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Sex biases in bird and mammal natural history collections

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Natural history specimens are widely used across ecology, evolutionary biology and conservation. Although biological sex may influence all of these areas, it is often overlooked in large-scale studies using museum specimens. If collections are biased towards one sex, studies may not be representative of the species. Here, we investigate sex ratios in over two million bird and mammal specimen records from five large international museums. We found a slight bias towards males in birds (40% females) and mammals (48% females), but this varied among orders. The proportion of female specimens has not significantly changed in 130 years, but has decreased in species with showy male traits like colourful plumage and horns. Body size had little effect. Male bias was strongest in name-bearing types; only 27% of bird and 39% of mammal types were female. These results imply that previous studies may be impacted by undetected male bias, and vigilance is required when using specimen data, collecting new specimens and designating types.

1. Introduction

Museum specimens are used extensively in studies of taxonomy, systematics, biogeography, genomics, comparative anatomy, morphological variability, development, parasitology, stable isotope ecology, toxicology, morphological evolution and more [1–3]. They are also of vital importance for understanding how biodiversity responds to anthropogenic impacts [4]. Large studies of species phenotypes using museum specimens, especially in vertebrates, are becoming increasingly common (e.g. evolutionary dynamics in birds [5], ecomorphological diversification in squamates [6]) and are revealing new insights into the evolution of diversity. These studies require large amounts of data, which can mean the focus is on collecting data from as many species as possible, to the detriment of other sources of variation. Sex is an important factor that influences many aspects of an individual's ecology and life history (table 1), but it is often treated as a nuisance variable, overlooked entirely, or data collection focuses on just one sex (e.g. only measuring female rates of phenotypic evolution [7]) to avoid the issue. If natural history collections have unbiased sex ratios (i.e. close to 50% males and females, or reflective of the sex ratio for the species in the wild [8]) then this may not be a problem; if there is a bias in the sex composition of collections, this has implications for studies that assume their samples are representative of the whole population or species (table 1). No large-scale study of sex ratios in bird and mammal museum collections exists, therefore investigating this is of vital importance as the number of studies using museum specimens continues to rise (e.g. this recent special issue on using museum specimens to study biodiversity in the Anthropocene [4]).

Here, we investigate sex biases in natural history collections of birds and mammals using over two million specimen records from five major international museums. We find a slight bias towards males in both groups. Curators and

Table 1. Prominent uses of natural history specimens and how research outcomes may be influenced by sex biases.

use	might sex biases in birds and mammals affect research outcomes?
taxonomy	**Yes**. Sexes often have external differences; if these are used in the taxonomy of the group (e.g. male plumage coloration in birds [9]) then it may be more difficult to identify individuals to species-level in one sex than another. Consistent over-representation of one sex in samples used in taxonomic studies, and in selection of name-bearing types in particular, may mean that interspecific distinctions between taxa are framed most often for that sex, making the less-represented sex harder to identify and distinguish across species, even if important differences exist, a considerable practical problem.
systematics	**Maybe**. For standard molecular phylogenies, commonly used genes do not differ substantially among sexes (i.e. not to the extent that they would form different branches). In phylogenomic studies, however, gene trees may vary across a genome if sex chromosomes are included in the sample [10]. Morphological phylogenies are likely to be most affected, as morphological characters can vary extensively between males and females. This also has implications for total evidence phylogenies that use both morphological and molecular data. mtDNA is often used to investigate species limits (e.g. gentes limits in cuckoos [11]) and this may differ across sexes.
biogeography	**Maybe**. This depends on the scale at which you consider biogeography. In species where all reproduction is sexual, sexes (necessarily) do not differ in terms of large-scale historical biogeography, i.e. colonization of new regions will not succeed if only one sex colonizes. However, locally sexes may be spatially segregated (e.g. bat roosting sites [12]), and have different dispersal rates [13] or patterns of habitat use, and differential migration of sexes is common in birds [14].
genomics	**Yes**. Mammals and birds have chromosomal sex determination; in mammals XY male and XX female, in birds ZZ male and ZW female [15]. The X and Z chromosomes are larger and have more genes than W and Y, thus genome size differs among sexes. Many genes are also sex-linked, so genomes will differ between sexes.
comparative anatomy	**Yes**. Males and females have internal and external anatomical differences, thus sex biases will influence comparative anatomy studies.
development	**Maybe**. In most vertebrates, early developmental stages are almost identical in males and females, however later development and sexual maturation involve highly divergent growth to result in adult sex differences [16]. If research is focused on early development or juvenile life-history stages then sex biases are unlikely to pose a problem.
morphological variability	**Maybe**. Perceived wisdom is that males are more variable than females. However, many detailed morphometric studies do not find this (e.g. in mammalian dentition and skull variation [17,18] and references within) in birds or mammals when a large sample is included. In some groups females are more variable than males (e.g. in *Pyriglena* antbirds [19]).
parasitology	**Yes**. Males are commonly more susceptible to infection, have lower immune function, and higher parasite loads than females [20]. This is likely due to testosterone inhibiting the immune system [21]. However, this is not true for all species and all kinds of parasites, e.g. breeding female birds have more blood parasites than males [22]. Differences in either direction may cause parasite load and diversity to be misrepresented where collections are sex biased.
stable isotope ecology	**Yes**. The demands of producing eggs, brooding, pregnancy, and lactation can alter stable isotope ratios [23]. Many species also have sex-segregated diets, e.g. leopards [24], and foraging ranges, so stable isotope ratios may vary among sexes even in non-breeding individuals.
toxicology	**Yes**. As above, sexes may differ in foraging ecology, which has consequences for contaminant burden. Furthermore, females may be able to eliminate some contaminants via eggs (e.g. mercury [25]), an option not available to males.
morphological evolution	**Yes**. There is extensive sexual dimorphism in many of the traits used in studies of morphological evolution, for example, body size [26], thus tempo and mode of evolution may vary with sex.

collections managers do not as a rule discard specimens based on sex, thus any bias is likely related to what is collected in the field. Male bias may be related to active selection for males by collectors in the field, or active avoidance of females with young due to legislation, ethical or conservation considerations. In particular, a major suspected source of male bias in collections for some species is deliberate selection for large, 'impressive' male specimens, especially where males are larger or more colourful than females, or possess ornaments or weaponry such as horns or antlers. Given the age of most major natural history collections, some male bias may be related to the changes in attitudes towards sex through time, therefore, we expect male bias to decrease towards the present due to changes in collection methods and motivations over the last century. Alternatively, male bias may be accidental, for example, due to trapping biases (i.e. trapping method, season of collecting, conspicuous male behaviours or traits), difficulties identifying females to species-level, or in some cases simply because there were more males in a population. In some mammals, higher dispersal, and broader habitat use, in males may result in them being more likely to come into contact with hunters or traps; males may also exhibit lower levels of neophobia increasing their likelihood of being captured, though evidence for this is limited [27,28]. In some birds, male territorial calls are often used to bring individuals towards a trap, which may also bias collections towards males.

To investigate these biases further, we tested whether male bias differed among orders, with sexual size dimorphism, with the possession of colourful plumage (birds) or ornamentation or weaponry (mammals) in males, and through time. Note that these variables mostly test for deliberate selection for males, because these data are easier to collate, but our results are likely a combination of deliberate and accidental male-biased collecting.

2. Material and methods

(a) Data collection and cleaning

(i) Specimen data

We obtained museum bird and mammal collection records from the Global Biodiversity Information Facility (GBIF [29]). Specifically, we collated data from the American Museum of Natural History (AMNH; $n = 271\,407$ records [30,31]), Field Museum of Natural History (FMNH; $n = 182\,984$ records [32,33]), Muséum National d'Histoire Naturelle (MNHN; $n = 86\,126$ records [34,35]), National Museum of Natural History, Smithsonian Institution (NMNH; $n = 496\,735$ records [36]) and Natural History Museum, London (NHMUK; $n = 251\,409$ [37]). These specimens were obtained between 1751 and 2018, mostly through hunting or trapping, and sexed based on internal or external genitalia or secondary sexual characters, for example plumage coloration or antlers. All raw data can be downloaded from GBIF [29].

Prior to analyses we cleaned the data as follows: (i) record type: to avoid confusing specimens with archives describing specimens we selected only preserved specimen records; (ii) age: juveniles can be harder to sex so we excluded all juveniles, young and fetuses from the dataset; (iii) year: we removed collection years later than 2018 as these were clearly errors; (iv) taxonomy: we removed subspecies names and used species binomials because we were interested in species-level sex ratios. To ensure our results were not due to female specimens more frequently being identified to the genus-level only, we also created a dataset with all specimens with valid generic names. We corrected bird taxonomy using the GBIF backbone taxonomy [29], and mammal taxonomy using *Mammal species of the world* [38]; (v) type status: we split types into name bearing (holotype, syntype, lectotype, neotype) and non-name bearing (all others) types. Where the records did not specify the kind of type we define these as ambiguous types; (vi) sex: we standardized sex to either female, male or non-sexed, and removed intersex or hermaphrodite individuals. Note that we recognize that biological sex is a spectrum [39]. We focus here on specimens identified as females and males for simplicity because there were very few recorded intersex specimens in collections databases (only five remained after other data cleaning), but we recognize the importance of these individuals. We also excluded non-sexed individuals from the analyses. The final dataset contained 2496 611 specimens (1 395 748 birds and 1 100 863 mammals), 1 647 409 (708 355 birds and 939 054 mammals) of which were sexed (electronic supplementary material, table A1).

(ii) Sexual dimorphism, plumage coloration and ornamentation data

We extracted median body masses (g) for males and females from Lislevand *et al.* [40] for birds and Jones *et al.* [41] for mammals, then calculated sexual size dimorphism by dividing mean male body mass by female body mass. Note that the sample size for these variables is lower because sex-disaggregated body size data are rare (see electronic supplementary material, table A2).

To explore how 'showiness' might influence sex bias, we included a measure of plumage coloration for passerine birds taken from Dale *et al.* [42,43]. This measure is based on the mean RGB (red green blue) values for 400 randomly chosen pixels in six patches (nape, crown, forehead, throat, upper breast, and lower breast) for each sex. We then calculated a plumage dimorphism score by dividing male plumage score by female score for each species. For mammals, we used the *Handbook of mammals of the world* [44] to identify mammals where males have 'ornamentation'. We defined ornamentation as a feature that might increase the likelihood of a collector targeting an individual, specifically horns, antlers, tusks, well-defined manes (i.e. in lions and some baboons), enlarged nasal appendages (e.g. in elephant seals, proboscis monkeys and hammerhead bats), facial coloration (e.g. in mandrills) or large cheek extensions (e.g. orangutans). Where species had ornaments, we recorded whether both sexes or only males routinely possess them. Note that the majority of species with ornaments in our models were Artiodactyla (59 of 67 species).

Bird species in several groups show reverse sexual dimorphism, where females are larger or showier than the males. To see if we detect a different pattern in these species we also divided the bird data into species where the female is generally the larger or showier sex (the families Accipitridae, Falconidae, Scolopacidae, Charadriidae, Jacanidae, Stercorariidae, Sulidae, Fregatidae, Cuculidae, Trochilidae, Pipridae, and the orders Strigiformes and Struthioniformes—list taken from [44]), and species where the male is generally the larger or showier sex (all other species).

The final cleaned data are available on the NHM Data Portal [45].

(b) Analyses

We analysed bird and mammal data separately and performed all analyses in R v.3.5.0 [46]. Reproducible scripts are available on GitHub at https://github.com/nhcooper123/sex-bias-museums [47].

We first summarized the overall proportion of female, male and unsexed specimens, and calculated the median proportion of females across species (using the main species-level dataset) and genera (using the generic-level dataset). We then summarized differences in the proportion of female specimens across orders and types.

Unsexed specimens may bias our results towards males if the majority of unsexed specimens are female. We tested for this by fitting linear models to compare the percentage of unsexed specimens and the percentage of female specimens within species; if these unsexed specimens are generally female we expect to see a negative relationship between unsexed specimens and the proportion of females in a species. In addition, we investigated variation in the numbers of unsexed specimens by order, collection continent and collection decade (see electronic supplementary material).

Most species were represented by only a few specimens (electronic supplementary material, figure A1), with large skews towards either males or females at low numbers (electronic supplementary material, figure A2). To reduce problems this is likely to cause when fitting models, we used only species with 100 or more specimens in our models (see electronic supplementary material for more details), except in our change through time models. In these models, our response variable was the proportion of males and females in each species for each year from 1880 to 2010 (before 1880 and after 2010 we did not have any species with sufficient specimens to include). As there were only 55 bird species and 1216 mammal species with over 100 specimens in a year, change through time models instead used all species with more than 50 specimens in a single year to increase the sample size (see electronic supplementary material, table A2).

We fitted all models using generalized linear models (GLM) with quasi-binomial errors, with the proportion of female

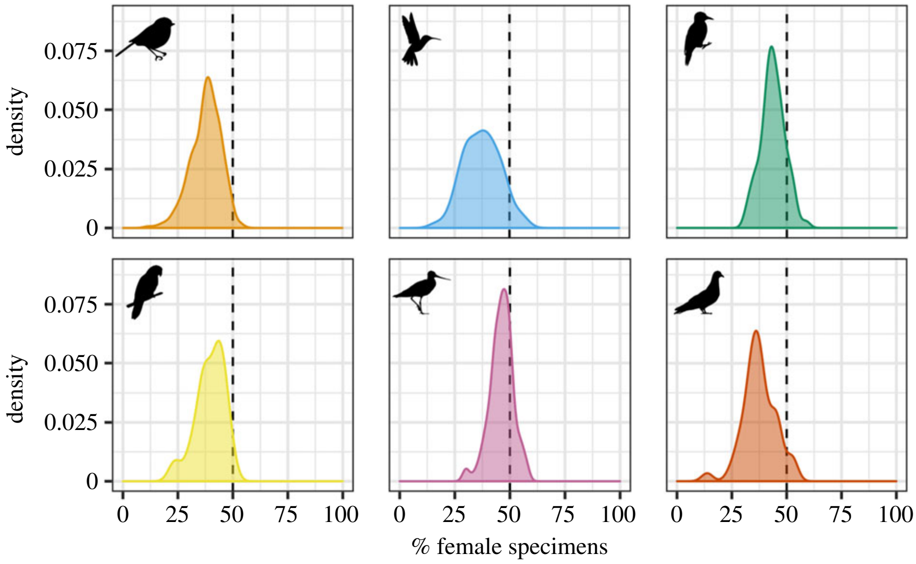

Figure 1. Kernel density plots showing the % female specimens in each species across the six largest orders of birds (from left to right, top to bottom: Passeriformes, Apodiformes, Piciformes, Psittaciformes, Charadriiformes and Columbiformes). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens. Silhouettes are from PhyloPic.org contributed by Ferran Sayol (parrot, hummingbird, tit), Steven Traver (woodpecker) and Alexandre Vong (shorebird). (Online version in colour.)

specimens (success) and the proportion of male specimens (failure) for each species as the response variable (i.e. a binomial response where the number of females and the number of males for each species were jointly modelled). Quasi-binomial rather than binomial errors were used due to overdispersion (all models have deviance/residual degrees of freedom far greater than two; see output on GitHub for exact values), and we assessed the significance of model terms using Type II sums of squares. We used standard model checks for GLMs (Q-Q plot, histogram of residuals, residuals versus linear predictors, response versus fitted values) to assess model fit. We tested whether the proportion of female and male specimens varied with (i) orders; (ii) collection years (1880–2010); (iii) male body mass (log-transformed); (iv) sexual size dimorphism (log transformed); (v) whether males were larger/more showy than females or vice versa (reverse sexual dimorphism; birds only); (vi) plumage dimorphism (log-transformed; passerine birds only); and (vii) ornamentation (mammals only). The number of specimens and species in each model are shown in electronic supplementary material, table A2.

3. Results and discussion

Of the 2 496 328 specimen records (1 395 748 birds and 1100 580 mammals) in our dataset, 20% of bird specimens were female, 31% were male and 49% were not sexed (electronic supplementary material, table A1). For mammals, the number of non-sexed individuals was much lower at 15%, likely because it is often easier to identify sex in mammals, with 41% female and 44% male specimens. If we consider only sexed specimens, 40% of bird and 48% of mammal specimens were female (electronic supplementary material, figure A3). In real terms, this represents 143 905 more male than female specimens in birds and 40 468 more male specimens in mammals. This male bias was not due to unsexed specimens mostly being female (see electronic supplementary material; figures A4–A8). Results were also qualitatively similar using the generic-level data (electronic supplementary material, table A1), so we focus only on species-level data below.

In the wild, adult sex ratios in many bird species are male skewed, though on average not as skewed as our results ($n = 187$ species, median 44.8% female [48]; see electronic supplementary material, figure A9), however, 48% is not a large deviation from the 50% expected in many natural populations of mammals [8]. Well-sampled species (i.e. those with at least 100 specimens) with the most extreme sex ratios in our data, i.e. species with fewer than 25% female or 25% male specimens, are shown in electronic supplementary material, table A3.

(a) Variation among orders

The proportion of female specimens varied across orders for both birds ($F_{24,1721} = 29.81$, $p < 0.001$; figure 1; electronic supplementary material, figure A10 and table A4) and mammals ($F_{24,1488} = 19.80$, $p < 0.001$; figure 2; electronic supplementary material, figure A11 and table A4). Most orders had more males than females (electronic supplementary material, table A4). In birds, of the 25 orders with sufficient data, only tinamous (Tinamiformes; 50.4%) had more females, but these represented just four species in the dataset. The most male-biased orders with more than 25 species were pigeons and doves (Columbiformes; 36.8% female), hummingbirds and swifts (Apodiformes; 37.2%; but see electronic supplementary material, figure A12) and passerines (Passeriformes; 38.4%). Adult sex ratios in Columbiformes and Passeriformes are generally male-skewed [48–50], but hummingbirds are often female-skewed in the wild [48,50]. This, along with evidence that, on average, Passeriformes are not as male biased as our results ($n = 54$ species, median 45.1% female [48]), suggests that greater availability of males alone cannot account for our results.

Seven of the 25 mammalian orders with sufficient data had more females, the most extreme being anteaters and sloths (Pilosa; 71.1% female). Most mammal species have a sex ratio of 1:1 at birth [8], though this can vary in adults. Several species of sloth have higher numbers of females (up to 68.8% females [51]) which may explain why we also found more females in collections; however, giant anteaters (*Myrmecophaga tridactyla*) show variable sex ratios in the field [52], but strong female bias in collections (71.3% female). Among

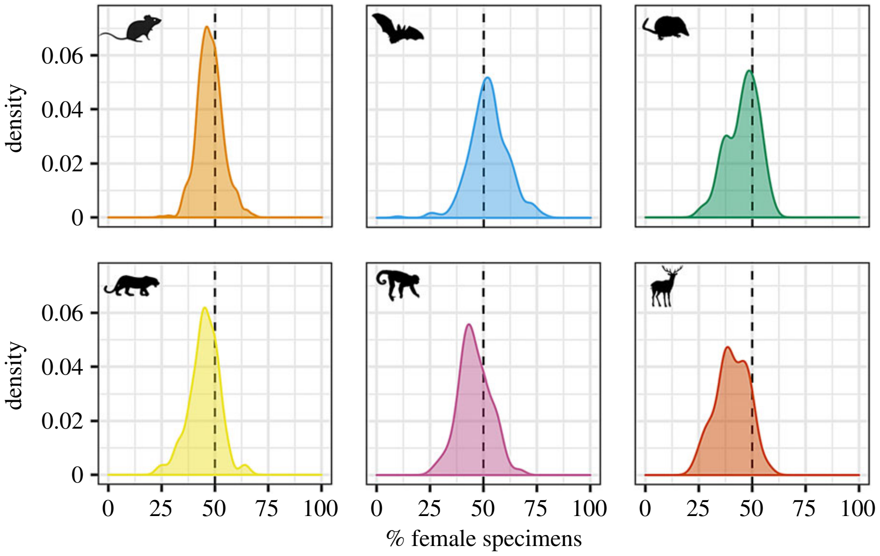

Figure 2. Kernel density plots showing the % female specimens in each species across the six largest orders of mammals (from left to right, top to bottom: Rodentia, Chiroptera, Soricomorpha, Carnivora, Primates and Artiodactyla). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens. Silhouettes are from PhyloPic.org contributed by Daniel Jaron (mouse), Yan Wong (bat), Becky Barnes (shrew), Lukasiniho (tiger), Sarah Werning (monkey) and Oscar Sanisidro (deer). (Online version in colour.)

the orders represented by more than 25 species in our data, only bats have more females (Chiroptera; 52.2% female; figure 2), despite reportedly balanced adult sex ratios in the wild [12]. This is likely related to widespread sex segregation in bat roosting sites, with many roosts containing individuals of only one sex [12]. In the past, bats were often trapped by collecting all individuals in a roost site, and female bats may use fewer roost sites than males (e.g. in *Myotis daubentonii* [53]), so skew towards females is not surprising. The most male-biased order of mammals were the even-toed ungulates (Artiodactyla; 39.7% females), but although they exhibit a great deal of variation in adult sex ratio, on average, there are more females than males in wild populations [54] suggesting strong selection for male specimens in this order derived from the deliberate hunting of large males that was common in the nineteenth and early twentieth centuries.

(b) Changes through time

We found male bias increased for birds ($F_{1,389} = 7.167$, $p = 0.008$; electronic supplementary material, figure A13), but decreased for mammals ($F_{1,3426} = 6.86$, $p = 0.009$; electronic supplementary material, figure A13); however, the effect sizes were extremely small (birds: slope ± s.e. = −0.002 ± <0.001; mammals: slope ± s.e. = 0.001 ± <0.001), indicating very little change in either class, i.e. there has been no improvement in the sex balance of collecting over the last 130 years.

(c) Male body mass and sexual size dimorphism

We found significant effects of male body size on the proportion of female specimens in both birds and mammals (electronic supplementary material, table A5), however, the direction and strength of the relationship varied among classes and orders (electronic supplementary material, figures A14–A16 and table A5). Bird species with larger males tended to have more female specimens, whereas the reverse was true for mammals. In mammals, this was likely driven by a few orders with large males that have long been favoured in collections (e.g. Artiodactyla, Carnivora) and have low median percentages of female specimens (figure 2; electronic supplementary material, table A4). Interestingly, however, selection for males in these groups did not increase with increasing male body size (electronic supplementary material, figure A16), instead it appears male carnivores and artiodactyls were preferred over females, regardless of their body size.

Rather than selecting large males *per se*, collectors may favour males when the difference in size between females and males, i.e. sexual size dimorphism, is large. We found that as sexual size dimorphism increased, i.e. as males became increasingly larger than females, there was more bias towards male specimens (electronic supplementary material, table A5); however, this result was entirely driven by differences among orders (electronic supplementary material, figures A17–A18); when order was included in the models, sexual size dimorphism did not significantly influence specimen sex ratios over the effects of order (electronic supplementary material, table A5). As with body mass, this suggested certain orders were more likely to contain more male specimens, regardless of their size with respect to females, suggesting that other characteristics were driving their selection.

In birds that show reverse sexual dimorphism we found that the median percentage of females for species where the male was the larger or showier sex was 40%, the same as for the whole dataset. For species where the female is the larger or showier sex the median percentage of females was 44.6%, closer to the expected 50:50 ratio. There were significantly more females in species where the female is the larger or showier sex ($F_{1,1744} = 167.9$, $p < 0.001$; electronic supplementary material, figure A19).

(d) Plumage and ornaments

In passerine birds, as males became increasingly more colourful than females, the proportion of female specimens decreased (figure 3; $F_{1,828} = 58.95$, $p < 0.001$; slope ± s.e. = −0.416 ± 0.054). This relationship was not strong, but fits with anecdotal evidence of collectors preferentially selecting colourful male specimens, especially where plumage differences are large, for example in birds of paradise. Although the numbers are

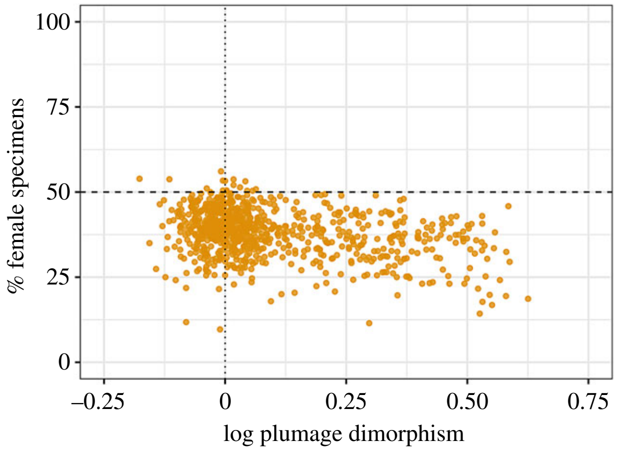

Figure 3. Relationship between the % female specimens for each species and log plumage dimorphism scores in passerine birds. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens; the dotted line is the point at which males and females have the same plumage coloration. Plumage dimorphism scores were calculated by dividing male plumage scores by female plumage scores (see Methods). (Online version in colour.)

too small to drive the differences seen here, there is also bias towards displaying male specimens in exhibits [55].

For mammals, species with ornaments (horns, antlers, tusks, manes etc.) had significantly fewer female specimens than those without ornaments (figure 4; $F_{1,1510} = 46.98$, $p < 0.001$; slope ± s.e. = -0.328 ± 0.048). Note, however, that only 67 species across four orders in our analyses had ornamentation (electronic supplementary material, table A6). Most of the species with ornaments in our models were artiodactyls, and most artiodactyls have horns, antlers or tusks, suggesting that the strong male bias in Artiodactyla (39.7% female; figure 2) was due to selection for males with these features. Within ornamented species there was no significant difference if both sexes or only males possessed the ornament (figure 4; $F_{1,65} = 0.725$, $p = 0.398$), suggesting that even where females are phenotypically different, preference is still given to collecting males. This is particularly concerning since most artiodactyl species are female skewed in the wild [54]. We note, however, that artiodactyls only make up 4% of our dataset, and just over 4% of all mammal species [38], so while deliberate hunting of large males may be a driver in this order, it is unlikely to drive all the male biases we see.

(e) Type specimens

Perhaps our most notable finding focused on name-bearing type specimens (holotypes, syntypes, lectotypes and neotypes). Here, the bias towards male specimens was extreme; only 25% of bird and 39% of mammal types were female (electronic supplementary material, figure A3). Although in some instances, males might be considered the appropriate sex for holotypes because male characters such as plumage or bacula are diagnostic (e.g. in bats [56]), we see no reason to not also designate a female paratype to represent the phenotypic range of a species—with the exception that in rare species, or species with few specimens for another reason, this may not be possible. In mammals, paratypes were almost 49% female, but bird paratypes were 38% female. Additionally, for newly discovered species, genetic identification of species limits may remove the need for male diagnostic characteristics, and thus male holotypes. Currently, sex does not form any part of the International Code for Zoological Nomenclature (ICZN) recommendations for designating types, although some historical instructions for collectors emphasize the importance of multiple types (e.g. the classical description of the type [57]). Adding this to the ICZN is of vital importance moving forwards.

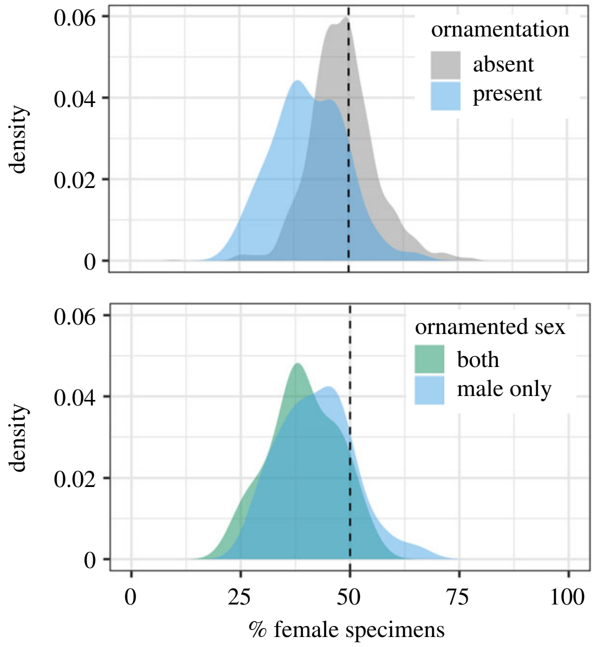

Figure 4. Kernel density plots comparing the % female specimens in each mammal species where ornaments, i.e. horns, tusks, antlers, manes, etc., are present or absent (*a*), and when species have ornaments, whether these are found in both sexes or only males (*b*). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens. (Online version in colour.)

(f) Conclusions and recommendations

Here, we tested for deliberate selection of large, showy males, especially in species with high levels of sexual dimorphism in these traits. Our analyses suggest that some male bias in collections is likely the result of historical active selection of males. In mammals, males are favoured in species with larger males, and in species with ornaments. These results, however, are driven by carnivores and artiodactyls, and do not account for male biases in species that are not actively targeted by hunters, for example, most rodents. In birds, showier males appear to be favoured within passerines, and species that exhibit reverse sexual size dimorphism show less bias towards males. As passerines make up 58% of our dataset (and around 60% of all bird species), active selection for males may be a much larger problem in birds than in mammals. To reduce these imbalances, collectors in the field should strive to avoid trapping biases and biases in selecting individuals to collect.

Much bias towards males is probably non-deliberate, and related to the characteristics of individual species and how they are trapped. In small mammals, for example, higher dispersal and broader habitat use in males may result in males being more likely to come into contact with hunters or traps [13]. In passerines, male calls are often used to draw birds towards a mist net, resulting in higher numbers of males being trapped (a simple solution to this is to also use playback of female calls, an active area of current research in ornithology [58]). Some trapping is also opportunistic, so characteristics that mean one sex is exposed to collectors more often may play a key role. For example, the slight female bias in Tinamiformes (50.4%) in this study may be because they are often collected on their nests. Similar patterns are likely for other conspicuous ground-nesting birds. Differential migration of sexes may also influence the numbers of males and females caught at certain locations throughout the year [14]. More ecological studies on species with strong biases towards males or females are needed to help explain these patterns. On top of these factors, females may be harder to identify than males—they may appear similar to juveniles, or lack diagnostic features such as bacula that make identification simpler. If this is the case, many of our unsexed specimens may be female. Our supplemental analyses (electronic supplementary material, figures A4–A8) suggest this does not cause the male bias, but until these 687 393 unsexed bird and 161 526 unsexed mammal specimens are sexed, we cannot say it would have no effect.

Museum professionals, and those using museum collections, should have an awareness of the biases within their collections (not just in terms of sex but also in terms of age, locality and other factors), and attempt to acquire material to best resolve those biases, whatever their cause. Natural history collections play a critical role in informing multiple research disciplines answering vital questions for the future of biodiversity [4] and are also key resources for public engagement and interaction with biodiversity [55]. Therefore, it is paramount that we continue developing these resources while using a more comprehensive and better-informed approach. Finally, researchers investigating broad-scale variation in species should account for these biases when designing data collection protocols and/or in downstream analyses and declare how they dealt with those biases in resulting publications. Our analyses place particular pressure on taxonomists to think more carefully about sex when defining name-bearing types, and suggest more designation of opposite sex paratypes would be desirable, particularly in birds.

Data accessibility. Data are available from the NHM Data Portal [45] and GBIF [29]. R code is available from GitHub (https://github.com/nhcooper123/sex-bias-museums; Zenodo DOI: 10.5281/zenodo.3459138).

Authors' contributions. N.C. performed the analyses and wrote the first draft. All authors contributed to study design, interpreted results, revised the manuscript and approved the submitted version.

Competing interests. The authors declare no competing interests.

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Supplementary Materials from: *Sex biases in bird and mammal natural history collections*; Proceedings of the Royal Society Series B: Biological Sciences, DOI: 10.1098/rspb.2016.0049

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Contents

1 Numbers of specimens for each species

We expect large skews in the proportion of male or female specimens when sample size is low, but the ratio of male:female specimens should approach 50:50 as more specimens are added if there is no bias. Most species in our dataset were represented by only a few specimens (Figure A1), with large skews in the percentage of female specimens (in both directions) at low numbers (Figure A2).

To test whether this may influence our analyses, we used generalised linear models (GLM) with binomial errors, with the proportion of female specimens (success) and the proportion of male specimens (failure) for each species as the response variable, and the log number of specimens per species as the explanatory variable. We then used standard model checks for GLMs (Q-Q plot, histogram of residuals, residuals vs. linear predictors, response vs. fitted values) to assess model fit. The model showed massive heteroscedasticity in the residuals, due to the skew in proportions when sample size is low. We therefore repeated the analysis, removing species with fewer than 20, 50, 100, 150 and 200 specimens in turn. The best fitting model, without losing too much data, was a model with species with more than 100 specimens. There is still a significant positive relationship between the number of specimens and the proportion of female specimens but this is not unusual with such a large dataset, and the effect size is extremely low ($slope \pm SE = 0.034 \pm 0.001$, $z_3 257 = 24.86$, $p < 0.001$) so we exclude this variable from further analyses.

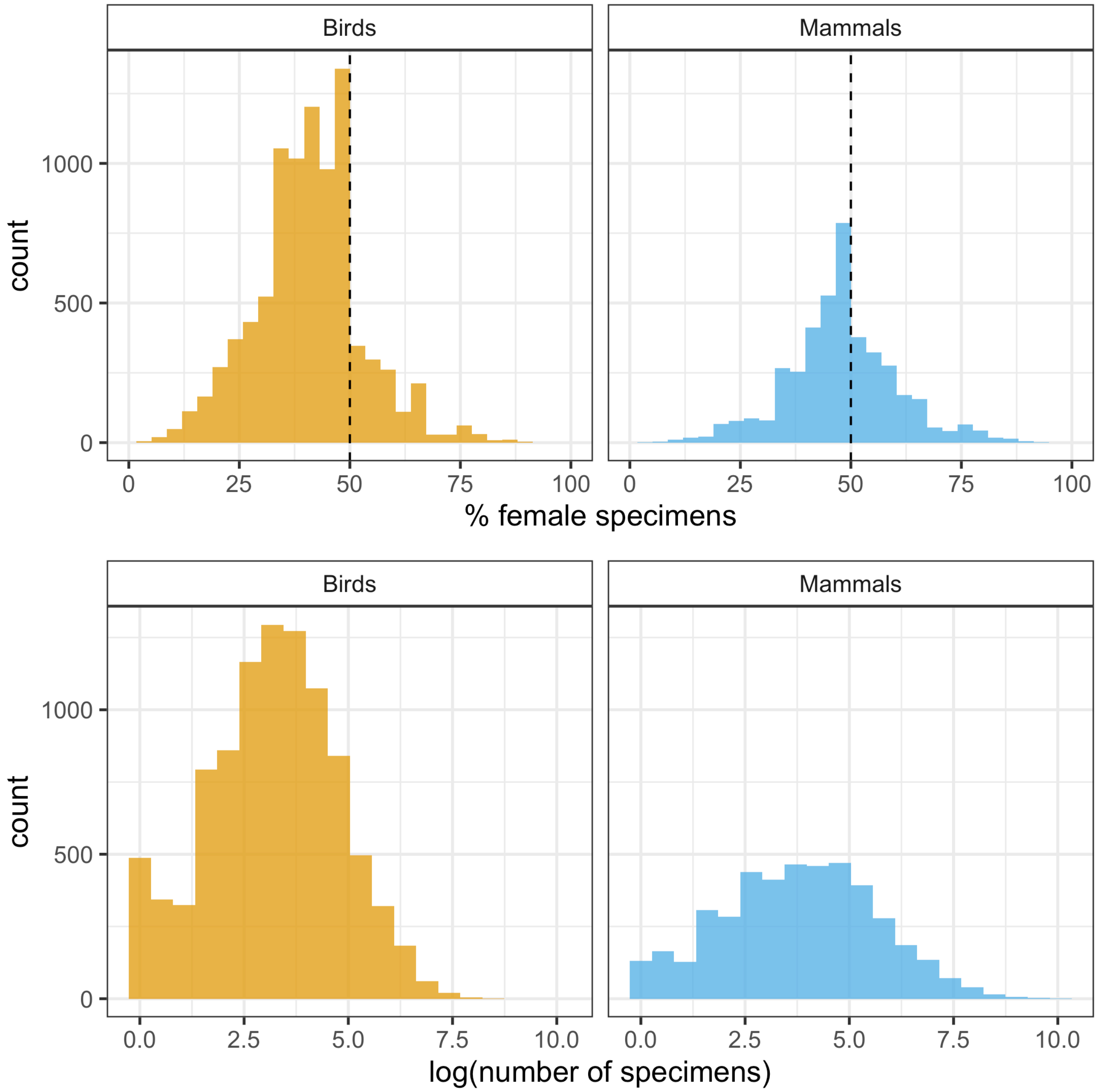

Figure A1: Histograms showing the distribution of percentage female specimens and log number of specimens for each species across birds and mammals.

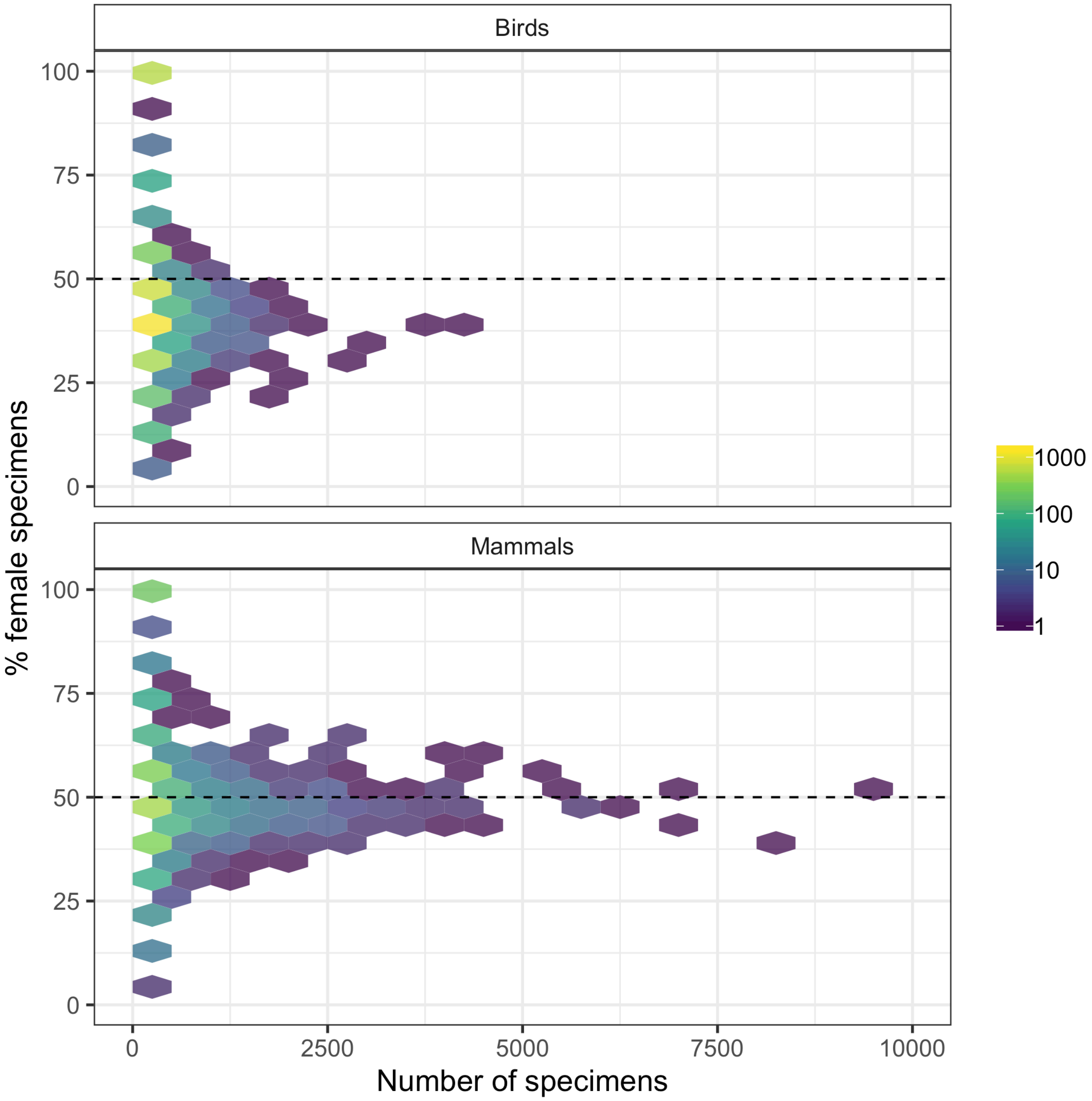

Figure A2: Relationship between the percentage female specimens in each species and the number of specimens for each species. Hex bins are used rather than points to make the plot easier to read.

2 Genus-level data

Table A1: Numbers of specimens in our dataset at species and genus-level divided by sex.

BIRDS				
All specimens				
	Species-level		**Genus-level**	
	N specimens	**%**	**N specimens**	**%**
Total	1,395,748	NA	1,498,129	NA
Sexed	708,355	50.75	791,140	52.81
Unsexed	687,393	49.25	706,989	47.19
Male	426,130	30.53	475,957	31.77
Female	282,225	20.22	315,183	21.04
Sexed specimens only				
	Species-level		**Genus-level**	
	N specimens	**%**	**N specimens**	**%**
Total	708,355	NA	791,140	NA
Male	426,130	60.16	475,957	60.16
Female	282,225	39.84	315,183	39.84
Sexed specimens from species/genera with $\geq$ 100 specimens				
	Species-level		**Genus-level**	
	N specimens	**%**	**N specimens**	**%**
Total	497,923	NA	751,510	NA
Male	299,859	60.22	452,343	60.19
Female	198,064	39.78	299,167	39.81
MAMMALS				
All specimens				
	Species-level		**Genus-level**	
	N specimens	**%**	**N specimens**	**%**
Total	1,100,580	NA	1,187,738	NA
Sexed	939,054	85.32	1,011,143	85.13
Unsexed	161,526	14.68	176,595	14.87
Male	489,674	44.49	527,574	44.42
Female	449,380	40.83	483,569	0.71
Sexed specimens only				
	Species-level		**Genus-level**	
	N specimens	**%**	**N specimens**	**%**
Total	939,054	NA	1,011,143	NA
Male	489,674	52.15	527,574	52.18

Female	449,380	47.85	483,569	47.82
Sexed specimens from species/genera with $\geq$ 100 specimens				
	Species-level		**Genus-level**	
	N specimens	**%**	**N specimens**	**%**
Total	857,384	NA	991,826	NA
Male	447,237	52.16	517,419	52.17
Female	410,147	47.84	474,407	47.83

3 Numbers of species and specimens in each analysis

Model	Specimens	median % female	Species
Birds			
orders	497,923	39.78	1,746
years	30,525	38.56	390
mass/SSD	277,179	39.82	829
plumage	258,326	37.34	850
Mammals			
orders	857,384	47.84	1,512
years	386,476	48.20	3,417
mass/SSD	548,514	47.97	717

Table A2: Numbers of specimens and species in each of our models. SSD is sexual size dimorphism. All species have order data, all birds have reverse sexual size dimorphism (presence/absence) data, and all mammals have ornamentation (presence/absence) data.

4 Total numbers of female specimens and female type specimens

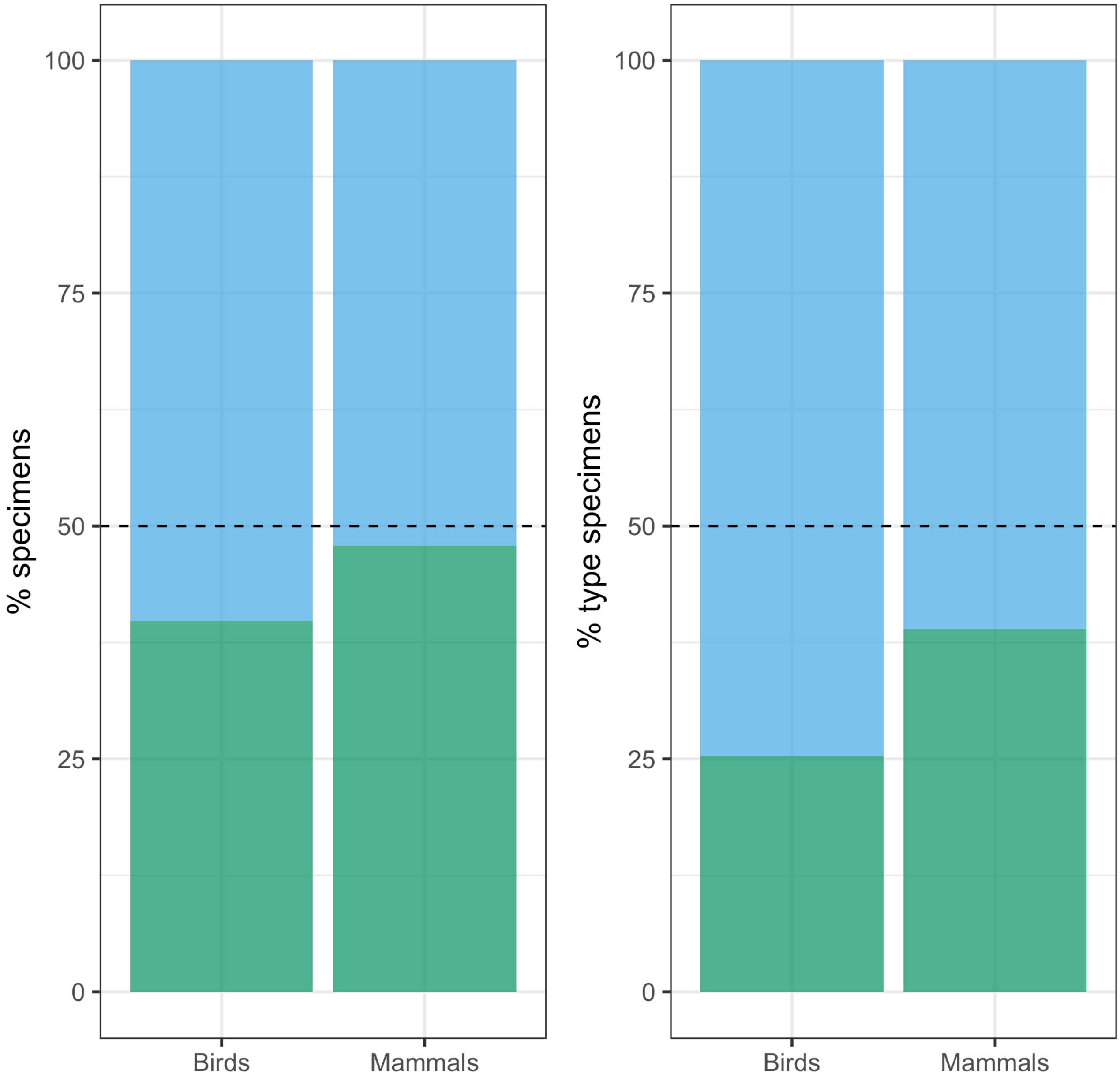

Figure A3: Percentages of female (green) and male (blue) specimens in bird and mammal collections for all specimens (left hand panel) and for name-bearing type specimens only (right hand panel). The dashed line represents 50% female specimens.

5 Exploring the unsexed specimen data

49% of bird specimens and 15% of mammal specimens had no data on their sex at all. This is likely related to a number of factors. First, sexing birds and mammals is not always straightforward. Some species do not have clear external diagnostic features, so require dissection or close inspection by experts. In some bird species, for example, juvenile males and adult females may have very similar plumage, making differentiation difficult. Not all collectors or curators will have the skills to make these decisions, so collections remain unsexed. Second, historical collections often have poor metadata, in part because no-one imagined a time when you might examine the records without the specimen in front of you - as such many obviously male and female specimens are not recorded as such in specimen catalogues (this is common in the NHM collections *pers. comm*). Curators and collections managers are often too busy to add these data when collections are massive and in need of much care and attention.

We cannot sex all of the 687,393 unsexed bird and 161,526 unsexed mammals specimens in this study, instead we investigated variation in the numbers of unsexed specimens by order, collection continent and collection decade. Note that the figures below use all unsexed specimens, i.e. we did not exclude species with fewer than 100 specimens.

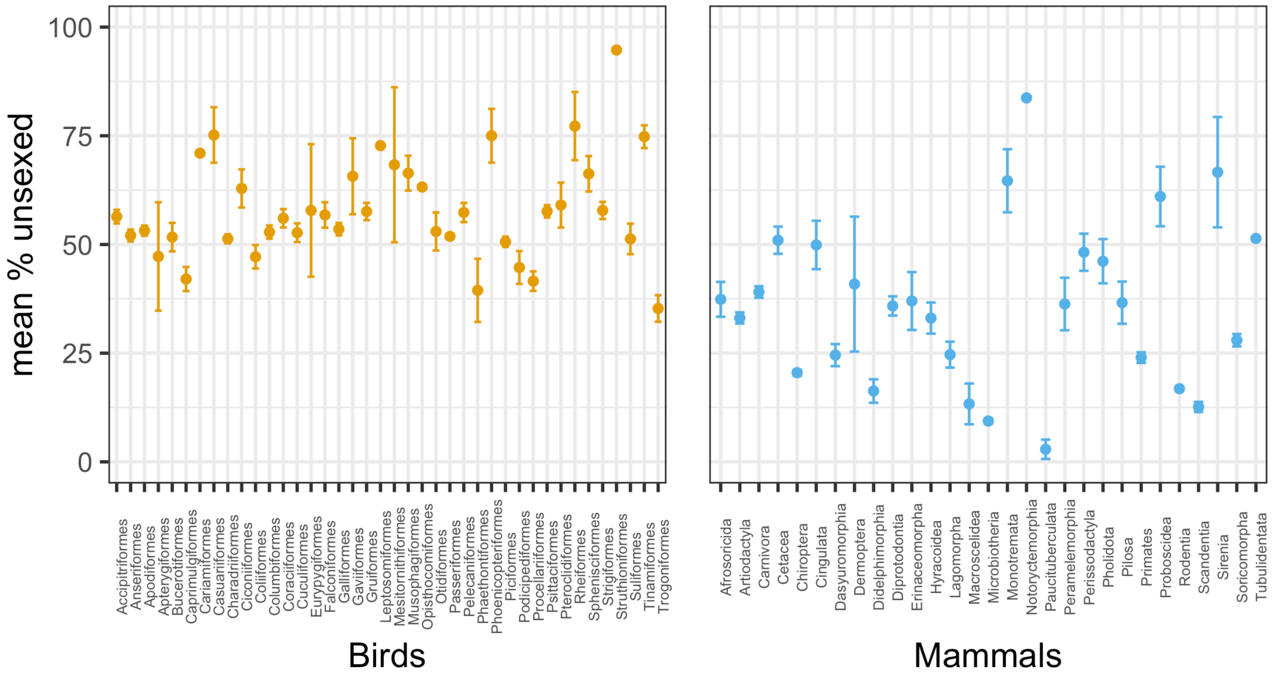

Figure A4: Unsexed specimens across orders of birds and mammals. Points are the mean percentage of unsexed specimens across all species within an order. Error bars are standard errors.

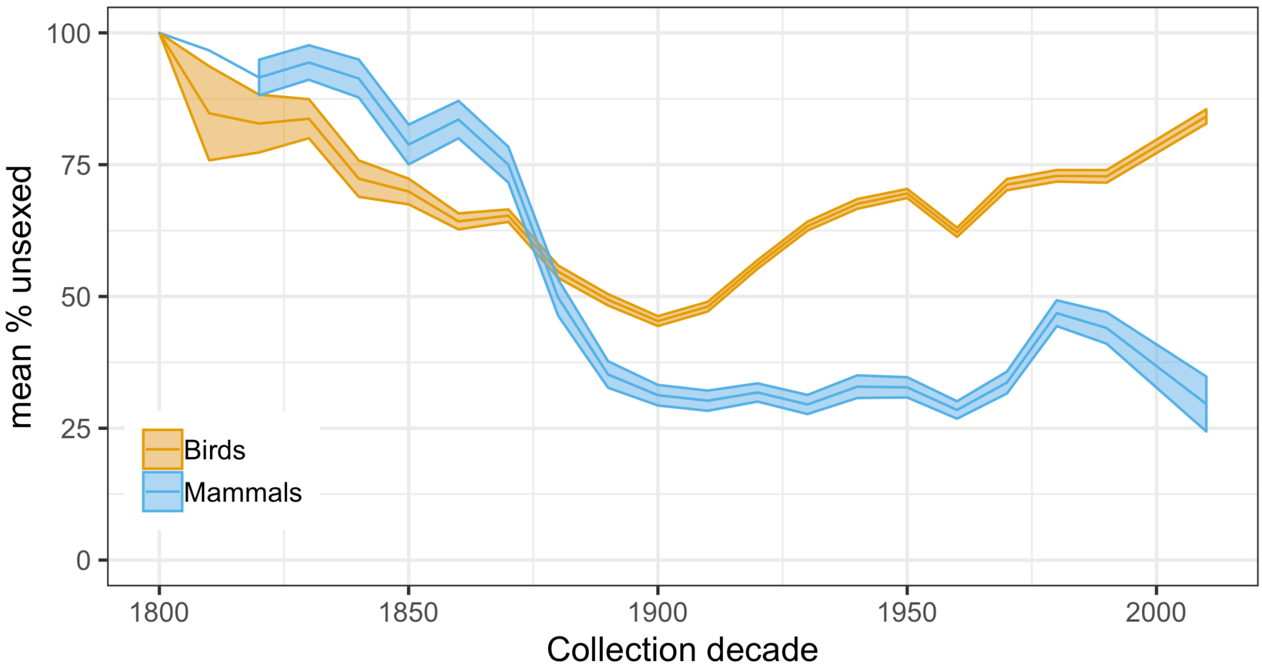

Figure A5: Unsexed specimens of birds and mammals across decades. Lines show the mean percentage of unsexed specimens across all specimens collected within a given decade with 95% confidence intervals.

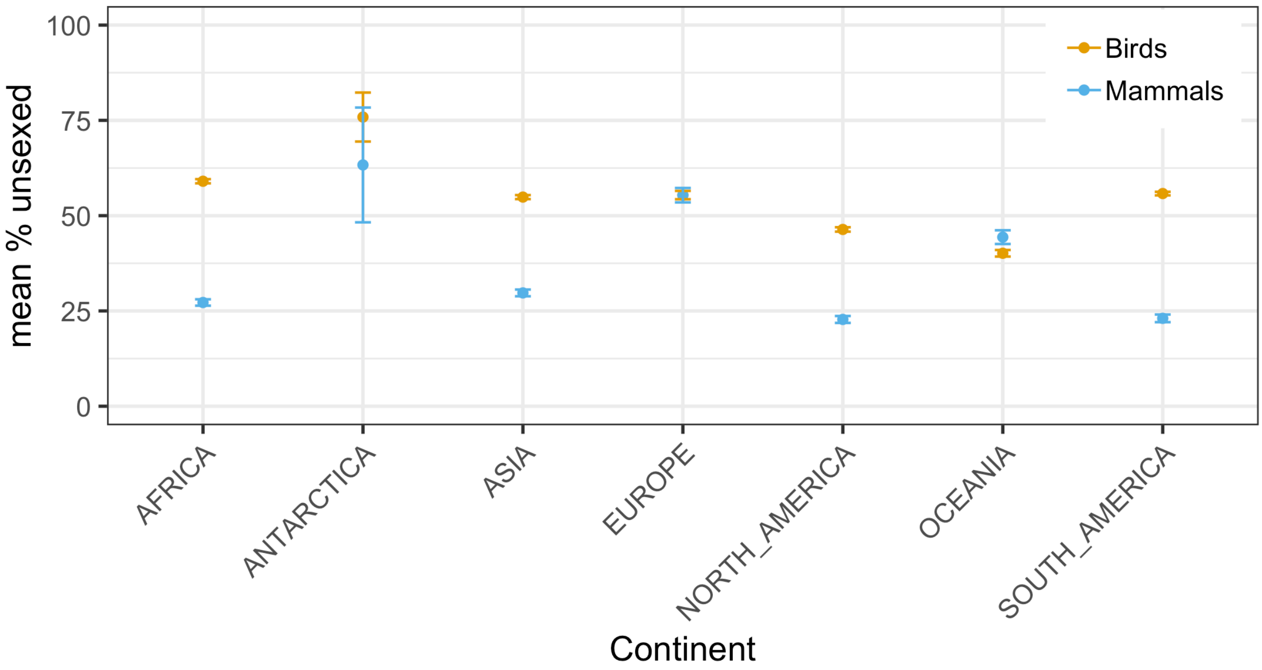

Figure A6: Unsexed specimens of birds and mammals across continents they were collected in. Points are the mean percentage of unsexed specimens across all species collected within a continent. Error bars are standard errors.

There is a lot of variation in the percentage of unsexed specimens across orders (Figure

A4), regions (Figure A6) and through time (Figure A5). Interestingly, while the percentage of unsexed mammals has steadily decreased through time, in birds there is a steady decrease until 1900 followed by a slow increase towards the present. Patterns across orders and regions are not easily explained by the presence of hard to sex species.

Do unsexed specimens bias our results towards males?

The presence of unsexed specimens may bias our results in various ways, but the worst possible scenario is that the majority of unsexed specimens are females, leading to the male bias we report in the main text. If this were true, we would expect the percentage of unsexed specimens to be strongly negatively correlated with the percentage of female specimens when we only consider female and male specimens. So, for example, a species with 50% female and 50% male specimens would have a higher percentage of unsexed specimens than one with 90% female and 10% male.

We tested this by fitting linear models to compare the percentage of unsexed specimens (in species with more than 100 specimens overall) and the percentage of female specimens (in species with more than 100 sexed specimens). We investigated the correlation at two taxonomic levels 1) mean percentages within each order and 2) mean percentages within each species.

Within orders

There were no significant correlations between the percentage of unsexed specimens and the percentage of female specimens across orders in either birds (linear regression: $slopeSE = 0.143 \pm 0.359$, $t = 0.398$, $df = 23$, $p = 0.694$; Figure A7) or mammals (linear regression: $slope \pm SE = 0.225 \pm 0.513$, $t = 0.439$, $df = 23$, $p = 0.665$; Figure A7).

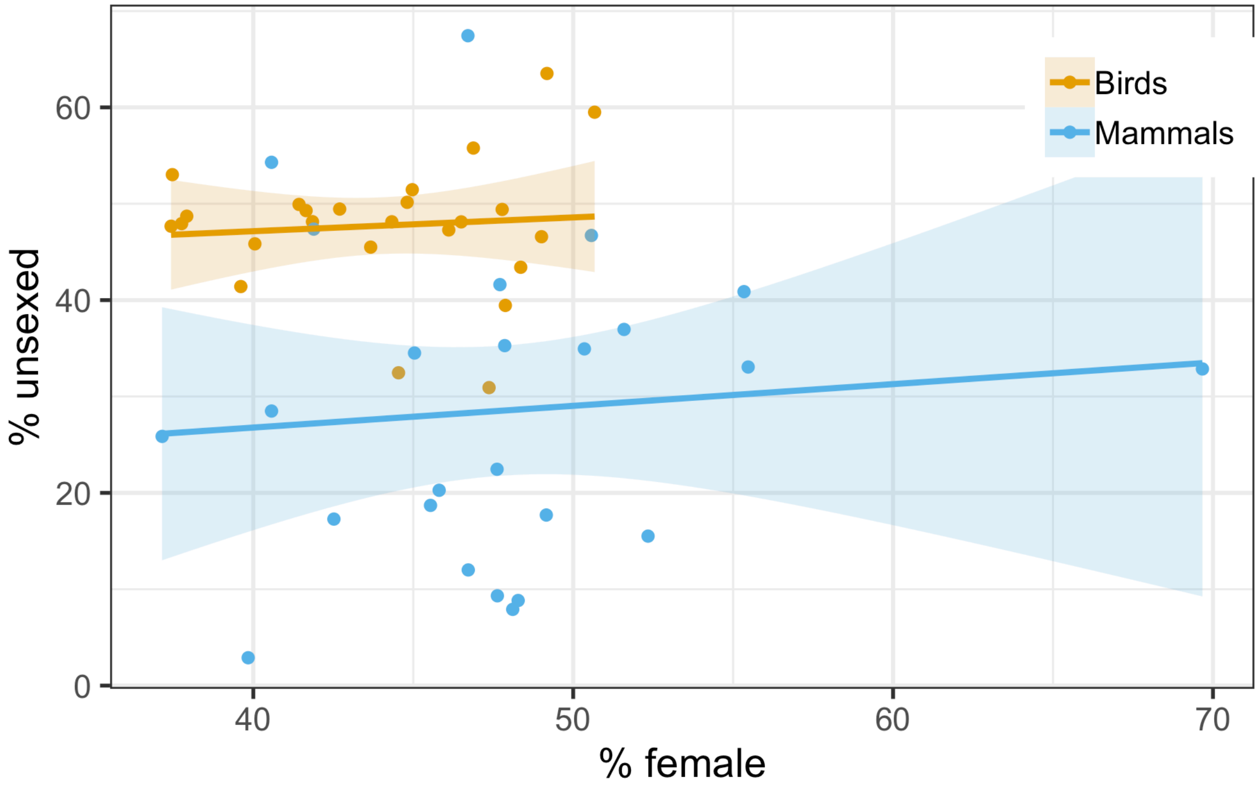

Figure A7: The relationship between the percentage of female specimens and percentage of unsexed specimens across orders of birds and mammals. Lines are from a linear regression, and shaded bars represent 95% confidence intervals on the model.

Within species

There was no significant correlation between the percentage of unsexed specimens and the percentage of female specimens across species in birds (linear regression: $slope \pm SE = 0.092 \pm 0.050$, $t = 1.876$, $df = 1743$, $p = 0.061$; Figure A8), but there was a weak negative correlation in mammals (linear regression: $slope \pm SE = -0.120 \pm 0.042$, $t = -2.852$, $df = 1487$, $p = 0.004$; Figure A8). The effect size was very small, however, so we do not place much emphasis on this result.

Note that without sexing the unsexed specimens we cannot be sure a bias does not exist, but the lack of correlation (except the weak one within species for mammals) makes us believe our results are likely not driven by unsexed specimens being predominantly female.

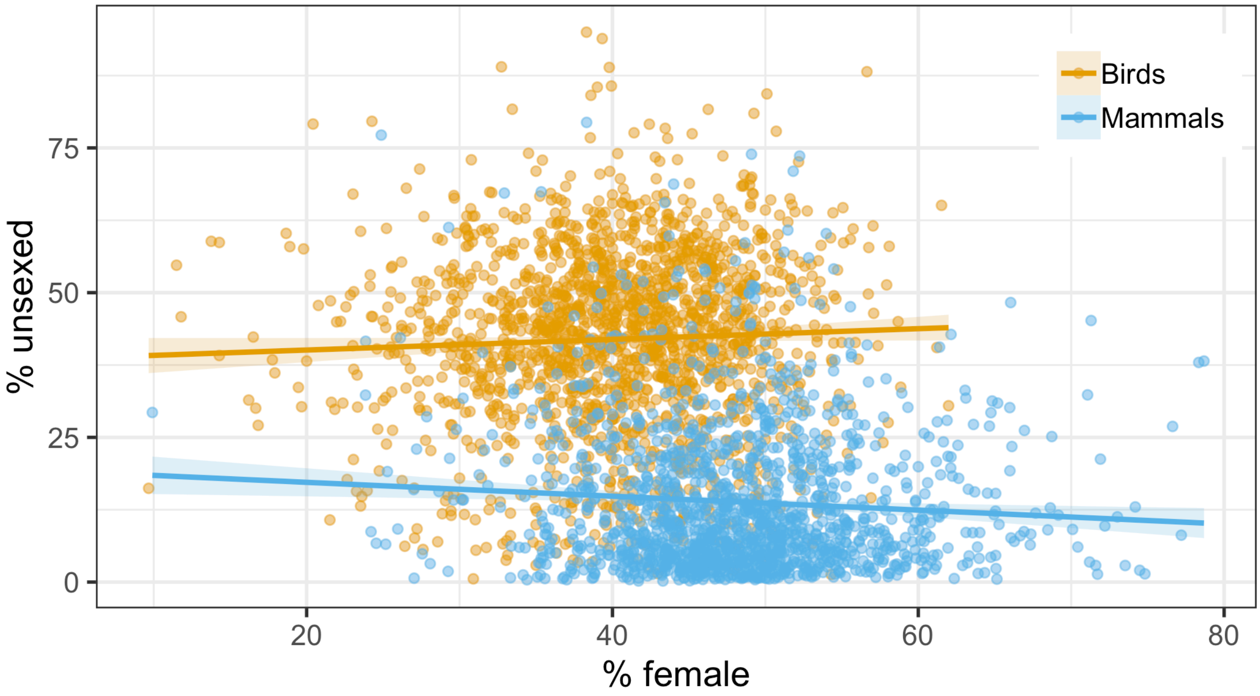

Figure A8: The relationship between the percentage of female specimens and percentage of unsexed specimens across species of birds and mammals. Lines are from a linear regression, and shaded bars represent 95% confidence intervals on the model.

6 Comparing our sex ratios to wild adult sex ratio data for birds

There is very little available data on sex ratios in wild bird populations. The study which has collated the most data so far is Szekely et al. (2014). We took their data and compared the wild adult sex ratios (number of males/ number of males + number of females) to the sex ratios of the matching species in our dataset.

Overall we found 119 overlapping species out of the 187 in Szekely et al. (2014).[1] Of these 88 (74%) have less male biased sex ratios in the wild compared to museums, while the remaining 31 (26%) have more male biased sex ratios in the wild compared to museums. This difference was significant (paired t-test: $t_{118} = -6.768$, $p < 0.001$; Figure A9)

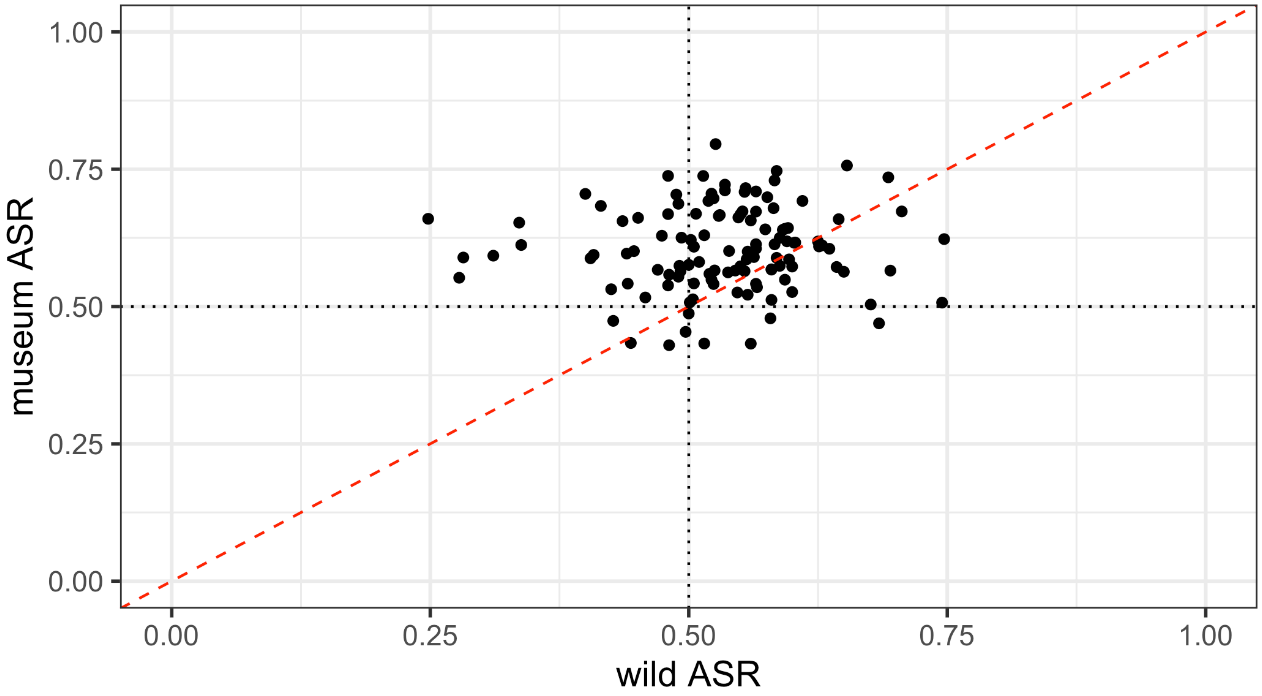

Figure A9: Adult sex ratio (ASR) in wild populations versus ASR in our museum dataset for 119 bird species. Wild ASR values come from Szekely et al. (2014).[1] For the museum dataset only species with at least 100 specimens are included. The dotted lines represents 50% female specimens in either the wild or museum ASR data. The red dashed line is the 1:1 line representing where points would sit of wild ASR and museum ASR are identical for a given species. Points above this line indicate species where museum ASR is more male biased than in wild populations.

7 Species with the most extreme sex ratios

Table A3: Species of birds and mammals with the most extreme sex ratios in our data, i.e. species with fewer than 25% female or fewer than 25% male specimens, for species with at least 100 specimens in total. Species with fewer than 25% male specimens are highlighted in bold.

class	**order**	***binomial***	**n specimens**	**% female**
Birds	Passeriformes	*Pardalotus striatus*	300	9.67
Birds	Passeriformes	*Ficedula hypoleuca*	148	11.49
Birds	Passeriformes	*Camaroptera brachyura*	195	11.79
Birds	Columbiformes	*Streptopelia tranquebarica*	109	13.76
Birds	Passeriformes	*Euplectes progne*	112	14.29
Birds	Passeriformes	*Cinnyris asiaticus*	112	14.29
Birds	Passeriformes	*Cinnyris mariquensis*	253	16.21
Birds	Apodiformes	*Chlorostilbon mellisugus*	109	16.51
Birds	Passeriformes	*Saxicola rubicola*	156	16.67
Birds	Passeriformes	*Cicinnurus regius*	202	16.83
Birds	Passeriformes	*Aethopyga siparaja*	321	17.76
Birds	Passeriformes	*Vireo plumbeus*	106	17.92
Birds	Passeriformes	*Euplectes macroura*	134	18.66
Birds	Passeriformes	*Cinnyris mediocris*	127	18.90
Birds	Passeriformes	*Euplectes albonotatus*	221	19.46
Birds	Passeriformes	*Aethopyga shelleyi*	122	19.67
Birds	Passeriformes	*Aethopyga nipalensis*	101	19.80
Birds	Passeriformes	*Emberiza citrinella*	390	20.00
Birds	Passeriformes	*Junco hyemalis*	1959	20.42
Birds	Passeriformes	*Rupicola peruvianus*	130	20.77
Birds	Passeriformes	*Acrocephalus atyphus*	158	21.52
Birds	Passeriformes	*Cinnyris chloropygius*	218	21.56
Birds	Passeriformes	*Cyanocompsa parellina*	111	21.62
Birds	Passeriformes	*Paradisaea minor*	174	21.84
Birds	Passeriformes	*Cinnyris venustus*	387	21.96
Birds	Apodiformes	*Campylopterus hemileucurus*	144	22.22
Birds	Passeriformes	*Emberiza cirlus*	152	22.37
Birds	Passeriformes	*Chalcomitra senegalensis*	536	22.57
Birds	Passeriformes	*Cinnyris chalybeus*	181	22.65
Birds	Passeriformes	*Oenanthe hispanica*	175	22.86
Birds	Passeriformes	*Cinnyris pulchellus*	139	23.02

Birds	Psittaciformes	*Psittacula krameri*	152	23.03
Birds	Passeriformes	*Myzomela cardinalis*	581	23.06
Birds	Passeriformes	*Euplectes ardens*	299	23.08
Birds	Passeriformes	*Aethopyga gouldiae*	117	23.08
Birds	Passeriformes	*Cyanerpes lucidus*	129	23.26
Birds	Passeriformes	*Nectarinia famosa*	176	23.30
Birds	Passeriformes	*Cinnyris habessinicus*	120	23.33
Birds	Passeriformes	*Lichmera incana*	119	23.53
Birds	Passeriformes	*Euplectes axillaris*	119	23.53
Birds	Passeriformes	*Troglodytes musculus*	144	23.61
Birds	Apodiformes	*Phaethornis longirostris*	192	23.96
Birds	Passeriformes	*Prunella modularis*	174	24.14
Birds	Passeriformes	*Piranga olivacea*	505	24.16
Birds	Passeriformes	*Sporophila minuta*	132	24.24
Birds	Columbiformes	*Treron calvus*	103	24.27
Birds	Psittaciformes	*Forpus passerinus*	111	24.32
Birds	Passeriformes	*Setophaga dominica*	704	24.43
Birds	Passeriformes	*Malurus lamberti*	126	24.60
Birds	Passeriformes	*Aimophila rufescens*	142	24.65
Birds	Passeriformes	*Nectarinia johnstoni*	101	24.75
Mammals	Chiroptera	*Nyctiellus lepidus*	111	9.91
Mammals	Artiodactyla	*Ovis ammon*	109	23.85
Mammals	Carnivora	*Mustela nivalis*	570	23.86
Mammals	Rodentia	*Allactaga sibirica*	252	24.21
Mammals	Chiroptera	*Emballonura raffrayana*	167	24.55
Mammals	Primates	*Homo sapiens*	138	24.64
Mammals	Chiroptera	*Pteronotus personatus*	410	24.88
Mammals	Pilosa	*Tamandua tetradactyla*	261	**76.63**
Mammals	Chiroptera	*Chaerephon major*	193	**77.20**
Mammals	Pilosa	*Tamandua mexicana*	157	**78.34**
Mammals	Chiroptera	*Myotis oxyotus*	136	**78.68**

8 Variation among orders

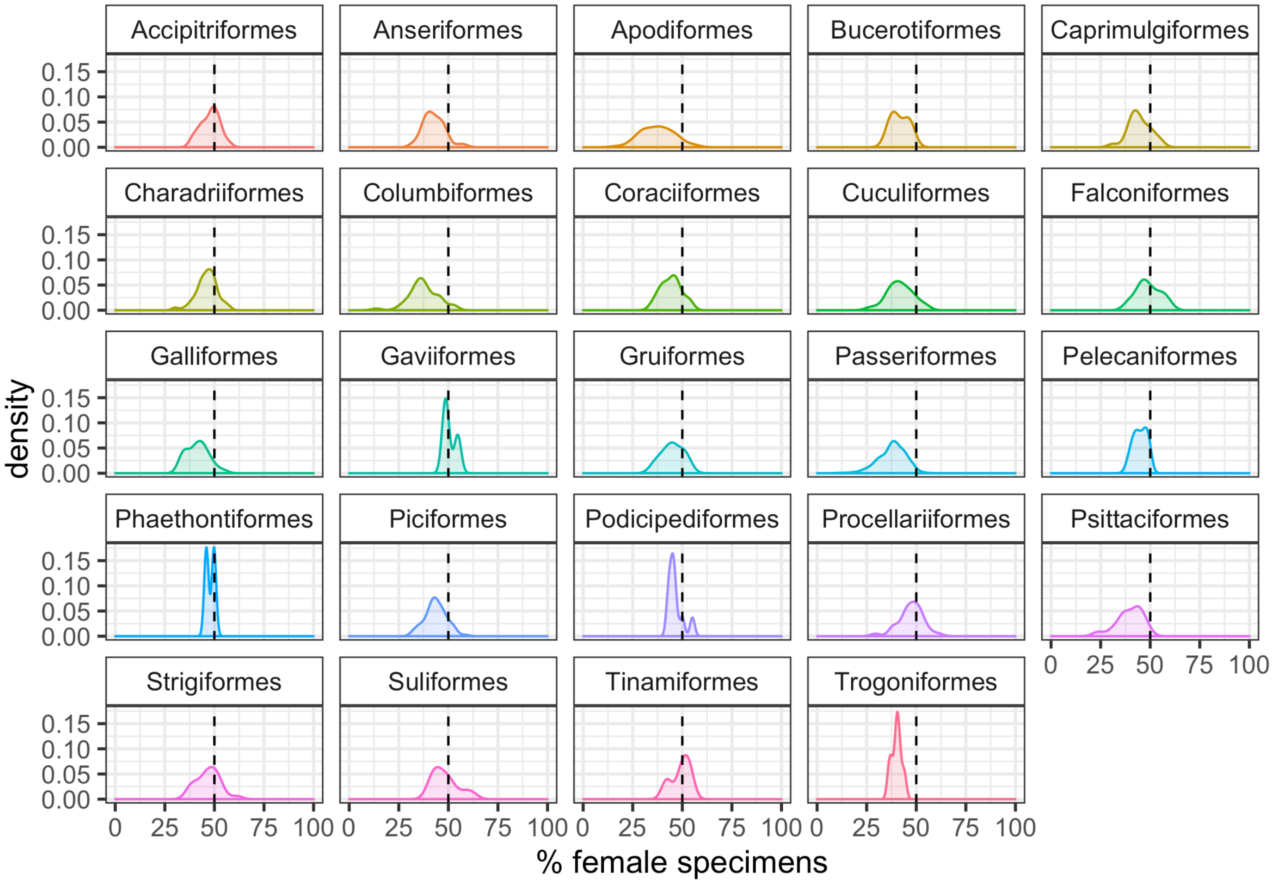

Figure A10: Kernel density plots showing the % female specimens in each species across orders of birds with at least three species in the dataset. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens.

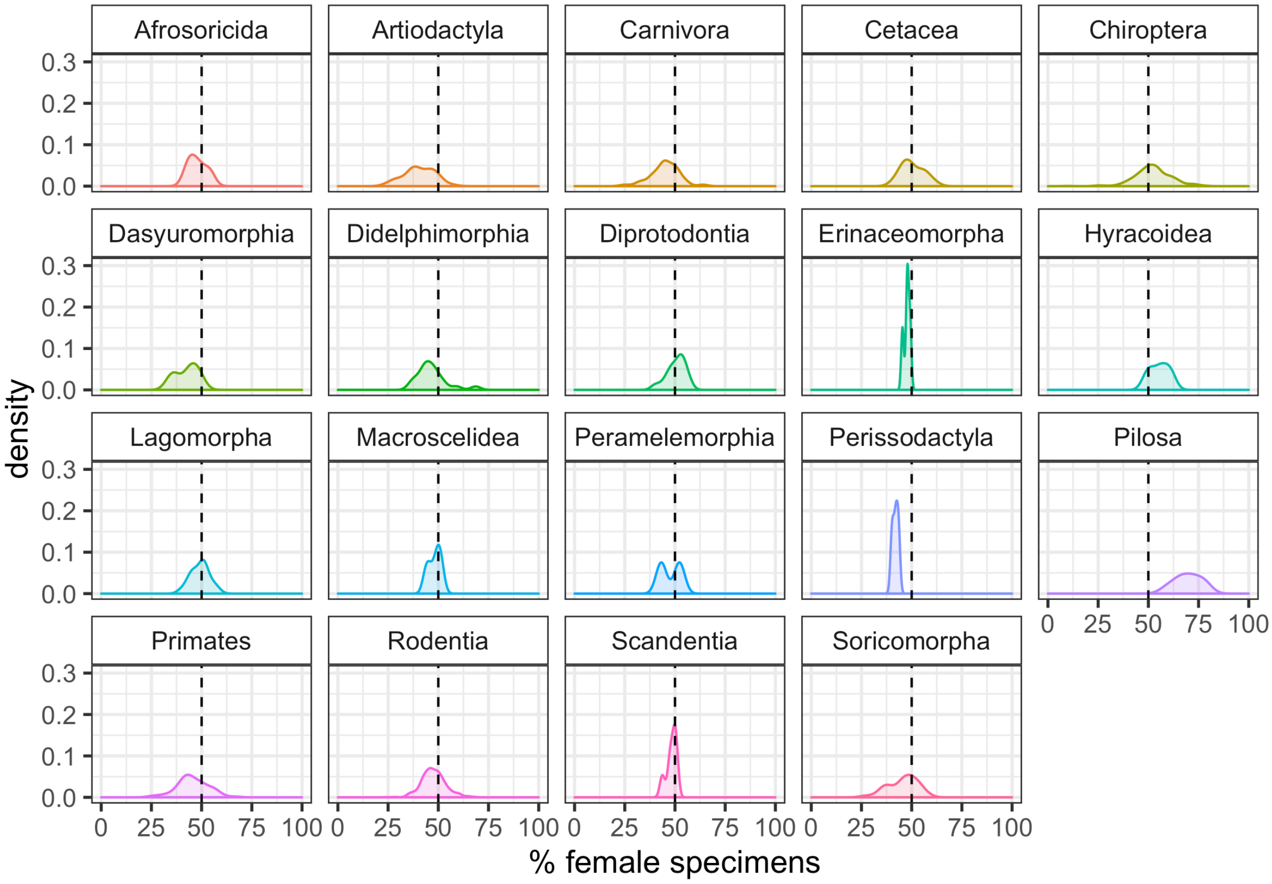

Figure A11: Kernel density plots showing the % female specimens in each species across orders of mammals with at least three species in the dataset. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens.

Table A4: Median percentages of female specimens within species with at least 100 specimens, or each order of birds and mammals. Orders with median percentages of female specimens of over 50% are in bold.

class	order	n species	n specimens	% female
Birds	Accipitriformes	37	9738	48.76
Birds	Anseriformes	45	12301	42.48
Birds	Apodiformes	64	10914	37.18
Birds	Bucerotiformes	5	919	40.70
Birds	Caprimulgiformes	24	5565	44.19
Birds	Charadriiformes	148	43393	46.32
Birds	Coliiformes	2	491	37.92
Birds	Columbiformes	46	8464	36.77
Birds	Coraciiformes	27	7377	44.71
Birds	Cuculiformes	29	6223	41.32
Birds	Falconiformes	14	5577	47.70
Birds	Galliformes	37	13062	40.99
Birds	Gaviiformes	3	585	49.03
Birds	Gruiformes	20	5082	45.22
Birds	Passeriformes	1021	317414	38.39
Birds	Pelecaniformes	26	6355	44.81
Birds	Phaethontiformes	2	684	47.88
Birds	Piciformes	74	19003	43.27
Birds	Podicipediformes	9	1746	45.41
Birds	Procellariiformes	33	6842	47.90
Birds	Psittaciformes	33	5011	40.57
Birds	Strigiformes	24	6570	47.33
Birds	Suliformes	12	2929	47.19
Birds	Tinamiformes	4	608	**50.36**
Birds	Trogoniformes	7	1070	40.50
Mammals	Afrosoricida	4	459	47.25
Mammals	Artiodactyla	60	15855	39.71
Mammals	Carnivora	91	46610	45.37
Mammals	Cetacea	16	8929	49.30
Mammals	Chiroptera	366	195777	**52.19**
Mammals	Cingulata	2	613	37.15
Mammals	Dasyuromorphia	3	436	43.75
Mammals	Dermoptera	1	103	**55.34**
Mammals	Didelphimorphia	20	9240	45.40

Mammals	Diprotodontia	15	3303	**52.33**
Mammals	Erinaceomorpha	4	1176	47.88
Mammals	Hyracoidea	3	831	**55.70**
Mammals	Lagomorpha	25	12127	**50.22**
Mammals	Macroscelidea	9	2412	48.93
Mammals	Monotremata	1	106	40.57
Mammals	Paucituberculata	2	484	39.84
Mammals	Peramelemorphia	2	465	47.71
Mammals	Perissodactyla	3	498	42.00
Mammals	Pholidota	1	126	**51.59**
Mammals	Pilosa	7	1293	**71.07**
Mammals	Primates	80	19856	44.79
Mammals	Rodentia	701	488124	47.34
Mammals	Scandentia	6	1929	48.95
Mammals	Sirenia	1	152	46.71
Mammals	Soricomorpha	90	46618	46.78

9 Apodiformes

The order Apodiformes consists of three families hummingbirds (Trochilidae), swifts (Apodidae) and treeswifts (Hemiprocnicadae). Hummingbirds are sexually dimorphic, but swifts are not. To investigate this in more detail we split this order into the three families and look at the percentage of females in each family. As suspected if sexual plumage dimorphism affects the percentage of female specimens, we see that on average hummingbirds have fewer female specimens than swifts (hummingbirds = 35.4% from 51 species; swifts = 48.2% from 10 species; tree swifts = 47% from 3 species; Figure A12).

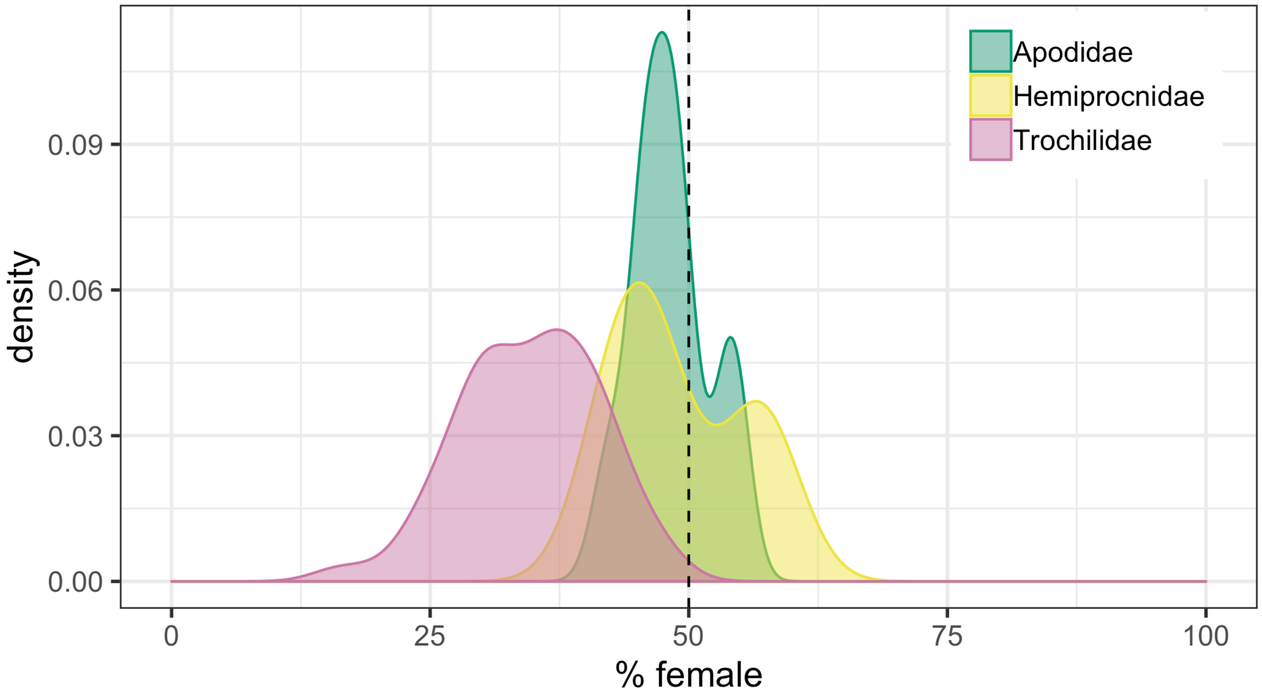

Figure A12: Kernel density plots showing the % female specimens in each species across the three families of the order Apodiformes. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens.

10 Changes through time

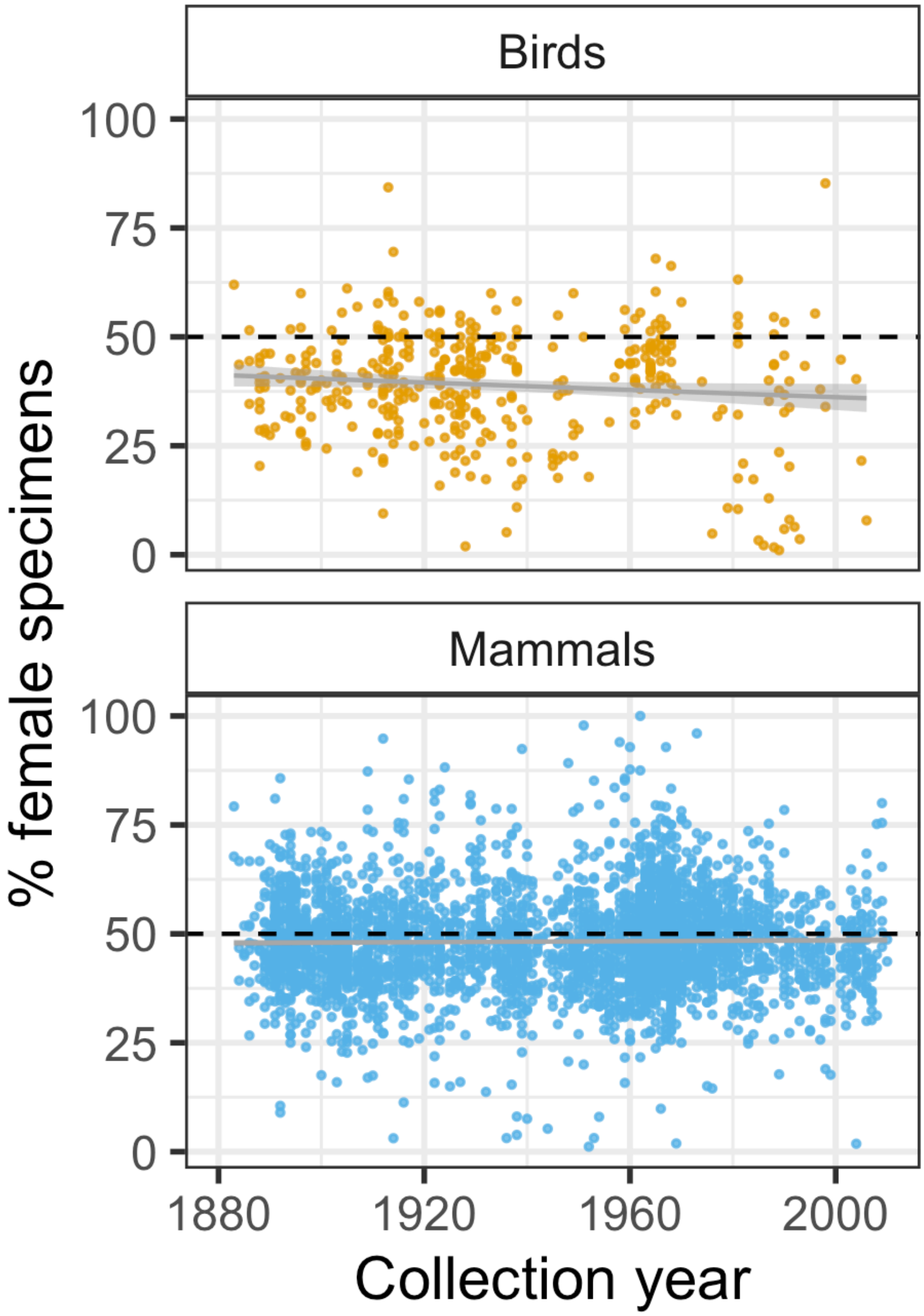

Figure A13: Changes in the proportion of female specimens for each species collected each year between 1880 and 2010. Best fit lines and 95% confidence intervals from quasibinomial generalized linear models are shown in grey. Data points represent species with at least 50 specimens collected in a given year. The dashed line represents 50% female specimens.

11 Male body mass and sexual size dimorphism.

Figure A14: Relationship between the percentage of female specimens for each species and log male body mass (g) for the species. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens. Note that the x-axis scales are different for birds and mammals.

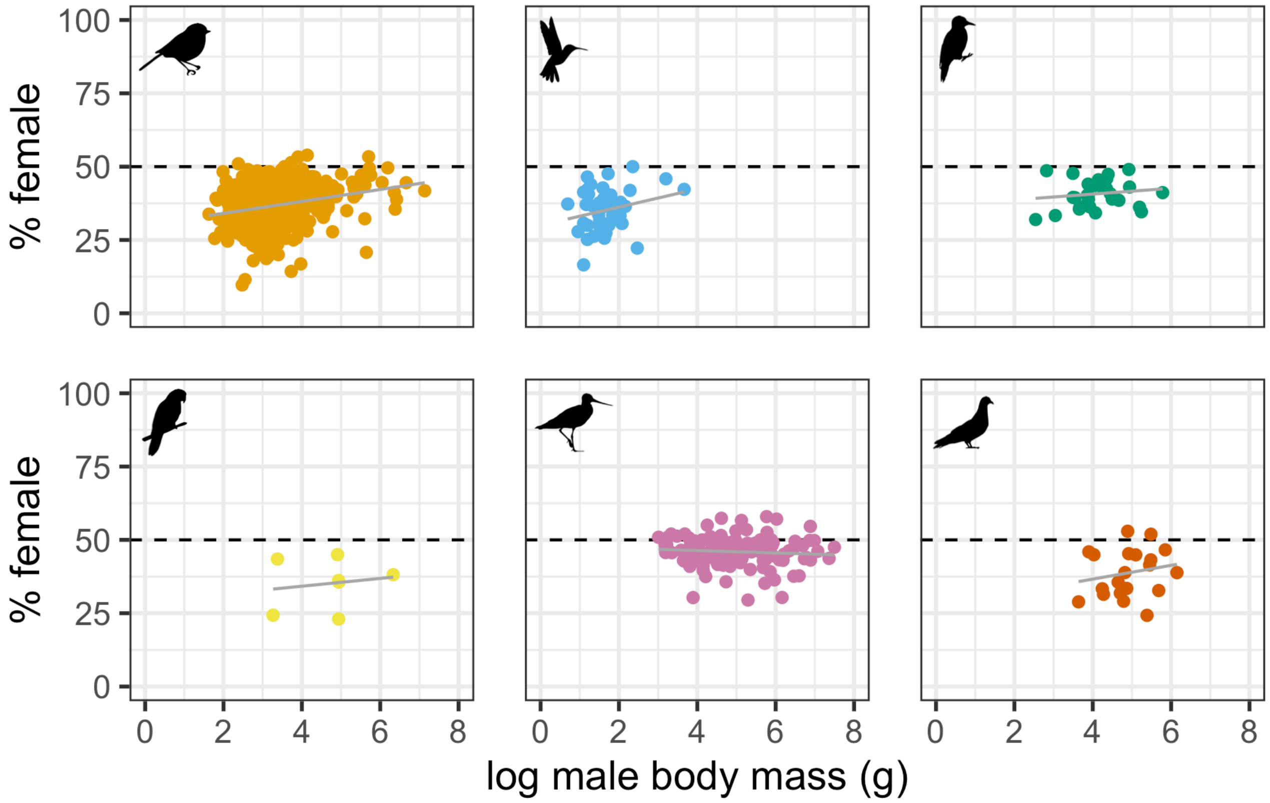

Figure A15: Plots showing how % female specimens in each species varies with male body mass (g) across the six largest orders of birds (from left to right, top to bottom: Passeriformes, Apodiformes, Piciformes, Psittaciformes, Charadriiformes, and Columbiformes). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens; grey lines show relationship between the variables using a simple linear regression and are for reference only. Silhouettes are from PhyloPic.org contributed by Ferran Sayol (parrot, hummingbird, tit), Steven Traver (woodpecker) and Alexandre Vong (shorebird).

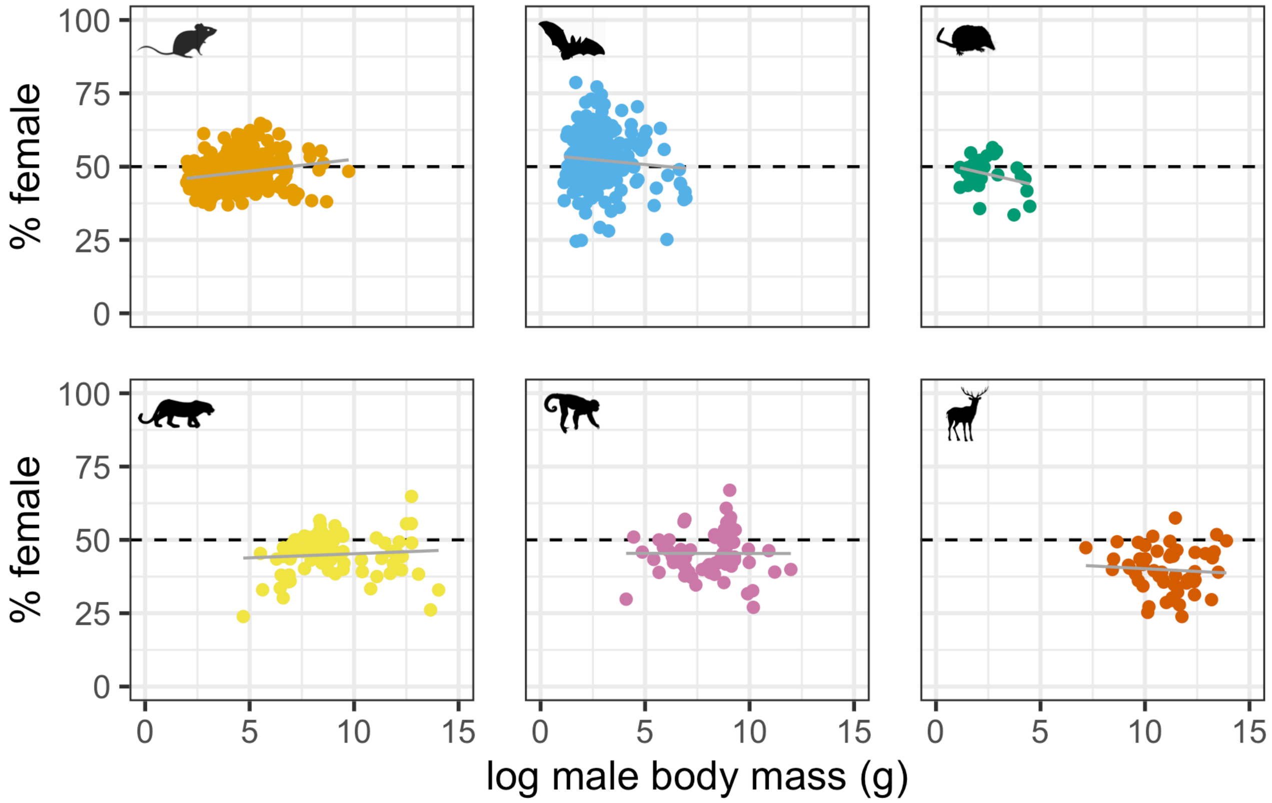

Figure A16: Plots showing how % female specimens in each species varies with male body mass (g) across the six largest orders of mammals (from left to right, top to bottom: Rodentia, Chiroptera, Soricomorpha, Carnivora, Primates, and Artiodactyla). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens; grey lines show relationship between the variables using a simple linear regression and are for reference only. Silhouettes are from PhyloPic.org contributed by Daniel Jaron (mouse), Yan Wong (bat), Becky Barnes (shrew), Lukasiniho (tiger), Sarah Werning (monkey), and Oscar Sanisidro (deer).

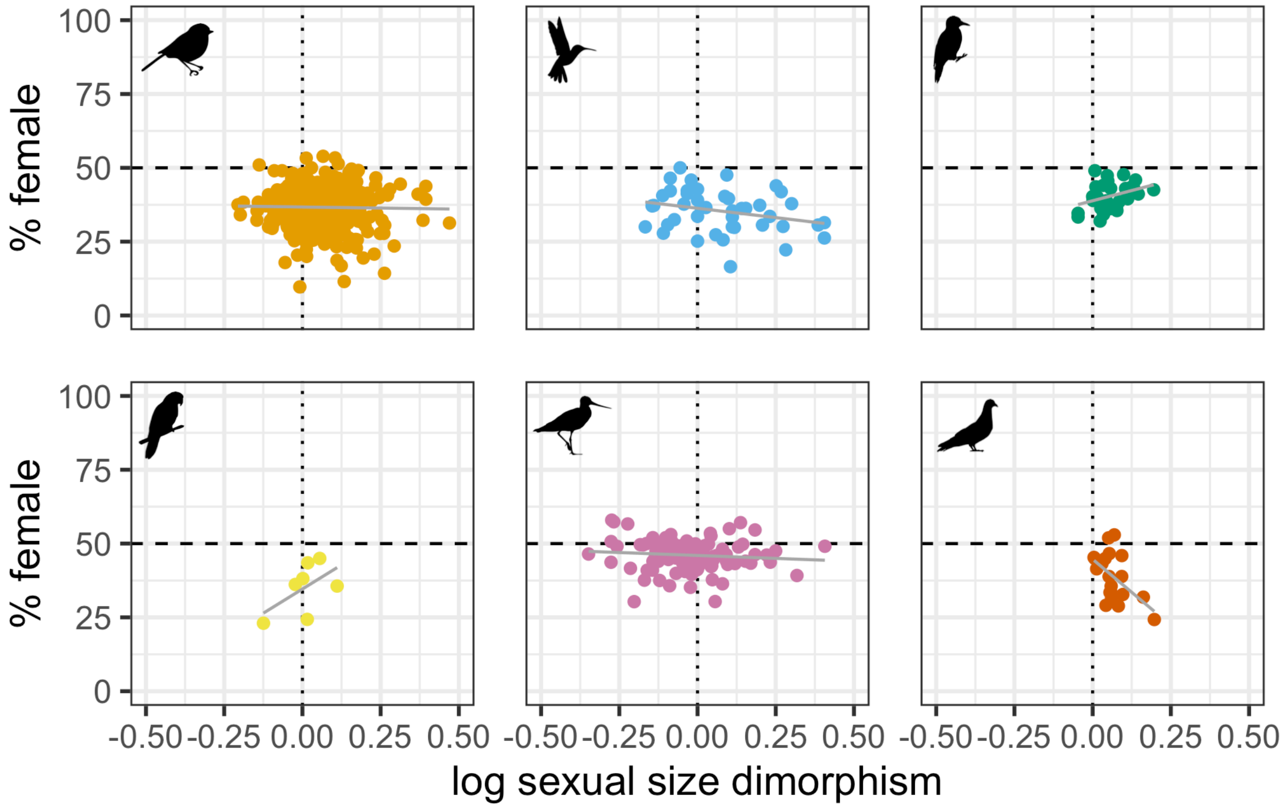

Figure A17: Plots showing how % female specimens in each species varies with sexual size dimorphism across the six largest orders of birds (from left to right, top to bottom: Passeriformes, Apodiformes, Piciformes, Psittaciformes, Charadriiformes, and Columbiformes). Sexual size dimorphism is male mass divided by female mass. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens; the dotted line is the point at which males and females have the same body size; grey lines show relationship between the variables using a simple linear regression and are for reference only. Silhouettes are from PhyloPic.org contributed by Ferran Sayol (parrot, hummingbird, tit), Steven Traver (woodpecker) and Alexandre Vong (shorebird).

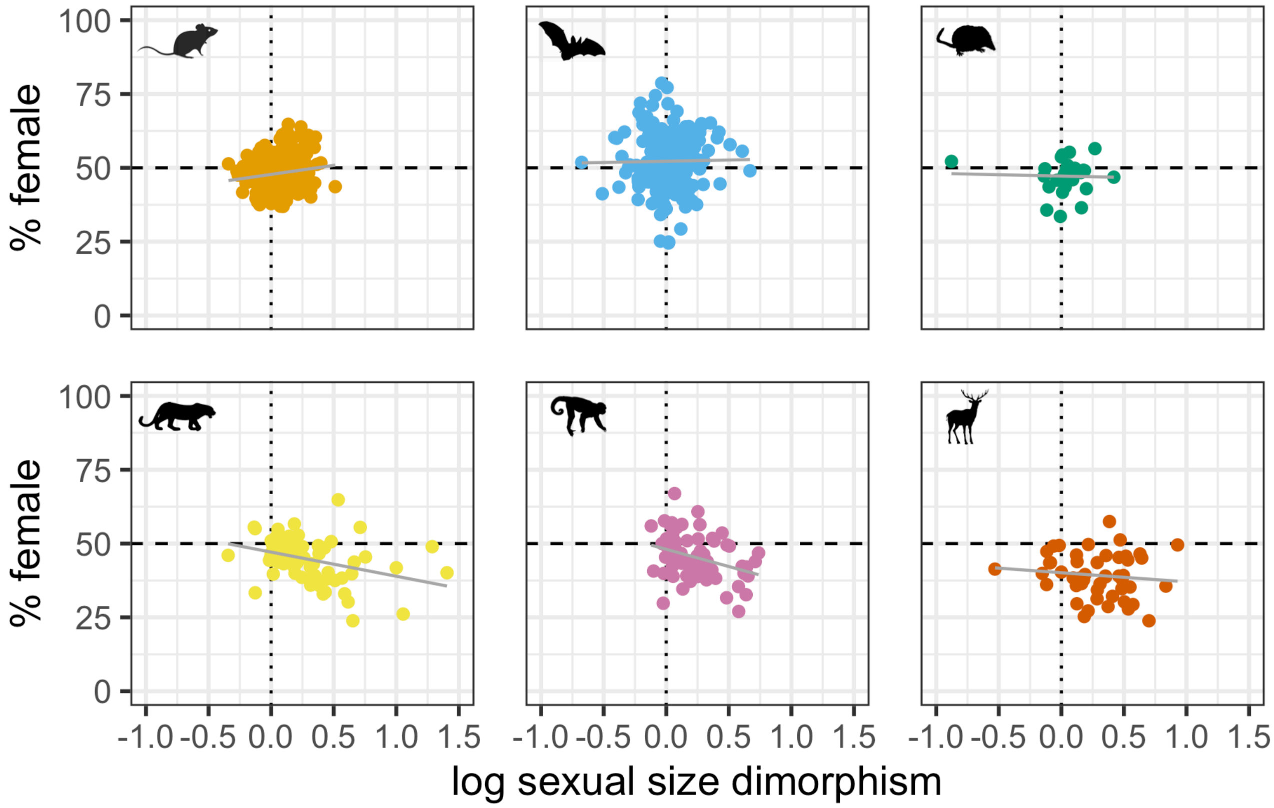

Figure A18: Plots showing how % female specimens in each species varies with sexual size dimorphism across the six largest orders of mammals (from left to right, top to bottom: Rodentia, Chiroptera, Soricomorpha, Carnivora, Primates, and Artiodactyla). Sexual size dimorphism is male mass divided by female mass. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens; the dotted line is the point at which males and females have the same body size; grey lines show relationship between the variables using a simple linear regression and are for reference only. Silhouettes are from PhyloPic.org contributed by Daniel Jaron (mouse), Yan Wong (bat), Becky Barnes (shrew), Lukasiniho (tiger), Sarah Werning (monkey), and Oscar Sanisidro (deer).

Table A5: Outputs from generalised linear models (GLMs) with quasibinomial errors where the response variable is the number of male and female specimens for each species, for species with more than 100 specimens. mass = log male body mass (g); SSD = log male body mass/female body mass. Significance testing uses Type II ANOVA. df = degrees of freedom; SE = standard error.

Birds

coefficients	**F**	**df**	**p**	$slope \pm SE$
mass	273.1	1, 849	<**0.001**	0.102 ± 0.006
mass	40.33	1, 803	<**0.001**	NA
order	10.06	24, 803	<**0.001**	
mass:order	1.183	22, 803	0.254	
SSD	41.23	1, 827	<**0.001**	-0.436 ± 0.068
SSD	0.317	1, 782	0.574	NA
order	18.92	24, 782	<**0.001**	
SSD:order	1.501	21, 782	0.069	
SSD	2.269	1, 741	0.132	NA
mass	41.40	1, 741	<**0.001**	
order	6.800	24, 741	<**0.001**	
SSD:mass	0.073	1, 741	0.787	
SSD:order	1.070	20, 741	0.376	
mass:order	0.918	20, 741	0.563	
SSD:mass:order	0.989	19, 741	0.472	

Mammals

coefficients	**F**	**df**	**p**	$slope \pm SE$
mass	46.24	1, 785	<**0.001**	-0.025 ± 0.004
mass	21.15	1, 751	<**0.001**	NA
order	14.13	19, 751	<**0.001**	
mass:order	2.802	15, 751	<**0.001**	
SSD	27.34	1, 715	<**0.001**	-0.244 ± 0.047
SSD	0.052	1, 681	0.819	NA
order	13.68	19, 681	<**0.001**	
SSD:order	1.339	15, 681	0.173	
SSD	0.672	1, 660	0.413	NA
mass	31.31	1, 660	<**0.001**	
order	14.38	19, 660	<**0.001**	
SSD:mass	5.247	1, 660	**0.023**	
SSD:order	1.979	10, 660	**0.033**	
mass:order	4.094	10, 660	<**0.001**	

SSD:mass:order	0.810	9, 660	0.607

12 Reverse sexual dimorphism in birds

Some bird species show reverse sexual dimorphism, where females are larger or showier than the males. This occurs in hawks and vultures (Accipitridae), falcons (Falconidae), sandpipers and snipe (Scolopacidae), phalaropes (Charadriidae), jacanas (Jacanidae), skuas (Stercorariidae), boobies (Sulidae), frigate birds (Fregatidae), owls (Strigiformes), cuckoos (Cuculidae), hummingbirds (Trochilidae), manakins (Pipridae), and some ratites (Struthioniformes) (Swaddle et al. 2000[2]). The sexual size dimorphism and sexual plumage dimorphism analyses in the main text deal with this quantitatively and within the same framework as more typical male based sexual dimorphism. This is a better technique than lumping species into male versus female dominated dimorphism groupings, as the variation among sexes can vary hugely within these. For example, in European grouse species where the male capercaillie (*Tetrao urogallus*) are more than twice the mass of females, while hazel grouse (*Tetrastes bonasia*) females are only a gram heavier than males (Amadon, 1959[3]). However, our method had limitations - we did not have male and female body size for all species, and we only had plumage data for Passeriformes. As such we may have missed important patterns.

To deal with this, we divided the bird data into species where the female is generally the larger or showier sex (the families Accipitridae, Falconidae, Scolopacidae, Charadriidae, Jacanidae, Stercorariidae, Sulidae, Fregatidae, Cuculidae, Trochilidae, Pipridae, and the orders Strigiformes and Struthioniformes), and species where the male is generally the larger or showier sex (all other species). We then compared the median percentage of females within species of the two groups, and fitted generalized linear models with quasibinomial errors to test for significant differences.

Overall we found that the median percentage of females for species where the male was the larger or showier sex was 40%, the same as for the whole dataset. For species where the female is the larger or showier sex the median percentage of females was 44.6%, closer to the expected 50:50 ratio. There were significantly more females in species where the female is the larger or showier sex (quasibinomial GLM: $F_{1,1744} = 167.9$, $p < 0.001$; Figure A19)

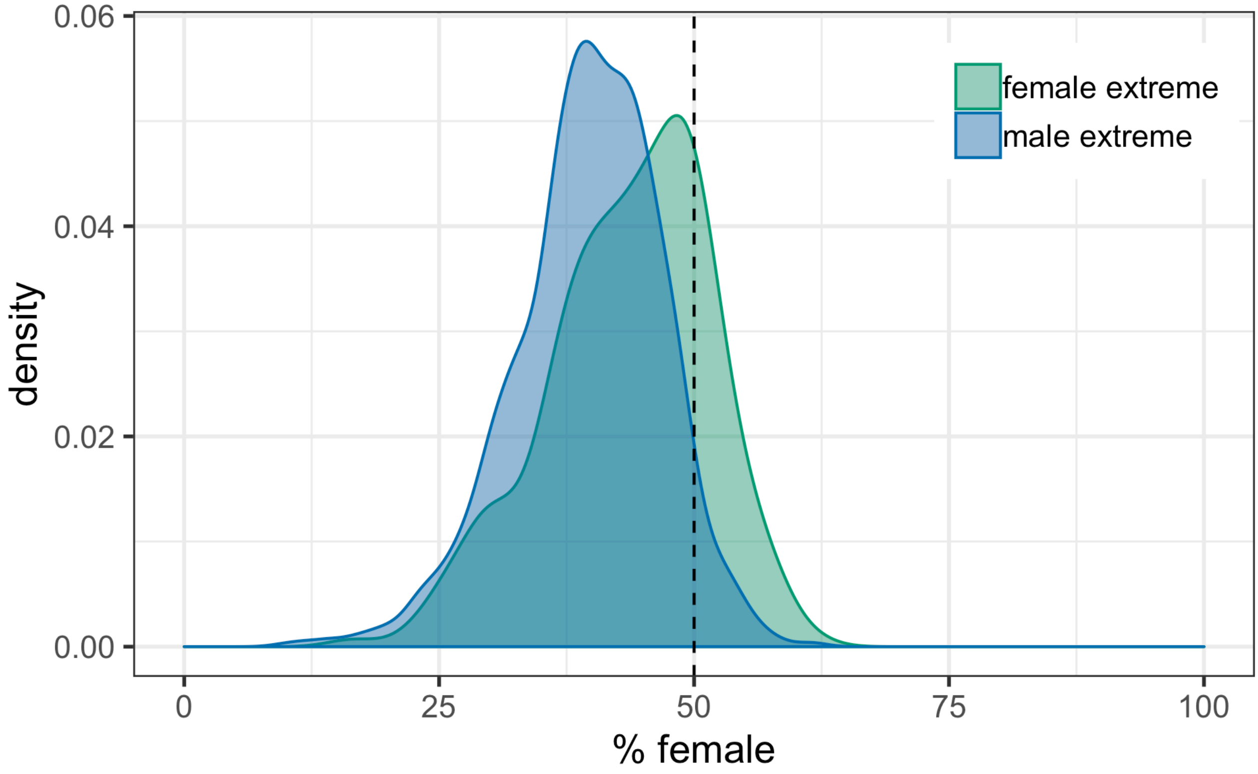

Figure A19: Kernel density plots showing the % female specimens in each species of bird for species where females are the larger or more showy sex (female extreme), or where males are the larger or more showy sex (male extreme). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens.

13 Ornamentation analyses in mammals

Model	**Specimens**	**median % female**	**Species**
Absent	839,981	48.32	1,445
Present	17,403	39.52	67
Feature			
cheek extensions	287	39.02	1
horns or antlers	13,506	38.86	50
manes	752	32.67	3
nasal protrusions	474	55.85	3
ossicones	157	49.68	1
tusks	2,227	48.05	9
Order			
Artiodactyla	15,726	39.52	59
Carnivora	663	45.20	3
Chiroptera	188	55.85	1
Primates	826	35.85	4

Table A6: Numbers of specimens and species with ornaments, divided by ornament type and order.

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[1] Székely T, Liker A, Freckleton RP, Fichtel C, Kappeler PM. Sex-biased survival predicts adult sex ratio variation in wild birds. Proceedings of the Royal Society of London B: Biological Sciences. 2014;281(1788):20140342.

[2] Swaddle JP, Karubian J, Pruett-Jones S. A novel evolutionary pattern of reversed sexual dimorphism in fairy wrens: implications for sexual selection. Behavioral Ecology. 2000;11(3):345–349.

[3] Amadon D. The significance of sexual differences in size among birds. Proceedings of the American Philosophical Society. 1959;103(4):531–536. Available from: `http://www.jstor.org/stable/985554`.