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# Female North American passerine birds have lower apparent survival than males

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Survival is a fundamental organismal trait which can vary by sex, yet the extent of sex-biased survival is largely unknown across most taxa. To address this information gap, we leveraged 563 414 capture–mark–recapture records in 92 North American bird species—spanning 17 families across the orders Passeriformes and Piciformes—to estimate sex-specific apparent survival using transient Cormack–Jolly–Seber models. We found significantly lower apparent survival in females in 35 species. Adult apparent survival was, on average, 12.4% lower for females (0.479 ± s.e. 0.009) than males (0.538 ± 0.008), corresponding to adult lifespans (i.e. longevity having survived to adulthood) of 1.36 years for females and 1.61 years for males (18.5% higher than females). Exploration of potential mechanisms underlying sex-biased survival indicated that the female–male survival gap was greater in long-distance migratory species, lower in species with greater dispersal-associated morphology, and higher in species where males had relatively more fat, lending weight to the hypotheses that social dominance and lower movement costs in males contribute to male-biased survival. Our analysis demonstrates a pervasive male bias in adult apparent survival across a large swath of Nearctic breeding birds and provides possible explanations for previous observations of skewed adult sex ratios in birds.

## 1 . Introduction

Given the extent and pace of human-caused biodiversity loss, it is critical to understand the causes underlying ongoing population declines [1,2]. Population change is fundamentally driven by two demographic parameters: survival—the probability of surviving from one time period to the next [3]—and fecundity—the number of offspring produced per time period [4]. Across vertebrate species, adult survival typically has a bigger impact on population growth in longer-lived species, whereas fecundity has a bigger impact in species that mature early and have high reproductive output [5,6]. Though the mechanisms that shape population demographics are nuanced, an individual's sex is a key characteristic which can affect survival, fecundity and population trajectories.

Female and male organisms are subject to different biological processes, such as sexual selection, reproductive demands and physiological and genetic pressures [7–10]. Their divergent life histories thus lead to different factors affecting mortality [11,12]. Survival rates that differ according to sex, which we call sex-biassed survival, can affect the ratio of reproductively active females to males in a population (i.e. operational sex ratio) [12]. Such unbalanced operational sex ratios can reduce reproductive output and



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**Table 1.** We predict that species with higher movements, female reproductive costs, and where females have lower social status will have reduced female apparent survival.

| hypothesis | trait[a] | prediction[b] | result[b] |
|---|---|---|---|
| movement costs | migration tendencies (avg) | + | + |
| | hand-wing index (HWI; avg) | + | – |
| | Δwing:mass ratio (F to M) | + | 0 |
| reproduction costs | clutch size | + | 0 |
| | relative egg load | + | 0 |
| social dominance | mass (g; avg) | +/– | 0 |
| | Δmass (g; F to M) | + | 0 |
| | Δfat (F to M) | + | + |
| | sexual size dimorphism (SSD) | + | 0 |

[a]Each testable hypothesis was evaluated by one or multiple measurable, uncorrelated species traits.
[b]A positive (+) value indicates greater male-biased apparent survival ($\Delta\phi$), while a negative (–) value indicates lower $\Delta\phi$. Null (0) values in our results indicate no evidence for a relationship.

negatively impact population growth [13–16]. However, most demographic models are single sex, accounting only for the dynamics of females in the population [4,17], or assume equal sex ratios and life histories between sexes [18]. This assumption of equal sex ratio or rate of survival across sexes is rarely valid across the tree of life [19]. While many demographic modelling studies do not consider sex-specific survival parameters, some that do have found that incorporating sex effects can change inferences and conclusions [20,21].

Data on survival of both sexes can improve demographic model precision and clarify when a particular sex has a larger influence on population trajectory. A better understanding of sex bias in survival within birds is important for conservation and management to target the direct drivers of population change, particularly for declining and endangered species [22–24]. For example, the sexes of giant petrels (*Macronectes* spp.) respond differently to climate variation and longline fishing, and accounting for these sex differences is critical to predicting the species' future demography [25]. The lack of sex-specific survival estimates can impede a full understanding of what limits populations. Consequently, to understand population trajectories, managers must understand how to improve survival in the limiting sex.

Multiple non-exclusive hypotheses for sex-biased survival exist. One prevalent hypothesis is that the heterogametic sex (i.e. females in birds or males in mammals) suffers from potentially deleterious mutations on the reduced sex chromosome [26,27]. Empirical evidence across a diversity of species, including mammals, birds, reptiles, amphibians, fish, and invertebrates, supports this theory [19,28,29]. A second hypothesis postulates that the sex with greater movements, which tends to be females in passerine birds [30–32], incurs a higher risk of mortality due to increased physiological costs and overall mortality risks such as collision and predation [33]. A third hypothesis is that reproductive costs (e.g. carrying embryos or caring for young) may reduce one sex's survival (typically females) relative to the other [34–36]. Finally, a fourth hypothesis is that social dominance by one sex, coupled with differential access to resources, may lead to reduced body condition in the subordinate sex that can amount to reduced survival over time [37,38]. Each of these hypotheses has evidence in some systems, yet their relative total contributions to sex-biased survival remain poorly understood.

Birds represent a strong study system for determining the extent of sex-biased survival and for evaluating evidence for the above hypotheses. Birds are widespread, diverse, and have larger available monitoring datasets than many other animals. Yet even though birds are one of the most well-researched taxa overall, direct estimates of sex-specific survival are not always calculated [39]. This oversight may be because the standard methods to calculate survivorship require recapturing marked individuals [40,41]; these calculations end up extremely data-hungry since most individual birds are never encountered again [42]. For example, 6–10 recaptures are needed to obtain reasonably accurate annual survival estimates [43]. To calculate survival rates for both sexes effectively requires roughly doubling one's sample of recaptured individuals, which can be a limiting factor. As a result of data limitations, there have been few large-scale, multi-species studies of sex-specific survival rates in birds. To our knowledge, primary analyses on sex-biased survival in birds have been taxonomically limited to 8–15 species [44–47]. In contrast, the number of species modelled in species-level analyses (i.e. ignoring sex-biased survival) are orders of magnitude larger [48]. Several reviews suggest that survival is lower in female than male birds, although these inferences largely derive from observations of adult sex ratios [35,49] or meta-analyses [12,50]. Because rigorous analyses of sex-specific survival are typically too data-intensive to be conducted on a large scale, we currently lack direct comparisons of survival rates between female and male birds at large taxonomic and spatial scales.

In this study, we modelled adult apparent survival rates of female and male passerines and woodpeckers across the USA and Canada over 27 years and explicitly tested for sex-biased survival in these species while controlling for transient individuals and potential sex-specific biases in capture–recapture probability. In addition to determining the extent and magnitude of the difference in apparent survival between sexes, we also explored some functional traits that may explain species-specific variation in these survival differences. We hypothesized that female birds would have overall lower apparent survival than male birds. We subsequently sought to examine three of the four hypothesized origins of sex-biased survival by relating

species traits to the estimated magnitude of sex bias in each species' survival probability. The theories we explored were (i) movement costs, (ii) reproductive costs, and (iii) social dominance (table 1); we were not able to test the theory of homogametic advantage because this trait does not vary among species within Aves. For costs associated with (i) long-distance movement, we examined three traits as proxies: migratory class, hand-wing index (HWI; a measurement of wing aspect ratio associated with dispersal ability [51]), and sex-based differences in wing-to-weight ratio. Because female passerines disperse farther and are therefore expected to incur greater movement costs than males, we predicted that sex-biased survival would be greater for more migratory species, for species with larger HWI, and for species where females have larger wing-to-weight loading than males. For (ii) reproductive costs, we evaluated two proxy traits—clutch size and relative egg size—with the prediction that the increased quantity of eggs or energy needed for females to produce eggs would produce physiological costs leading to male-biased survival. For (iii) social dominance costs, we assessed four proxy traits: three measurements of body size as well as sex difference in fat storage among breeding individuals. Our indirect variables assume that larger differences in size or condition between sexes will signify strength of dominance hierarchies—where males are typically socially dominant over females in passerines [10,52]—which could result in male-biased survival. Evaluating these hypotheses to improve our understanding of mechanisms underlying sex-biased survival will support better population management and conservation in an era of massive environmental changes.

## 2. Methods

### (a) Bird capture methods

We conducted sex-specific apparent survival analysis using nearly three decades of capture–mark–recapture bird banding data across the USA and Canada spanning 1992–2018 to conduct sex-specific survival analysis on 92 bird species from 17 families (electronic supplementary material, table S1) [53]. The Monitoring Avian Productivity and Survivorship (MAPS) programme is a rigorous, constant-effort bird banding programme that collects standardized capture–mark–recapture data across a network of over 1200 US and Canadian sites beginning in 1989 [53,54]. At a typical MAPS station, 10 mist nets were opened once every 10 days during the local breeding season, generally between 1 May and 8 August. Banding effort at all stations was approximately equal and carefully standardized across all years following MAPS protocols [53]. Each banding day comprised six hours of net operations. For each individual captured (mostly of passerine species), banders recorded the species identity, band number, age, sex, measurements, moult condition and reproductive status [54]. Banding data and data on station operations were provided by the Institute for Bird Populations (IBP) [55].

### (b) Data filtering

Our analysis included stations that meet rigorous IBP-established suitability criteria for survivorship analysis (e.g. operated for at least four years, had early and late season sampling, operated for at least three 10-day periods in a year; see [54] for full details). Because juvenile mortality is higher and more variable among species than adult mortality, and because estimation of meaningful first-year survival rates of birds marked as juveniles is difficult due to few recaptures as adults because of high natal dispersal rates [56], we filtered data to adult birds, retaining individuals classified as after-hatching-year (AHY) or older. We kept only individuals of known sex (84% of AHY birds across our sample) for analyses. At least 10 individuals with recaptures in subsequent time steps are recommended to fit survival models to a species with MAPS data [57]; given that we aimed to model sex-specific survival, we retained only species with at least 20 total recaptured individuals with a minimum of five recaptured individuals per sex.

Following these filtering steps, our banding data comprised a total of 563 414 unique adult birds of known sex. Of these, 22 415 were recaptured 'residents' (explained below). Individuals represent 92 species from two orders (Piciformes and Passeriformes) and 17 families (electronic supplementary material, table S1). Banding data spanned 1229 stations across the continental USA and Canada. Raw captures consisted of 48.4% ($n$ = 272 486) females and 51.6% ($n$ = 290 928) males across retained species.

### (c) Modelling sex-specific apparent survival for all species

We modelled apparent annual survival ($\phi$) for adult birds of each species using the Cormack–Jolly–Seber model [3,58] in program MARK via the R package 'RMark' v. 3.0.0 [59]. We parametrized the model to distinguish between individuals of known and unknown residency status [60]. Since the model cannot distinguish between permanent emigration and death, we modelled apparent survival primarily for individuals of known residency status to minimize the influence of emigrants on survival estimates. To do this, we classified an individual bird as a 'resident' if it was caught at least twice on occasions more than 6 days apart in the year it was banded. Data from these known residents informed survival estimates across all years after initial capture. All other individuals were considered to be of unknown residency status (i.e. a mixture of residents and transients), and data from this group only informed survival estimates subsequent to the initial capture year [57]. This approach minimizes the influence of transient individuals in the sample on survival estimates.

We fit one model for each species. We coded sex ($M$; 0 = female; 1 = male) and residency ($T$; 0 = resident; 1 = unknown residency status) as binary variables. The model estimates apparent survival probability ($\phi_i$) for individual $i$ as a logit-linear function of sex, residency status and their interaction:

$$\text{logit}(\phi_i) = \beta_0 + \beta_1 M_i + \beta_2 T_i + \beta_3 M_i T_i, \quad (2.1)$$

where $\beta_0$ is the intercept (for a female resident), $\beta_1$ is the additive effect of being a male (resident), $\beta_2$ is the additive effect for being of unknown residency status during the first year after banding and $\beta_3$ is the interactive effect of being both male and of unknown residency status in the first year after banding. Parameter $\beta_1$ thus directly estimates the direction and magnitude of sex-biased apparent survival (among the target (resident) population).

Cormack–Jolly–Seber models also account for imperfect capture probability when estimating survival [40]. We modelled the probability of capture ($p$) as a function of sex ($M$) and effort ($E$). Effort is a year- and station-specific term that denotes whether each station was operated in a given year ($E = 1$) or not ($E = 0$). Because a relatively standardized netting effort among years was required for a station to be included in analyses [54], and missed station-years were accounted for by setting recapture probabilities for those instances to zero, we considered stations as functionally equivalent and did not seek to model additional variation in capture probability. While we acknowledge that minor among-station variation in netting effort may exist, to maintain a tractable and consistent modelling framework among species, we thus chose to model capture probability as variable between sexes, but constant among stations. In addition to being consistent with past work [61], we believe the assumption of constant station-level capture probability is justified given that any existing station-level capture heterogeneity is unlikely to disproportionately affect one sex versus another in a systematic way.

Our fitted model predicts apparent survival rates ($\phi$) for each sex and residency status. We retained species with models that converged (due to sufficient data density) and produced estimable parameters [43]. We then calculated $\Delta\phi$, or the difference in apparent survival between male and female residents,

$$\Delta\phi = \phi_m - \phi_f, \quad (2.2)$$

where a positive $\Delta\phi$ indicates a higher apparent survival rate for males compared to females of the species. We calculated mean lifespan of birds once they reach adulthood (second year; SY) as the negative inverse of the log of annual sex-specific survival [3,36]: $-\log(\phi)^{-1}$. Summarizing across species, we used a meta-analytic fixed-effects model on estimates of $\beta_{1,j}$ for each species $j$ and associated uncertainties ($\sigma_{\beta_1,j}$) to test whether there is an aggregate trend in $\Delta\phi$ across all evaluated species [62]. This meta-analytic test was also conducted on each taxonomic family for which our analysis included two or more representative species.

## (d) Impact of life history traits on sex-biased apparent survival

In order to evaluate our main hypotheses, we modelled sex differences in apparent survival as a function of nine predictors that served as proxies for movement costs, reproductive costs, or social dominance costs (table 1). For the movement-cost hypothesis, we examined three proxy variables: migration tendency (with three categories: 'non-migrant', 'partial migrant' or 'long-distance migrant', from AVONET [63]); HWI (table 1; from AVONET [63]), a trait which correlates with flight and dispersal abilities [51]; and sex-based difference in wing-to-mass ratio (Δwing:mass; male minus female within a species), calculated directly from our banding data (details in electronic supplementary material, Methods). Since a higher wing-to-mass ratio indicates less mass loading, positive Δwing:mass values indicate males have less loading than females of a species, and negative values indicate females have less loading. For the reproductive cost hypothesis, we examined two proxy variables: mean clutch size from [10]; and relative egg load per female, standardized by female weight (table 1; details in electronic supplementary material, Methods). For the social dominance hypothesis, we examined four proxy variables: average species-level body mass (from banding data); sex-specific differences in body mass (from banding data); sex-specific differences in average body fat scores (from banding data); and sexual size dimorphism (SSD) [10], which integrates across multiple morphological measurements. Though there is variation among species, size is often related to social dominance and resource access in birds, where larger individuals are socially dominant [10,52]. See electronic supplementary material, Methods, for additional details.

Since we did not have *a priori* justification for which of the nine traits would be most important, we used $AIC_c$-based model selection [64] to narrow down to a limited set of strongly supported covariates. Thus, with the nine predictors (table 1), we constructed a full set of 512 candidate models—including all additive combinations of predictors—in a Gaussian linear model. We then used the 'dredge' function in the R package 'MuMIn' [65]. All models were then compared by $AIC_c$, and 504 models with uninformative parameters (i.e. models that were more complex versions of a model without an improvement in $AIC_c$) were removed [66], after which $AIC_c$ weights were recalibrated.

We examined the role of phylogeny by modelling phylogeny as a random effect using Pagel's correlation structure ($\lambda$) via the 'gls' function in the R package 'nlme' [67]. We downloaded 1000 phylogenetic trees with the Hackett backbone from BirdTree.org [68] and chose a tree at random for 15 iterations. Since we found no phylogenetic structure in the residuals of the linear model, no improvement in model fit of the phylogenetic model compared to a simple linear model, and no phylogenetic structure as evidenced by low Pagel's correlation ($\lambda = -0.06$ to 0.01), we did not include phylogeny in the subsequent modelling step.

After multi-model comparison with $AIC_c$, we retained the top-supported candidate model structure for formal model inference. In this second stage, we modelled $\phi$ as a function of $AIC_c$-selected species traits in a Bayesian regression framework, which allowed us to fully propagate uncertainty in $\phi$ from the individual species' Cormack–Jolly–Seber models. Here, we used the program JAGS [69] via the R package 'R2jags' [70]. We tested for multicollinearity using the 'vif' (variance inflation factor) function in the 'car' package [71] and a correlation matrix ('corr' function), and centred and scaled the species traits to allow for direct comparisons of relative effect sizes. VIF values between predictors were <2.2 and inter-variable correlations were low,

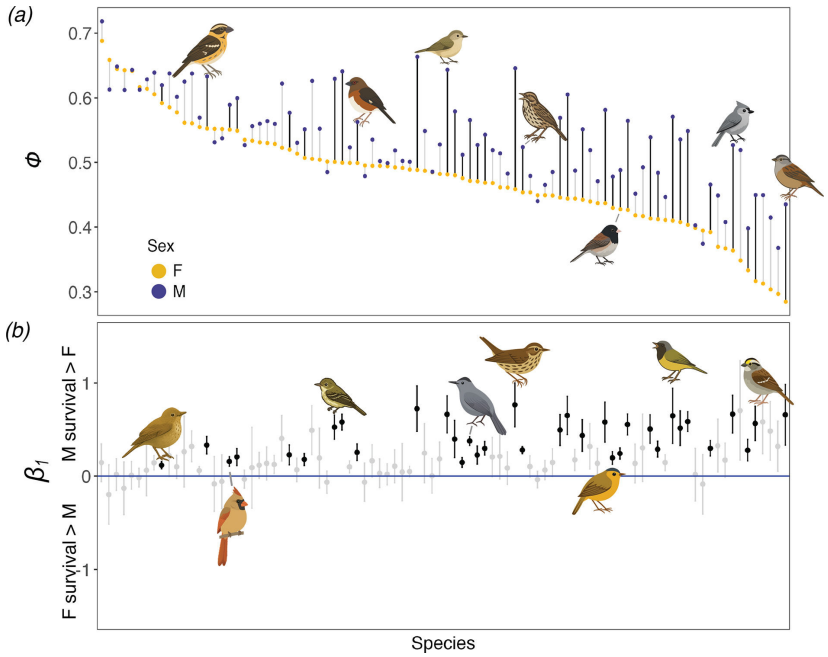


**Figure 1.** Females generally showed lower apparent survival than males in 82 of 92 Nearctic bird species, with statistically significant differences in 35 species. (*a*) Annual apparent adult survival ($\phi$) estimates for females (yellow) and males (purple). Black lines indicate a significant $\Delta\phi$ between the sexes ($p < 0.05$), and grey lines indicate a non-significant $\Delta\phi$. (*b*) Mean estimated effect sizes and 95% confidence intervals of $\beta_1$ of the 35 species with significantly lower female apparent survival ($p < 0.05$; black points and lines). The blue horizontal line denotes parity in apparent survival between sexes. Across both plots, species are ordered by female apparent survival rate. Labelled birds in (*a*) with significant differences, from left to right, are black-headed grosbeak (*Pheucticus melanocephalus*), spotted towhee (*Pipilo maculatus*), Bell's vireo (*Vireo bellii*), song sparrow (*Melospiza melodia*), dark-eyed junco (*Junco hyemalis*), tufted titmouse (*Baeolophus bicolor*) and swamp sparrow (*Melospiza georgiana*). In (*b*), labelled birds are Swainson's thrush (*Catharus ustulatus*), northern cardinal (*Cardinalis cardinalis*), Acadian flycatcher (*Empidonax virescens*), grey catbird (*Dumetella carolinensis*), northern waterthrush (*Parkesia noveboracensis*), Wilson's warbler (*Cardellina pusilla*), mourning warbler (*Geothlypis philadelphia*) and white-throated sparrow (*Zonotrichia albicollis*). See electronic supplementary material for bird figure credits.

with a median correlation of 0.02 and the highest correlation (between reproductive load and clutch size) of matrix values was <–0.58, indicating no autocorrelation [72,73] (see electronic supplementary material, Methods, for VIF ratios and correlation matrix).

Our Bayesian model assumed that the model-estimated sex-biased apparent survival parameter, $\phi_j$, for species $j$ was drawn from a normal distribution with a latent, true mean and model-estimated uncertainty, $\varepsilon_j$:

$$\phi_j \sim Normal(S_j, \varepsilon_j). \tag{2.3}$$

Species-specific precision $\varepsilon_j$ of the estimate $\phi_j$ was derived through error propagation of uncertainty ($\sigma$) attached to survival estimates for each sex:

$$\varepsilon = \left(\sigma_{\phi_f}^2 + \sigma_{\phi_m}^2\right)^{-1}. \tag{2.4}$$

The latent $S_j$ was then modelled via normal linear regression:

$$S_j \sim Normal(\mu_j, \tau), \tag{2.5}$$

with expected value $\mu_j$ representing a linear combination of species-level traits using only the set of traits selected for in the top $AIC_c$ model. In this case, because the selected traits included the categorical variable migration status, we coded each level (i.e. non-migrant, partial migrant or full migrant [63]) as its own intercept. Priors for all parameters were drawn from vague distributions (i.e. $\mu = 0$, $\tau = 0.001$ for normal; $r = 0.001$, $\lambda = 0.001$ for gamma). We ran three chains, each with 80 000 iterations including a burn-in of 30 000, followed by a thinning of 30, retaining 5000 total posteriors. All chains converged with Gelman–Rubin statistic = 1 [74] and posterior-prior overlap for all parameters was <0.6%. Inference on parameters was made using 95% Bayesian credible intervals (CrI), where 'strong confidence' in an effect was inferred when the 95% CrI did not cross zero. We checked *post hoc* whether a single outlier (tree swallow), which has a relatively extreme HWI value, exerted undue leverage in the regression.

## 3. Results

### (a) Survivorship

Across 92 species, annual adult apparent survival of resident birds was pervasively lower for female than male birds (meta-analytic test of $\beta_1$; $z = 17.4$, $p < 0.001$). On average, female apparent survival was 0.479 ± 0.009 (mean ± s.e.), compared to 0.538

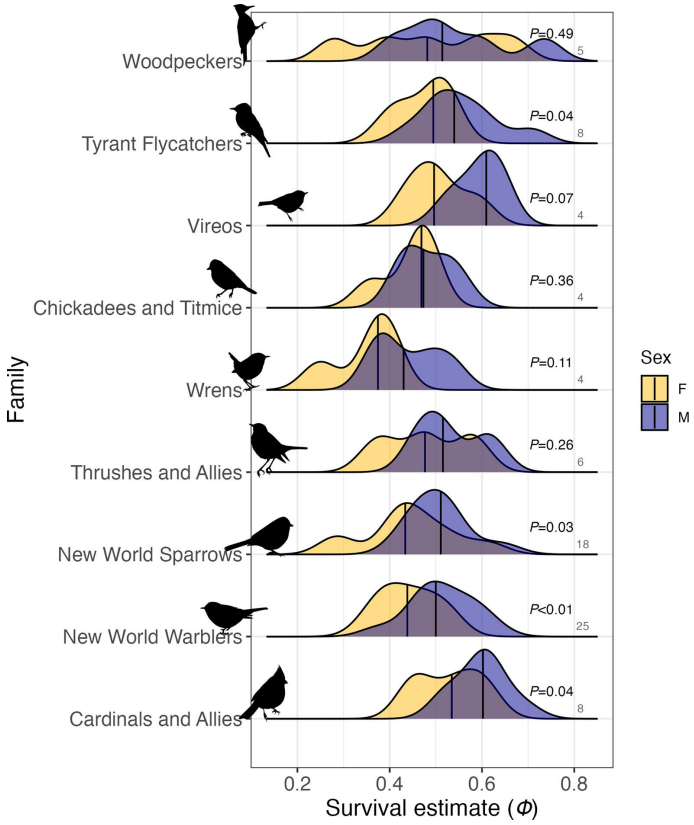


**Figure 2.** Distribution of female and male apparent annual survival estimates ($\phi$) by family. Values of $p$ indicate results of meta-analytic z-tests on the model-estimated difference in apparent survival by sex ($\beta_1$) for species tested within each family. Mean $\phi$ by sex within each family is indicated by the black vertical lines. The number of species within each family is represented at the bottom right. Families were only evaluated when >2 species were included in the sample.

± 0.008 for males, indicating that adult apparent survival was on average 12.4% lower for females than males. The survival difference was 12.9% lower for the 87 passerine species (excluding woodpeckers). Females had lower apparent survival in 82 of 92 species based on the sign of $\beta_1$, with significant effects ($p < 0.05$) observed in 35 of those species (figure 1). Of the remaining 10 species where mean apparent survival estimates were higher for females than males, none showed significantly different apparent survival (figure 1). We estimated mean lifespan of adult birds (i.e. birds that have already lived one year) across species as 1.41 ± 0.04 years for females and 1.67 ± 0.04 years for males, suggesting that of the species we analysed, adult males live, on average, 18.5% longer than adult females. Results for all species are presented in electronic supplementary material, table S1 [75].

Comparing across taxonomic families, we analysed apparent survival rates between sexes in 9 of 17 families that had more than two species represented per family in our analysis. We found apparent survival to be significantly lower in females than males in eight families: flycatchers (Tyrannidae; $z = 6.0$, $p < 0.001$), vireos (Vireonidae; $z = 5.7$, $p < 0.001$), chickadees and titmice (Paridae; $z = 2.8$, $p = 0.004$), wrens (Troglodytidae; $z = 6.7$, $p < 0.001$), thrushes (Turdidae; $z = 4.5$, $p < 0.001$), New World sparrows (Passerellidae; $z = 9.8$, $p < 0.001$), New World warblers (Parulidae; $z = 7.1$; $p < 0.001$) and cardinals and allies (Cardinalidae; $z = 6.3$, $p < 0.001$; figure 2). Female apparent survival rate was similar to males only in woodpeckers (Picidae; $z = 1.1$, $p = 0.25$; figure 2)—the only non-passerine family we were able to examine.

## (b) Impact of life history traits on sex-specific apparent survival differences

Based on $AIC_c$ comparison, the best model of variation in sex-biased apparent survival included effects of HWI, migration tendency and fat difference by sex (table 2; see electronic supplementary material, figure S1, for parameter estimates and electronic supplementary material, table S2, for full table of 512 model parametrizations). Our Bayesian error propagation model indicated that adult apparent survival was the most male-biased in full migrants (0.072; CrI = 0.058 to 0.085; value indicates the average difference in apparent survival for males compared to females), followed by partial migrants (0.055; CrI = 0.017 to 0.092), then non-migratory species (0.027; CrI = −0.0005 to 0.055; figure 3*a*). Full migrants, as a group, showed strong evidence for more male-biased apparent survival than non-migratory species (Pr>0 = 1). Male-biased apparent survival was positively related to sex difference in fat scores (slope = 0.015; CrI = 0.002 to 0.029; figure 3*c*), suggesting that species where males had higher fat scores than females also had greater male-biased apparent survival. Male-biased apparent survival was negatively related to HWI (slope = −0.021; CrI = −0.036 to −0.006; figure 3*b*), indicating that species with less pointy wings (associated with lower dispersal ability) exhibit greater sex biases in apparent survival. This result remained robust even when removing a single species with extremely high HWI (tree swallow; electronic supplementary material, figure S4). See electronic

supplementary material for Bayesian probability of direction (electronic supplementary material, figure S1) and posterior predictive checks (electronic supplementary material, figure S23).

## 4. Discussion

Though we are not the first to report lower apparent survival in female than male passerines [44,46,76,77], our study presents sex-specific apparent survival rates at broad temporal (27 year), spatial (USA and Canada) and taxonomic (92 species) scales, all using a single, standardized data-collection method. It is common to lump sexes together when evaluating survivorship in studies of animals [12,35,48], but this practice could occlude important ecological differences between the sexes. When we analysed the sexes separately in a broad survival analysis, we found that adult apparent survival was, on average, 12.4% lower for females than males across 92 species of North American (mostly) passerine birds. If we assume apparent survival translates to survival, this results in an average 18.5% longer lifespan for males than females after their first year. A caveat of modelling survival via mark–recapture is that death can be confounded with permanent emigration, leading to underestimates in true survival [40,78,79]. To minimize this risk, we only report the apparent survival of 'resident' individuals [80] that are likely to return year-after-year to breed. While there may be some residual permanent emigration and sex differences in breeding dispersal (i.e. females breeding elsewhere in subsequent years) [79,81], we believe true differences in survival are likely an underlying cause of our estimated between-sex apparent survival differences because of three lines of evidence. First, our results are consistent across eight of nine bird families (figure 2). Second, our estimates of survival are corroborated by prior studies finding male-biased adult sex ratios in 14/15 (93.3%) of our study species (electronic supplementary material, table S1). Although studies of adult sex ratios have their own ambiguities, sex ratio surveys are methodologically free of the problem of emigration and thus the agreement of our findings with past work suggests that male-biased survival is one mechanism that leads to biased adult sex ratios [12,49]. Third, we searched the literature for evidence of female-biased dispersal between successive breeding seasons in our study taxa ($n$ = 15 species). We found male-biased apparent survival in four species with female-biased dispersal and in 11 species with no or male-biased breeding dispersal (electronic supplementary material, table S1). Thus, permanent emigration does not appear to be conflated with sex-biased survival in 73.3% of the 15 species with known breeding dispersal tendencies, though its effects outside these species warrants further study.

With the finding of significant differences in eight out of nine examined families, our analyses demonstrate just how pervasive male-biased apparent survival can be in Nearctic-breeding passerines. In the context of the literature on sex-specific survival estimates (reviewed in [12,34]), our data may be particularly valuable for specific taxa, including the New World sparrows (Passerellidae; 18 species), wood-warblers (Parulidae; 25 species) and vireos (Vireonidae; 4 species). Future studies of sex-specific survival have important opportunities to expand geographically beyond North America and phylogenetically across non-passerines. Woodpeckers are the only taxon for which we did not find sex-biased apparent survival. This finding could be because of their larger body size, or differences in territoriality, migration, resource use or other factors. Across a broader suite of passerine and non-passerine species, such potential life history and survival correlates warrant further study.

### (a) Influence of life history traits on sex-biased apparent survival

Of the four primary hypotheses explaining potential mechanisms for sex-biased survival, we found support for the hypotheses that movement costs and social dominance may influence the female-to-male survival difference, but we did not find strong evidence in support of reproductive costs. One reason females may bear greater costs of longer-distance migration is that female passerines sometimes migrate farther than males [30,82,83], which likely exposes them to greater mortality risk. For example, of 13 species in our study shown to exhibit sex-based latitudinal segregation during the non-breeding season [84–87], we found significantly lower female apparent survival in 6: Swainson's thrush (*Catharus ustulatus*), ovenbird (*Seiurus aurocapilla*), dark-eyed junco (*Junco hyemalis*), song sparrow (*Melospiza melodia*), white-throated sparrow (*Zonotrichia albicollis*) and Wilson's warbler (*Cardellina pusilla*). Wood-warblers (Parulidae) are one of the families that show the largest degree of sex bias (figure 2). All 25 warbler species in our analysis are highly migratory and 11 species (44%) have significant male-biased apparent survival (electronic supplementary material, table S1). The synergistic effects of both being the more migratory sex [30,88] and being a fully migratory species appear to strongly predict higher female mortality. Another non-exclusive hypothesis could be that habitat use differs between sexes on non-breeding grounds. Female warblers often use secondary habitats compared to males [37,38,89–92], which could negatively impact their body condition, especially in a changing world where anthropogenic change is exacerbated in marginal habitats [93,94]. Migratory birds can spend most of their life on their non-breeding grounds [95], but this time period and its demographic implications are understudied [96]. More research is needed to understand sex-segregated habitat use on non-breeding grounds [38,97,98] and whether it has differential survival impacts on sexes across migratory species.

In addition to migratory tendency, we found that species with lower HWI have greater male-biased apparent survival. This relationship was well supported in our Bayesian model and via model selection, despite the important caveat that the next best competing model based on $AIC_c$ did not contain HWI. HWI is often positively associated with migration tendency [51] and so we predicted a positive relationship with male-biased survival when considered in isolation. However, the relationship between HWI and migration is actually more complex. Wing pointiness comprises a set of morphological traits that are additionally restricted by evolutionary, ecological and behavioural constraints such as latitude, flocking behaviour, response to wind and other factors [99]. Species of similar HWI can have different migration strategies and species with similar migration strategies can have different HWI; for example, the partial-migrant song sparrow has a greater HWI than the full-migrant clay-coloured

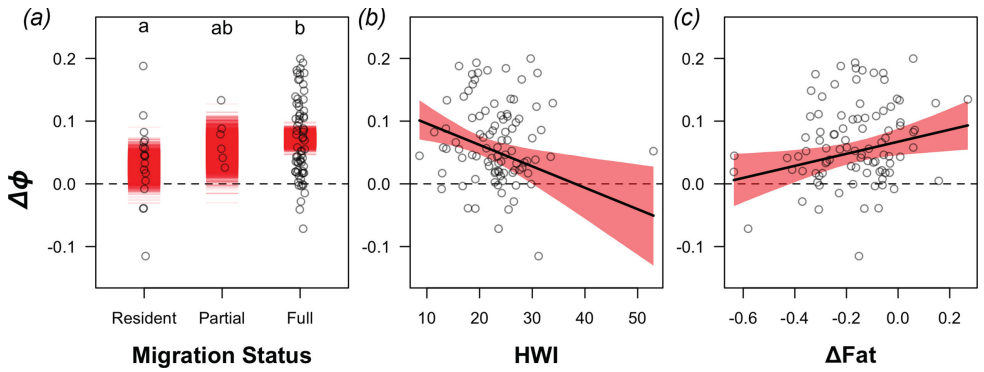


**Figure 3.** Among passerines, three species traits showed strong relationships with the extent of sex bias in apparent survival. (*a*) Species with greater migratory propensity showed greater $\Delta\phi$. Letters denote group differences with >95% credible evidence in support. Red lines show posterior distributions of the estimated intercept. (*b*) $\Delta\phi$ is negatively related to HWI, indicating species with pointier wings exhibit less male-biased apparent survival. (*c*) Male-biased apparent survival is positively related to fat differences between sexes; species where males have relatively more fat stored show a greater $\Delta\phi$. In (*b*,*c*), solid black lines show estimated mean effect and red strips are 95% posterior predictive credible intervals. In all plots, open circles show mean estimates of $\Delta\phi$ without uncertainty for each species. See electronic supplementary material, figure S4, for partial residual plots.

**Table 2.** Models explaining the extent and direction of species-specific sex-biased apparent survival were compared via $AIC_c$. We do not show model parametrizations with uninformative parameters (i.e. competing models without an improvement in $AIC_c$) per [66]. The top model contained migration, HWI, and fat difference by sex during the breeding season (Δfat). $AIC_c$ weight is the relative weight of the models in the set. See electronic supplementary material, table S2, for the full 512 model set.

| model parametrization | K | logLik | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight |
|---|---|---|---|---|---|
| migration + Δfat + HWI | 5 | 130.03 | −249.37 | 0.00 | 0.51 |
| migration + Δfat | 4 | 128.10 | −247.75 | 1.62 | 0.23 |
| migration + Δfat + Δwing:mass | 5 | 128.60 | −246.51 | 2.86 | 0.12 |
| Δfat + clutch | 4 | 126.60 | −244.75 | 4.62 | 0.05 |
| migration | 3 | 125.17 | −244.07 | 5.29 | 0.04 |
| Δfat | 3 | 125.13 | −243.99 | 5.38 | 0.03 |
| clutch | 3 | 124.28 | −242.28 | 7.08 | 0.01 |
| null model (intercept only) | 2 | 122.86 | −241.59 | 7.78 | 0.01 |

sparrow (*Spizella pallida*). It is thus possible that species with better flight abilities incur smaller male-biased apparent survival costs than species with relatively worse flight abilities, all else being equal. In other words, in species with a low HWI, if the female needs to migrate farther than the male and does so on more rounded wings, females may incur a higher survival cost. Ultimately, migration distance is a more direct predictor of movement tendencies than HWI, and as both are modelled in our results, the relationship with HWI should be interpreted in the context of simultaneous control for broad migratory categories. Future studies using (individual- or) sex-specific migration distance and HWI values, which were not available for this study, could possibly lead to stronger (or different) conclusions.

We found some evidence in support of the male social dominance hypothesis, although our proxies are imperfect, and more direct measures of sex-biased dominance would enhance future analyses. Species where males had a relatively higher fat score during the breeding season than females exhibited greater male-biased apparent survival. Male American redstarts (*Setophaga ruticilla*) [38,100], prairie warblers (*Setophaga discolor*) [101] and Cape May warblers (*Setophaga tigrina*) [102] have been found to be socially dominant to females, sometimes excluding them from prime habitat, and being in better body condition—as measured by mass, pectoral muscle or fat levels—at the end of the non-breeding season. However, in our study, weight (average or sex difference) and sexual size dimorphism either did not indicate social dominance and/or had no effect on sex-based survival. Weight is an ambiguous metric of body condition, particularly during the breeding season where female weight varies depending on whether she is gravid. Our finding that a sex difference in fat predicts survival may be because fat is directly associated with body condition [103]. However, differences in fat stores are further complicated by variation in reproductive investment [104], resource and environmental variation [105,106] and other factors, and thus may be an imperfect indicator of social dominance. Future studies that use more direct measures of sex-based social dominance (e.g. behavioural observations) may find different results.

There are several possible explanations for why we did not find evidence within our *a priori* traits supporting the theory of reproductive costs leading to reduced female apparent survival (table 1). Although unexpected, there is ample empirical literature corroborating these findings. For example, an analysis of mortality rates and parental investment in 194 bird species failed to find support for the hypothesis that reproductive costs drive female mortality in birds [34]. One possible explanation is that the cost of post-hatching care (i.e. feeding, nest defence) may be greater than that of pre-hatching care (i.e. physiological costs to females, nest building and incubation) [107], and across most passerines, post-hatching care is provided fairly evenly

by both sexes [10,108]. It was outside the scope of our study to test post-hatching care, but this hypothesis is worthy of further study. As a second point, species may already be maximizing their physical load on an evolutionary scale [109] such that further increasing reproductive investment would be too costly for females [110]. Additionally, if reproductive costs are similar among females across our set of largely socially monogamous, predominately passerine species, there might not be enough interspecific variation in reproductive costs to explain intraspecific survival differences. Finally, a myriad of ecological factors, such as trophic level, nestling development (altricial versus precocial), nest-predation rate, migration distance and body size, affect clutch size [111]. Our finding that birds with larger clutch sizes or higher relative egg loading do not see greater male-biased apparent survival suggests that the physiological costs of egg-bearing are not disproportionately contributing to reduced female survival.

Finally, we cannot judge how strongly homogametic advantage potentially structures sex-biased survival. Among the evaluated species, none credibly showed female-biased apparent survival, so homogametic advantage could provide an overall benefit to all male birds. However, the presence of such variation within (figure 2) and across (figure 1) families indicates that more mechanisms are at play than just homogametic advantage.

### (b) Other considerations

Here, we took a conservative approach to reduce biases due to emigration by allowing for differential apparent survival between residents and individuals of unknown residency status in the first year after capture [80], the latter of which account for 85% of all capture records. The modelled apparent survival rates of unknown individuals across species were near zero, which reflects their tendency to emigrate rather than true survival. However, true survival is difficult to ascertain without tracking individuals over their lifespan, which has only recently become considered possible for most passerines. Future studies can build on this by explicitly modelling dispersal, such as with a spatial mark–recapture model (s-CJS) [79], though doing so at a multi-taxa scale is currently challenging.

Additionally, our survival models treat space and time as static, but there is evidence of changes in survivorship over time [112] and space [113]. For one, demographic responses can vary across a bird's spatial range and annual cycle [114]. Clarifying survival variation across space, seasons, or life stages benefits from integrated population models [114,115], but differentiating this variation further by sex poses additional data requirements. Second, variation in survival over space and time is likely to be exacerbated by anthropogenic change, including but not limited to climate change and habitat change in non-breeding and breeding grounds. Climate change can affect sexes differently, such as in extreme flood or heat events [116], as well as gradual shifts, such as by affecting migration timing differently [117]. Anthropogenic habitat change can also affect sexes differently, such as with golden-winged warblers (*Vermivora chrysoptera*) in Central America where female-dominated non-breeding habitats were lost at twice the rate of that of the primary forests that males occupied [89]. It is unknown if this and other anthropogenic actions have sex-biased fitness consequences, in which case sex-biased survival following a migrant's first year may contribute to the male-biased survivorship we observe.

## 5. Conclusion

Our study estimates sex-specific apparent survival rates for a large number of passerine and near-passerine species breeding in North America. We find female apparent survival to be generally lower than male apparent survival and that interspecific variation in this sex bias may be related to higher movement costs in females and the cost to females of male social dominance. Given the discrepancy in this fundamental demographic parameter between sexes, we suggest that population studies of birds should model sexes separately where possible. Sex-specific apparent survival rates from our study, for example, can be used in population projection models [118,119] to determine the demographic parameter(s) that would be most effective to target for management and conservation.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data, code, and electronic supplementary material are available at Figshare [75].

Declaration of AI use. Bird icons in figure 1 were simplified from photographs (from Flickr Creative Commons under 'modifications allowed' licences) by ChatGPT. AI was not used in the conception, analysis and writing in any other way.

Authors' contributions. J.X.W.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; J.F.S.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, supervision, validation, writing—review and editing; M.H.C.N.-C.: investigation, methodology, resources, software, supervision, validation, writing—original draft, writing—review and editing; M.W.T.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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