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Fetal sex misidentification and adaptive sex ratio behavior in large whales

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ABSTRACT

There are many theories about how mammals divide their reproductive effort between males and females, including how individuals may adapt fetal sex ratios to ensure their lifetime reproductive success. These theories are difficult to test without large sample sizes because differences from equal sex ratios are often small. Whaling data provides one of the largest fetal sex ratio datasets for non-domesticated mammals and could be used to test some of these theories. One issue with whaling data, however, is the potential misidentification of the sex of small fetuses. To estimate the extent of this issue, we fit Bayesian models to estimate the lengths at which >99% of fetuses are correctly sexed for seven great whale species, finding evidence for frequent sex misidentification at lengths shorter than 30–120 cm (1–4 ft), with females recorded as males in Antarctic blue, fin, sperm, humpback, and sei whales, and males recorded as females in Antarctic minke whales. Using fetal sex data for fetuses longer than lengths where misidentification occurred, we tested whether female rorqual whales adapt the sex ratio of their offspring in relationship to their size with Bayesian generalized linear mixed models (GLMM). Longer females should be able to devote proportionately more resources to lactation and growth, and hence should have calves that grow faster and reach sexual maturity earlier. If longer females produce more male offspring, this implies that size differences between adults provide a greater advantage to male-male competition than female fecundity; while if longer females produce more female offspring, this implies that faster-growing and larger females enjoy much greater lifetime reproductive success than smaller females. We found some evidence in rorqual whales that longer mothers produced a lower proportion of male offspring, with overall posterior probability ranging from 0.87 to 0.99 depending on the model formulation, although this relationship varied among species. This evidence favors the hypothesis that differences in female body size have a greater impact on reproductive success than differences in male body size and that individual female rorqual whales adapt the sex ratio of their offspring to facilitate lifetime reproductive success.

1 INTRODUCTION

There are a variety of theories about how mammals divide their reproductive effort between males and females. Mammalian fetal sex ratios have been an area of active research since the 19th century, when Charles Darwin was intrigued by how parents seemed to produce equal numbers of males and females, though he did not understand the mechanism for this (Darwin 1874). Fisher (1930) provided this mechanism, by suggesting that frequency dependent natural selection will lead to equal population sex ratios. This theory claims that if the sex ratio of the population was biased, parents who produced the rarer sex would have higher lifetime reproductive success, causing the trait of producing the rare sex to become more common, and thereby decreasing the bias in the sex ratio. Fisher's theory rests on the idea that when sex ratios are equal, investing parental resources in a single offspring of either sex will provide equal genetic returns (Frank 1990).

Since the 1930s, there have been many theories about how individuals might adapt fetal sex ratios in order to facilitate lifetime reproductive success including adapting sex ratios based on parental body condition, social hierarchy, local competition and cooperation (Clutton-Brock & Iason 1986, Hardy 1997). Trivers and Willard (1973) developed one of the first theories of adaptive fetal sex ratios. This theory rests on two fundamental ideas: 1) that the condition of mature females varies between good and

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poor, and that a female in good condition is better able to bear and nurse her calf, producing a healthier and stronger calf; 2) adult differences in body size affect the sexes differently, for example, female fecundity may be relatively stable across large and small mothers, but larger and stronger males may have a greater advantage and exclude smaller males from reproducing entirely. If these are both true, a female in good condition who produces a son would have higher lifetime reproductive success than a similar condition female who produced a daughter (Trivers & Willard 1973). Inherent to Fisher's theory about population-level fetal sex ratios is the assumption that individuals have equal parental resources to invest, and that male and female offspring benefit equally from a single unit of parental investment. The Trivers and Willard model, as well as other models for individual adaptation of fetal sex ratios, violate these assumptions and may actually lead to biased population-level sex ratios (Frank 1987, Frank 1990).

The Trivers and Willard model has been primarily tested in populations of large ungulates, which are an ideal test case since they exhibit polygyny, a mating system where males mate with many females and often exhibit male-male competition for mates. However, evidence from these studies has been mixed, and often the evidence appears in conflict even among the same species (Hewison & Gaillard 1999, Kohlmann 1999). Adaptive sex ratio theories are difficult to test in practice, partly because differences from equal sex ratios are likely to be very small and there are few mammals beyond domesticated species for which an extensive database of fetal sex ratios exists.

Baleen whales were targeted by commercial whaling throughout the 20th century, decimating many of their populations. From the 1920s onward, Norwegian and later international regulations required whalers to record the sex of any whales caught as well as pregnancy status and the sex of any fetuses. Whaling data, therefore, provide one of the largest databases of mammalian fetal sex ratios, with a sample size for fin whales of over 100,000 pregnancies. Measurement and recording biases must be accounted for when using fetal sex ratio data from historical catches. It has been hypothesized that sex-identification was difficult for small fetuses (Gambell 1968, Kato & Shimadzu 1983), causing a bias in the fetal sex ratio data, and this bias was found in Antarctic blue whales (*Balaenoptera musculus intermedia*) (Branch & Monnahan 2020). Adult sex data from whaling has been used to find sex-specific migration pathways for sperm (*Physeter macrocephalus*), humpback (*Megaptera novaeangliae*), and minke whales (*B. acutorostrata*) (Brown et al. 1995, Kasamatsu & Ohsumi 1981, Mikhalev 2019), but quantitative analyses of fetal sex ratios have only been completed for blue whales (Branch & Monnahan 2020, Drinkwater & Branch 2022).

Mating systems for baleen whales are still an open area of research. Most research has been conducted on humpback whales who demonstrate male-male competition for females through song and physical competition (Clapham 1996). The mating systems of other balaenopterids are still quite a mystery, though blue and fin (*B. physalus*) whale males also produce song that is likely associated with reproductive competition (Croll et al. 2002). Furthermore, male blue whales appear to occasionally compete for access to females (Schall et al. 2019). Male right whales (*Eubalaena* spp.) also demonstrate male-male competition for mates, but instead of direct competition for access to females, this occurs through sperm competition, where females mate with multiple males and competition is based on the quantity and quality of sperm (Brownell Jr & Ralls 1986, Mate et al. 2005). Reproductive competition between males suggests that the genetic returns of parental investment may vary between male and female baleen whales, with males benefitting more than females as larger body size would provide advantages in male-male competition. It has been demonstrated in Southern right whales (*E. australis*) that baleen whale body condition affects calf growth rates (Christiansen et al. 2018), which suggests that female baleen whales provide differing levels of parental investment depending on their size and body condition. These characteristics, in addition to the extensive database of fetal sex ratios collected during whaling, make baleen whales an ideal candidate to test the Trivers and Willard theory of fetal sex adaptation.

In this study, we use Bayesian models to identify and correct for potential fetal sex misidentification biases in all species and then fit hierarchical models to data from rorqual whales to test whether fetal sex ratios vary with the mother's body size in these. If differences in adult body size have greater impacts on male-male competition than female fecundity, we predict that the proportion of fetuses that are male should increase with longer maternal body size.

2 METHODS

Fetal sex data:

Fetal sex data from historical catches were obtained from the IWC database v.7.1 (Allison 2020). Fetuses that did not have sex information (coded as "unknown") were not used for analysis. Because most fetuses were measured in feet, all length measurements were converted to feet and models were fit using lengths measured in feet. Fetal sex data were available for 11 species of large cetaceans, however, gray whales (*Eschrichtius robustus*), bowhead whales (*Balaena mysticetus*), and right whales did not have sufficient fetal sex ratio data to draw meaningful conclusions (Figure 1), so only seven species were used in this analysis: blue whales, fin whales, sperm whales, humpback whales, sei whales (*B. borealis*), Antarctic minke whales (*B. bonarensis*), and common minke whales. Species identifications were used as indicated in the IWC catch database, except for Antarctic and pygmy blue whales. Pygmy blue whales were only identified in the 1960s (Ichihara 1961), therefore blue whale catches were separated into Antarctic and pygmy blue whales for this study using length frequencies and catch latitude (Branch et al. 2019), while limited data from blue whale populations in the South-East Pacific, North Pacific, and North Atlantic were excluded.

To account for potential bias from fetal sex misidentification, four models were fit for each species to predict fetal sex from fetal length: 1) constant fetal sex ratio across lengths, 2) linear relationship between fetal sex ratio and length, 3) constant fetal sex ratio with small fetuses misidentified, and 4) linear relationship between fetal sex ratio and length with small fetuses misidentified (Table 1). Sex misidentification was modeled using a logistic selectivity equation for the probability of correctly identifying the sex of a fetus ($p_{correct_i}$):

$$p_{correct_i} = \begin{cases} {1+e^{\frac{-\log(19)\cdot\left(L_i-L_{50}\right)}{L_{50}-L_{95}}}}^{-1} & if\ L_i \le L_{max} \\ 1 & otherwise \end{cases} \tag{1}$$

where L_{50}, and L_{95} are estimated parameters that represent the length at which 50% and 95% of the fetuses were identified correctly, and L_i is the length of fetus *i.* For models with a constant relationship between length and fetal sex ratio, it was assumed that all fetuses longer than 5 ft (1.53 m) were correctly identified (L_{max}). For models with a linear relationship between length and fetal sex ratio, L_{max} was set to be 50 ft (15.2 m), which was longer than any recorded fetal length, essentially applying the misidentification model to all lengths. The predicted proportion of male fetuses ($\hat{p}_{male}$) at a given length was converted to the observed proportion of male fetuses at that length by:

$$p^*_{male_i} = \hat{p}_{male_i} + \left(1-\ \hat{p}_{male_i}\right)\cdot\left(1-p_{correct_i}\right) \tag{2}$$

when female fetuses at small lengths are mistaken for males, and:

$$p^*_{male_i} = \hat{p}_{male_i}\cdot\ p_{correct_i} \tag{3}$$

when male fetuses at small lengths are mistaken for males. Depending on the pattern in the data, models were fit with either Equation 2 or Equation 3, but the model did not allow for species misidentification in both directions. For models assuming a constant sex ratio across length, p_{male} was modeled directly, and for models with linear relationships between sex ratio and length, p_{male} was modeled using logistic regression with a logit link function:

$$logit(p_{male_i}) = a + b \cdot L_i \tag{4}$$

where a and b are estimated parameters describing the intercept and slope of the sex ratio on the logit scale.

Table 1. Description of models fit to fetal sex ratio data by fetal length to test for fetal sex misidentification.

		Fetal sex ratio relationship with length	
		Constant	*Linear*
Misidentification of fetal sex	*No*	$p^*_{male} = \widehat{p}_{male}$ for all fetal lengths	$p^*_{male_i} = \widehat{p}_{male_i} = inv\_logit(a + b \cdot L_i)$ for all lengths
	Yes	$p^*_{male_i}$ calculated from Equation 2 or 3 for lengths $\leq$ 5 ft. $p^*_{male_i} = \widehat{p}_{male}$ for lengths > 5 ft	$\widehat{p}_{male_i} = inv\_logit(a + b \cdot L_i)$ $p^*_{male_i}$ calculated from Equation 2 or 3 for all lengths

Models were fit using Bayesian methods in Julia v1.8 (Bezanson et al. 2017) using the No-U-Turn-Sampler (NUTS) from the Turing package v0.24 (Ge et al. 2018), assuming Bernoulli likelihoods. The best model for each species was identified using the Widely-Applicable Information Criterion (WAIC). Convergence was checked using trace plots and $\widehat{R}$ values. Using the median parameter estimates of the above models, the length at which 99% of fetuses were correctly sexed for each species was calculated and only sex ratio data for fetuses at or above this length were used for subsequent analysis.

Relationship with mother length:

Lengths of pregnant whales and the sex of the corresponding fetus were obtained from the IWC individual catch database v7.1 (Allison 2020). Due to some uncertainty in whale measurements because of the various practices for measuring adult whales (e.g., rounding to the nearest 6 in. or 1 ft, measuring in feet or meters, etc.) mother lengths were converted to feet (if needed) and then grouped into 3-inch bins with cutoffs at 1.5, 4.5, 7.5, and 10.5 in. To allow for comparisons across species, these lengths were then centered and scaled by subtracting the mean length for each species and dividing by the standard deviation. To remove obvious issues with measurements (either incorrect species ID or incorrect measurements), only scaled and centered lengths between -4 and +4 standard deviations of the species mean were used.

Bayesian generalized linear mixed models (GLMM) were built to predict the number of male fetuses ($N_{male,i}$) out of the total number of fetuses (n_i) given mother length (L_i), with random effects for each species. Three versions of the model were fit: 1) a random intercept for each species, 2) a random slope for each species, and 3) a random intercept and slope for each species. Hierarchical models assume that the random effect comes from a shared distribution, and given the evolutionary differences between sperm whales (which have larger males) and rorquals (which have larger females), only rorqual species (family Balaenopteridae) were included in this analysis. All models assumed a beta-binomial likelihood to account for overdispersion and used a logit link function. Weakly informative priors were used for all estimated parameters (Table 2). An exponential prior was used for the variance parameters of the random effects rather than the often-used half-Cauchy prior in order to avoid floor and ceiling effects caused by the logit link function and improve convergence (McElreath 2020).

Table 2. Description of Bayesian generalized linear mixed models (GLMM) fit to the number of male fetuses at each length for 7 species of rorqual whales.

Model Part	**Random intercept**	**Random slope**
Linear predictor	$\text{logit}(p_i) = \alpha_{sp[i]} + \beta \cdot L_i$	$\text{logit}(p_i) = \alpha + \beta_{sp[i]} \cdot L_i$
Likelihood	$N_{male,i} \sim BetaBin(n_i, p_i, \theta)$	$N_{male,i} \sim BetaBin(n_i, p_i, \theta)$
Hyper-distribution	$\alpha_{Sp[i]} \sim Normal(\alpha, \sigma^2)$	$\beta_{Sp[i]} \sim Normal(\beta, \sigma^2)$
Estimated parameters	α = mean intercept across species σ^2 = between-species variation in intercept β = slope θ = overdispersion	α = intercept σ^2 = between-species variation in slope β = mean slope across species θ = overdispersion
Priors	$\alpha \sim Normal(0, 10)$ $\sigma_\alpha \sim Exponential(1)$ $\beta \sim Normal(0, 10)$ $\theta \sim Gamma(0.1, 0.1)$	$\alpha \sim Normal(0, 10)$ $\sigma_\beta \sim Exponential(1)$ $\beta \sim Normal(0, 10)$ $\theta \sim Gamma(0.1, 0.1)$
	Random intercept and slope	
Linear predictor	$\text{logit}(p_i) = \alpha_{sp[i]} + \beta_{sp[i]} \cdot L_i$	
Likelihood	$N_{male,i} \sim BetaBin(n_i, p_i, \theta)$	
Hyper-distribution	$(\alpha_{Sp[i]}, \beta_{Sp[i]}) \sim MVNormal\left(\begin{bmatrix} \alpha \\ \beta \end{bmatrix}, \boldsymbol{\Sigma}\right)$ $\boldsymbol{\Sigma} = \begin{pmatrix} \sigma_\alpha & 0 \\ 0 & \sigma_\beta \end{pmatrix} \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix} \begin{pmatrix} \sigma_\alpha & 0 \\ 0 & \sigma_\beta \end{pmatrix}$	
Estimated parameters	α = mean intercept across species σ_α = between-species variation in intercept σ_β = between-species variation in slope ρ = correlation between intercept and slope β = mean slope across species θ = overdispersion	
Priors	$\alpha \sim Normal(0, 10) \quad \beta \sim Normal(0, 10)$ $\sigma_\alpha \sim Exponential(1)$ $\sigma_\beta \sim Exponential(1) \quad \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix} \sim LKJ\ Corr(1)$ $\theta \sim Gamma(0.1, 0.1)$	

Models were fit using the *brms* package (Bürkner 2017) in R v4.2.2 (R Core Team 2022), using 4 chains, 4000 iterations, and a 50% warm-up. The adapt delta parameter for the No-U-Turn-Sampler, which controls the target acceptance rate, was set to 0.95. Convergence was checked using trace plots and $\widehat{R}$ values. Models were compared using posterior predictive checks and leave-one-out and leave-one-group-out cross validation (Vehtari et al. 2022). Model weights were calculated using the Bayesian stacking method.

3 RESULTS

Fetal sex misidentification:

Models to predict fetal sex ratio from fetal length were fit to seven species. Misidentification models were not fit to pygmy blue whales because almost all pygmy blue whale fetuses were greater than 5 ft (1.5 m), so there was insufficient data to estimate misidentification rates (Figure 1). In general, small female fetuses were mistaken for males across exploited cetaceans. In Antarctic minke whales, however, the opposite trend appeared to be true, and in common minke whales there was no bias due to sex misidentification (Figure 2). The lengths at which 99% of fetuses were correctly identified (L_{99}) for each species ranged from 0.74–3.64 ft (Table 3). Though no misidentification models were fit to pygmy blue whales, only fetuses greater than the estimated L_{99} for Antarctic blue whales (2.79 ft) were used for further analysis. Additionally, though the best model did not indicate sex misidentification for common minke whales, for consistency in the rest of the analysis, only data for fetuses greater than the estimated L_{99} for Antarctic minke whales (0. 74 ft) were used for further analysis.

Table 3. Lengths at which 99% of fetuses were estimated to be correctly identified for each species (L_{99}) based on median parameter estimates from the best model for each species. "Female" indicates small female fetuses were mistaken for males. *Indicates species for which L_{99} was not estimated, either because there were not sufficient data at small fetus lengths to fit data for this species (pygmy blue whales) or because no correction was estimated (common minke whales). In these cases, L_{99} estimated from another subspecies (Antarctic blue whales and Antarctic minke whales) were used to remove small fetuses for further analysis.

Species	**Sex misidentified**	**L_{99} (ft)**
Antarctic blue whale	Female	2.79
Pygmy blue whale*	Female	2.79
Fin Whale	Female	3.62
Sperm Whale	Female	1.72
Humpback Whale	Female	2.62
Sei Whale	Female	2.10
Antarctic Minke Whale	Male	0.74
Common Minke Whale*	Neither	0.74

Relationship with mother length:

All three model formulations provided similar fits to the data and leave-one-out cross validation performed point-wise suggested that all models performed equally well. However, leave-one-group-out cross validation, which reflects the model's predictive ability across species, demonstrated a preference for the model with random slopes (Table 4).

Table 4 . Differences in expected log pointwise predictive density (elpd) from leave-one-out and leave-one-group-out cross validation for each model, as well as the difference between the standard errors of elpd, and model weights calculated using Bayesian stacking.

	Leave-one-out C.V.			*Leave-one-group-out C.V.*		
Random effects	**Elpd diff.**	**SE diff.**	**Model weight**	**Elpd diff.**	**SE diff.**	**Model weight**
Intercept and Slope	0.0	0.0	0.299	-2.3	0.3	0
Intercept	0.0	0.8	0.467	-0.8	0.4	0
Slope	-0.1	0.7	0.235	0.0	0.0	1.0

All models estimated that the proportion of male fetuses decreased with increasing female length. The posterior probability that the mean slope, β, was negative (on the logit scale) was 0.87 in the model with random slope and intercept, 0.90 in the model with a random slope, and 0.99 in the model with a random intercept (Figure 3). In both the models with random slopes, there was some inter-species variability in the slope, with the standard deviation between species estimated as 0.02 (95% BCI: 0.0-0.06) for both models. This variability is reflected in the species-specific slope estimates. Sei whales had the highest posterior probability of a negative slope (0.85 and 0.84, random intercept and slope, and random slope models respectively). In the random intercept and slope model, the posterior probability of a negative slope for Antarctic blue whales was 0.38, for pygmy blue whales it was 0.47, for fin whales it was 0.56, for humpback whales it was 0.39, for common minke whales it was 0.50, and for Antarctic minke whales it was 0.36. In the random slope model, the posterior probability of a negative slope for Antarctic blue whales was 0.38, for pygmy blue whales it was 0.44, for fin whales it was 0.55, for humpback whales it was 0.42, for common minke whales it was 0.49, and for Antarctic minke whales it was 0.34 (Figure 3).

The mean intercept parameter, α, was estimated to be 0.505 (on the real scale) in all three models, though the credible intervals varied between models. This intercept value represents the overall mean proportion of males at mean mother length across all species. In the models with random intercepts, the median species-specific intercept ranged from 0.48-0.502 (Figure 3).

4 DISCUSSION

These results suggest that, in general, larger female rorqual whales produce more female fetuses than male fetuses, however the species-specific slopes suggest that there is variation within species and that this relationship may not be as strong for some species. Decreasing sex ratio with increasing female body condition and size has been observed in roe deer (*Capreolus capreolus,* Hewison & Gaillard 1996), and reindeer (*Rangifer tarandus,* Skogland 1986). However the opposite trend, increasing sex ratio with increasing female size and body condition, has also been found for these same species (Kojola & Eloranta 1989, Wauters et al. 1995), as well as in elk (*Cervus canadensis,* Kohlmann 1999). This suggests that there is a large range of inter-species variation for ungulates, and that these relationships are hard to detect.

When larger females are shown to produce more female offspring in ungulates, the mechanism that is often proposed is the local resource competition model for adaptive sex ratios, which suggests that mothers will bias the sex ratio towards the sex that competes least for limited resources such as food (Hardy & Boulton 2019). For ungulates, where males disperse widely and females remain closer together, this could lead to smaller/poor condition mothers producing more males because they will compete less for resources (Hewison & Gaillard 1999). This is unlikely to be true for rorqual whales, where sexes overlap greatly on the feeding grounds and therefore the amount of competition for resources is unlikely to vary with the sex of the offspring.

Instead, the decreasing sex ratio with increasing mother size trend that we observed may be an extension of the Trivers and Willard model. The Trivers and Willard model assumes that parental body condition impacts fetal body condition. This is a good assumption for baleen whales, as female minke, humpback, and Southern right whales have all been shown to reduce their energetic investment in their fetus in proportion to their condition and that lower maternal body condition can negatively affect calf growth rates (Christiansen et al. 2016, Christiansen et al. 2013, Christiansen et al. 2018). The Trivers and Willard model also assumes that adult differences in body condition have differing effects on reproductive success for each sex. Due to the model's development in the context of ungulates, it is assumed that male-male competition almost completely prevents small males from participating in reproduction. Consequently, males have a greater difference in reproductive success among body sizes. However, our results suggest that, unlike in ungulates, the differences in body size for adult rorqual whales may provide greater differences in reproductive success for females than males.

Baleen whales face substantial costs during the lactation period, and Southern right whales have been shown to lose around 25% of their body volume in the first three months of lactation (Christiansen et al. 2018). This suggests that only females above a certain size can ensure their calf's survival without a cost to their own survival. Additionally, females in poor condition may need many years to recover the energy stores lost during lactation, increasing their calving interval and lowering their lifetime reproductive success (Christiansen et al. 2020). Additionally, the catch data demonstrates that females must reach a certain length before they are able to reproduce (Figure 4). Therefore, larger females could reach the length at sexual maturity faster, and potentially have more calves throughout their lifetime. The catch data also suggests a potential decline in pregnancy rates at larger lengths, but this is likely an artifact of small sample sizes at extreme lengths and species misidentification (Figure 4). The high cost of lactation and the ability of faster-growing females to reproduce for more of their lifetime suggests that while males do compete for access to females through physical aggression and song (Clapham 1996, Croll et al. 2002), the reproductive advantages of large body size are higher for females than males.

While our results suggest that in general larger females adapt the sex ratios of their offspring to produce more females, there is a lot of variation between species and the trend for individual species is less clear. While body size does affect calf growth rates and condition, length is not necessarily a good indicator for inter-annual body condition, the scale at which individual fetal sex ratio adaptation is thought to occur. Individual adult lengths are unlikely to vary greatly from year to year and may more directly reflect access to resources in early life. Therefore, these results may reflect the average trend for fetal sex adaptation without reflecting the variation that may occur when longer whales are in poor condition and shorter whales are in good condition. This unaccounted for variation is likely obscuring the species-level trends to some extent. Blubber thickness may be a better measure of inter-annual body condition and may demonstrate a stronger trend, however, no information about the amount of blubber or oil from individual whales were collected in the catch records. The system for processing whales may have made collecting this information impossible, as many individuals were often processed at once. Additionally, while adaptive sex ratio behavior may be the best way to ensure lifetime reproductive success, the actual mechanism for adapting fetal sex ratios in mammals is unclear. It is likely that mammals only have limited control of the sex of their offspring (Hardy & Boulton 2019), and therefore the trends that appear in data are likely to be weaker than those predicted by theory.

Overall, our results suggest that female rorqual whales may adapt fetal sex ratios to ensure lifetime reproductive success, with larger mothers producing more females and smaller mothers producing more males. While this may subtly bias population-level fetal sex ratios, these relationships are complex, and it is not yet known how these individual adaptations may influence the population-level fetal sex ratios (Frank 1987). Furthermore, the observed effects are very small, and differ only slightly from equal sex ratios. Previous analyses for fetal sex ratios in baleen whales suggest that population-level fetal sex ratios are likely to be close to equality for most species or have a slight male bias (Branch & Monnahan 2020).

However, to connect these results to individual adaptations in the sex ratio requires more work to better understand baleen whale mating systems and reproduction.

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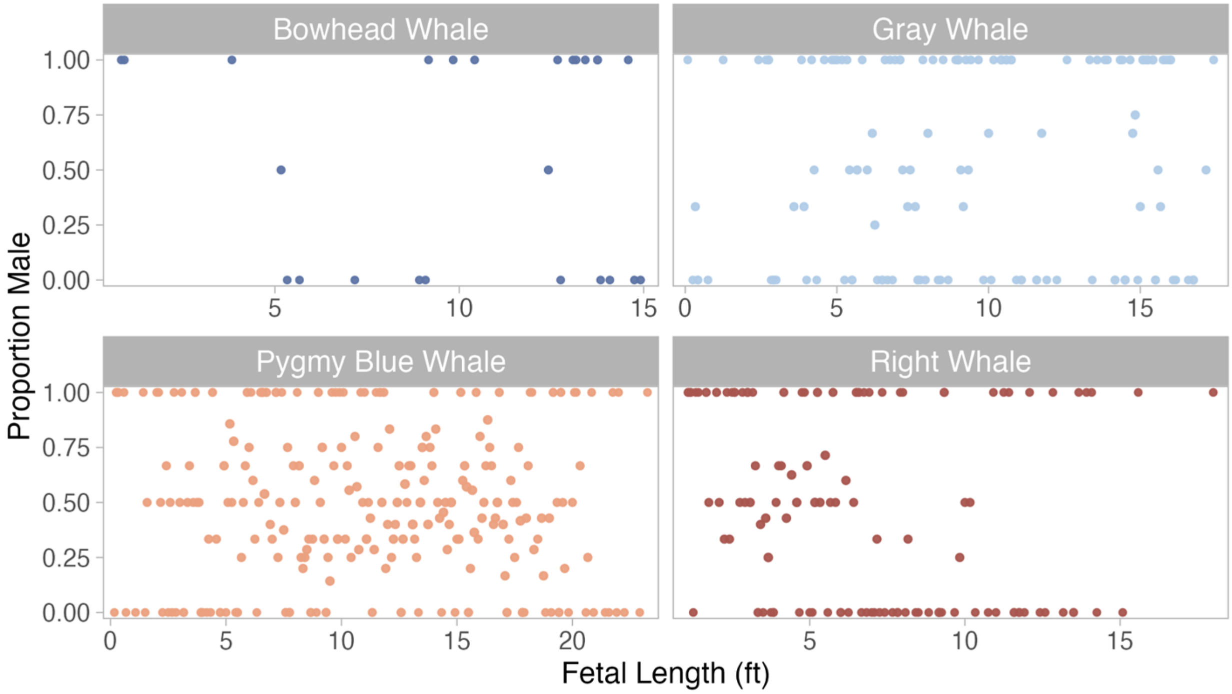

Figure 1. Fetal sex ratio (points) in one-inch bins for species not used in sex misidentification models due to small sample sizes of fetal sexes (bowhead, gray, and right whales) or lack of fetal data at small lengths (pygmy blue whales).

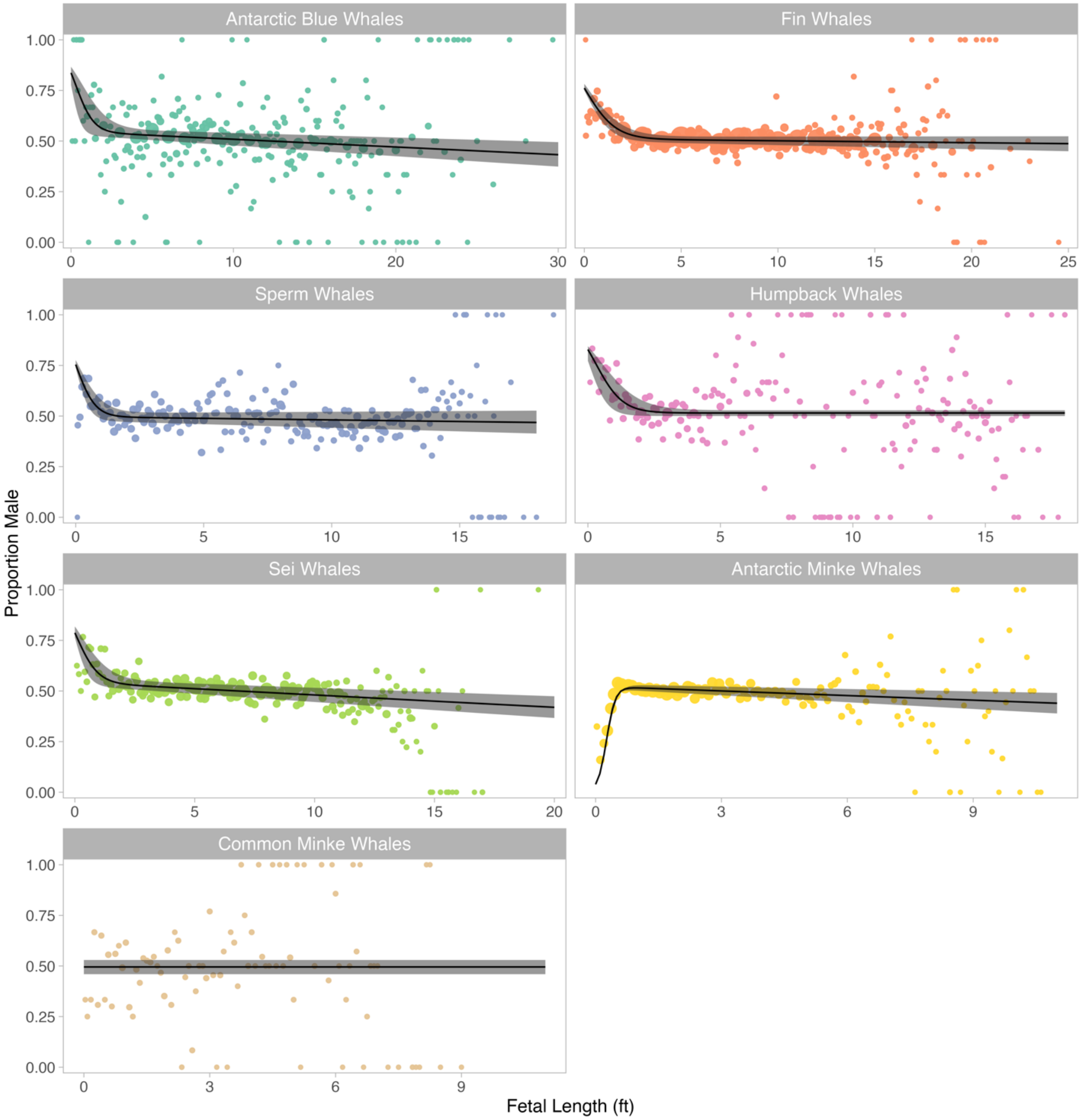

Figure 2. Fetal sex ratio (points) in one-inch bins for selected species, as well as Bayesian model fits (lines) and 95% credible intervals (shading) from the best model for each species based on WAIC. For most species, small female fetuses were mistaken for males, except for Antarctic minke whales, where small males were mistaken for females, and common minke whales where no bias due to sex misidentification was included in the best model.

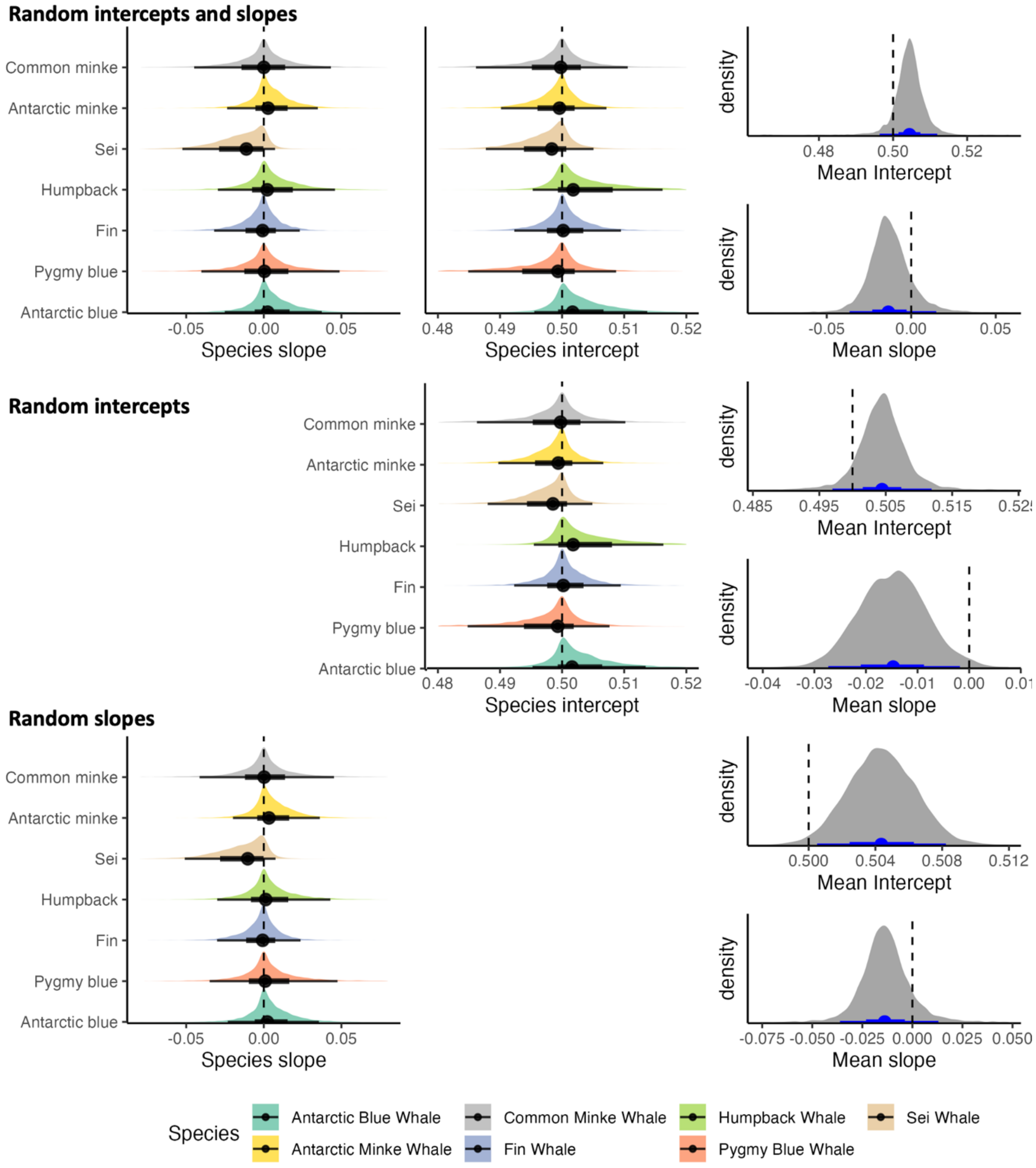

Figure 3. Posterior distributions for species-specific random intercepts (real scale) and slopes (logit scale) as well as posterior estimate of the hyperparameter for slope (logit scale) and intercept (real scale) for each model. Points represent medians and the solid lines represent the 66% (thick) and 95% (thin) credible intervals, and dashed lines represent 0.0 (logit scale) for slopes and 0.5 (real scale) for intercepts.

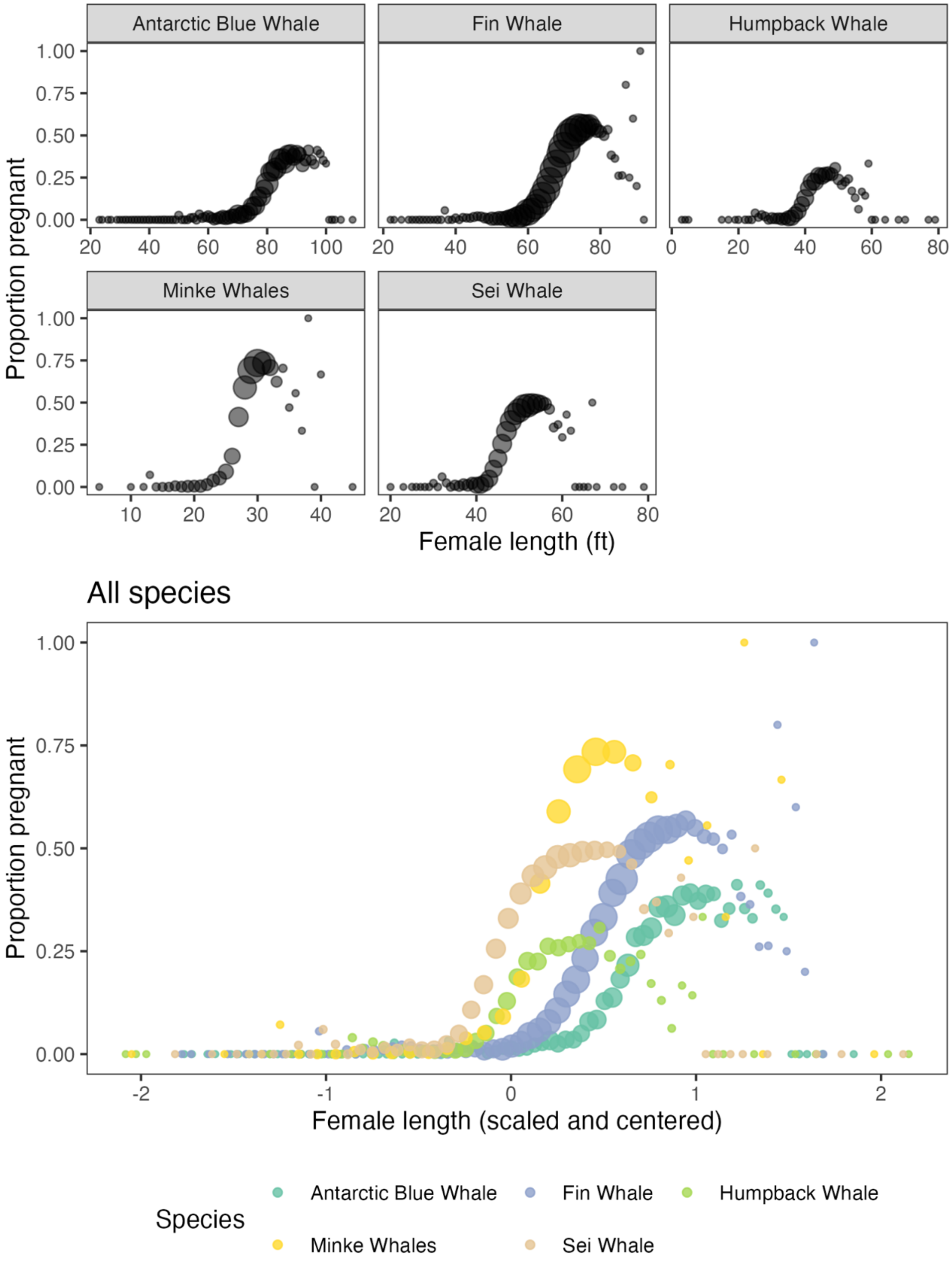

Figure 4. Proportion of female catches with pregnancies for 1 ft length bins for each species (top) and for scaled and centered 1ft length bins to compare across species (bottom).