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ARTICLE

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Modeling vital rates and age-sex structure of Pacific Arctic phocids: influence on aerial survey correction factors

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Abstract

To estimate abundance, surveys of marine mammals often rely on samples of satellite-tagged individuals to correct counts for the proportion of animals that are unavailable to be detected. However, naïve application of this correction relies on the key assumption that availability of the tagged sample resembles that of the population. Here, we show how matrix population models can be used to estimate stable age- and stage-proportions, and how these can be used to adjust aerial survey correction factors so that they represent population-level availability. We illustrate this procedure using data from ice-associated seals in the Bering, Chukchi, and Beaufort Seas. After compiling life history data for bearded (*Erignathus barbatus*), ribbon (*Histriophoca fasciata*), ringed (*Pusa hispida*), and spotted seals (*Phoca largha*), we find that correction factors ignoring age-sex composition can positively bias spotted seal abundance by an average of 13% and negatively bias ribbon seal abundance by an average of 5%. Note that we did not examine potential bias for bearded or ringed seals due to low sample sizes; as such, we urge caution in interpretation of abundance estimates for these species.

KEYWORDS
age and sex structure, availability, detection probability, *Erignathus barbatus*, *Histriophoca fasciata*, matrix population model, *Phoca largha*, *Pusa hispida*, stable stage distribution

1 | INTRODUCTION

Analysis of animal survey counts often include corrections for availability, the proportion of animals that are detectable while surveys are being conducted (Marsh & Sinclair, 1989). For marine mammals surveyed in water, availability consists of the proportion of animals that are at or near the surface while the survey vessel passes (e.g., Barlow et al., 1988; McLaren, 1961); for aural surveys of songbirds, it is the proportion of birds that sing while counts are conducted (Diefenbach et al., 2007); and for surveys of pinnipeds on land or on sea ice, it is the proportion of seals that are hauled out (e.g., Bengtson et al., 2005; Thompson & Harwood, 1990). If surveys are conducted while offspring are being born, availability may also encompass arrivals of offspring into the population (Bowen et al., 1987). In all cases, availability corrections are needed to prevent negative bias in abundance estimates (Nichols et al., 2009).

One possible avenue for estimating availability is to use data from satellite-linked time-depth recorders (TDRs) to estimate the proportion of time animals are available to a particular survey platform. For cetaceans, this would be the proportion of time an animal is at or near the surface (Heide-Jørgensen & Laidre, 2015). In certain types of pinniped surveys (e.g., line- and strip-transects; see Hammond et al., 2021 for a review), TDR data provide information on the proportion of time seals spend out of the water and are available to be detected (e.g., Bengtson et al., 2005). However, previous availability adjustments using TDR data have implicitly assumed that availability computed from a sample of telemetered animals was a good approximation to population-level availability—in other words, that the TDR data were not systematically biased in some way.

In this study, we investigate the potential for bias in availability corrections when analysis of TDR data is aggregated across age- and sex-classes. Although the problem is a general one relevant to multiple taxa, we were specifically interested in the potential for bias in aerial survey availability adjustments for surveys of ice-associated seals in the Bering, Chukchi, and Beaufort Sea region (hereafter, BCB). Previous estimates of abundance in BCB (e.g., Bengtson et al., 2005; Conn et al., 2014; Ver Hoef et al., 2014) relied on estimates of availability that did not control for age- and sex-specific differences.

Recently, London et al. (2022) examined the influence of environmental variables and age-sex class on haul-out probabilities of bearded, ribbon, and spotted seals in the Bering and Chukchi seas. For ribbon and spotted seals (sample sizes for bearded seals were insufficient), they demonstrated that haul-out probabilities differed considerably by age- and sex-class. Age- and sex-specific differences in availability are logical given biological constraints, with adult females needing to spend substantial time on ice for whelping and lactation (12–18 days for bearded seals; 21–28 days for ribbon seals; 14–35 days for spotted seals; reviewed in Oftedal et al., 1987). Similarly, adult male phocids mate with females shortly after parturition, and will mate with more than one female, if possible, known as polygyny (Stirling et al., 1983). Bearded seal males exhibit polygynous behavior and defend relatively stable underwater territories that are advertised to females via underwater vocalization (Van Parijs & Clark, 2006); we might, then, expect adult females to spend considerably more time hauled out than adult males during whelping season, but for adults to be concentrated near sea-ice haul-out locations. By contrast, subadults of all species have no reproductive constraints, though all age classes use sea ice as a platform to undergo an annual spring molt that ranges from ≈30 days in spotted and ringed seals to ≈120 days for bearded seals (Thometz et al., 2021).

Age- and sex-mediated differences in haul-out behavior suggest a potential for bias in availability if the age-sex structure of satellite-tagged seals differs from that of the population. For ice-associated seals in the Bering and Chukchi Seas, capture operations have largely been opportunistic (Boveng et al., 2020). Adult bearded seals, for instance, are wary of humans and are particularly hard to capture on ice. Most marking operations for bearded seals in BCB have thus focused on young animals (Cameron et al., 2018; Olnes et al., 2021). Similarly, spotted seals have sometimes been caught in coastal lagoons, a process that favors capture of young individuals (Lowry et al., 1998). There is thus reason to expect that age-aggregated availability estimates for these species will be biased towards younger age classes. If younger age classes haul out less frequently than adults, naïve application of such estimates as aerial survey correction factors will likely result in positively biased abundance estimates.

In this paper, we examine the potential for bias in ice seal availability estimates when the sample of satellite-tagged seals is biased towards young individuals, and when age-sex class is ignored during estimation. We compare age aggregation to an alternative approach that attempts to estimate population-weighted availability, where age- and sex-specific availability estimates are weighted by the proportion of animals thought to be in each age-sex class. To derive these weights, we rely on stable stage distributions estimated from matrix population models (Caswell, 2001). Parameterization of matrix population models requires knowledge of survival-at-age and female fecundity-at-age schedules, which are often unknown for individual pinniped populations. A secondary goal with this paper, then, was to assemble life history schedules for ice-associated seals in BCB that represent best available science. After this was accomplished, we illustrated our approach by applying both types of estimation approaches to TDR records of spotted and ribbon seals in the Bering Sea.

2 | METHODS

Our approach for constructing population-weighted availability correction factors relies on a number of steps (Figure 1).

First, stage-specific (pup, subadult, adult male, and adult female) availability estimates are generated from models fitted to wet/dry sensor data from TDRs affixed to seals. Second, survival- and fecundity-at-age schedules are used to predict stable age proportions with Leslie matrix models. Next, information on maturity-at-age is used to translate stable age proportions into stable stage proportions to match the resolution of availability predictions. Finally, stable-stage proportions are used to adjust stage-specific availability predictions to come up with a population-corrected availability estimate. We now describe these steps in further detail, including how we applied them to ice-associated seals in the BCB.

2.1 | Availability models

Several authors have used generalized linear mixed models (GLMMs; Wolfinger & O'Connell, 1993) to investigate factors affecting haul-out probabilities of Arctic and subarctic seals (e.g., Bengtson et al., 2005; Crawford et al., 2019; London et al., 2022; Olnes et al., 2021; Ver Hoef et al., 2010; Von Duyke et al., 2020). The GLMM framework is appealing because it allows one to include individual-level random effects, as well as autocorrelated error structures that are necessary to account for responses that are statistically dependent (as when seals haul-out consecutively for many hours). We summarized haul-out records as Bernoulli responses; for individual *i* and hour *t*,

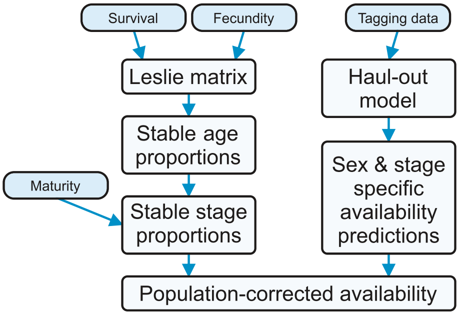


FIGURE 1 A conceptual diagram to illustrate our approach for calculating population-corrected availability correction factors for Arctic phocids.

we set $Y_{it} = 1$ if individual i has a dry tag for ≥50% of hour t. According to the GLMM framework, the expected value (i.e., prediction) for individual i at hour t is a function of both fixed effects specified by the investigator (e.g., choice of explanatory predictors) and random effects which are largely governed by the specific error structure assumed and variability in the observed data. Specifically, the expected values of haul-out observations given random effects can be given as

$$E(\mathbf{Y}|\boldsymbol{\eta}) = g^{-1}(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\eta})$$

where predictive covariates are codified in a design matrix, $\mathbf{X}$ (see McCullagh & Nelder, 2019), $\boldsymbol{\beta}$ represents a vector of regression parameters, $\mathbf{Z}$ gives a design matrix for random effects that links random effects to particular observations, and $\boldsymbol{\eta}\Delta$ is a vector of random effects. The function g^{-1} represents an inverse link function that will typically be used to convert the linear predictor to the scale of the observations (in our application, this is the inverse logit function).

In specifying alternative models for haul-out distributions, we will focus on the fixed effects structure, $\boldsymbol{\xi} = \mathbf{X}\boldsymbol{\beta}$, as it is here that researchers may specify different covariate effects (including age-sex effects). In particular, we consider two types of models, one with age-sex effects, and one without:

$$\text{Model 1}: \boldsymbol{\xi}_{as} = \mathbf{X}_1\boldsymbol{\beta}_1 + \mathbf{X}_2\boldsymbol{\beta}_2$$

$$\text{Model 2}: \boldsymbol{\xi}_0 = \mathbf{X}_1\boldsymbol{\beta}_1.$$

Here, $\mathbf{X}_2$ and $\boldsymbol{\beta}_2$ represent a design matrix and regression parameters for age- and sex-effects, and $\mathbf{X}_1$ and $\boldsymbol{\beta}_1$ represent a design matrix and regression coefficients for remaining covariates (e.g., weather, time-of-day), including an intercept. For specific examples of how such models can be formulated, see section 2.3 Ribbon and spotted seal analysis.

The GLMM models can be fitted directly to TDR records to estimate $\boldsymbol{\beta}_1$ and $\boldsymbol{\beta}_2$ (we designate such estimates as $\widehat{\boldsymbol{\beta}}_1$ and $\widehat{\boldsymbol{\beta}}_2$). However, for aerial survey corrections we need to make predictions of the proportion of seals that were hauled out at the particular time when aerial surveys were conducted. To make predictions, let $\mathbf{X}_1^*$ denote a design matrix where relevant entries correspond to the realized covariates at the time surveys were conducted. Availability predictions at the time of the survey can then be made using the fixed-effects structure $\boldsymbol{\xi}_0^* = \mathbf{X}_1^*\widehat{\boldsymbol{\beta}}_1$ for the model without age- and sex-effects. If random effects have mean zero as is standard, a vector of availability predictions ($\mathbf{a}_0^*$) can then be generated as $\mathbf{a}_0^* = g^{-1}(\boldsymbol{\xi}_0^*)$; variances of predictions are slightly more complicated; see Ver Hoef et al. (2014).

However, for models with age- and sex effects, we can only make predictions for specific age- and sex values. For instance, if we use a categorical fixed effect to represent age-sex class (e.g., pup, subadult, adult female, and adult male), we can only make predictions for each of these groups separately. Without loss of generality, let us assume that we have these four age-sex classes, and denote their predictions as $\mathbf{a}_{pup}^*$, $\mathbf{a}_s^*$, $\mathbf{a}_{af}^*$, and $\mathbf{a}_{am}^*$, respectively. In the usual case that aerial surveys are unable to discern age-sex class (possibly they would be able to discern differences between pup and other classes), it is necessary to average among availability predictions somehow, e.g.,

$$\widetilde{\mathbf{a}} = \pi_{pup}\,\mathbf{a}_{pup}^* + \pi_{sub}\,\mathbf{a}_{sub}^* + \pi_{af}\,\mathbf{a}_{af}^* + \pi_{am}\,\mathbf{a}_{am}^*, \tag{1}$$

where $\sum_i \pi_i = 1.0$. Ideally, the weights should reflect the age-sex composition of the population being surveyed. One possibility is to use stable stage proportions to help define these weights.

2.2 | Stable stage distributions

Our strategy for computing stable stage proportions (i.e., π_{pup}, π_{sub}, π_{af}, π_{am}) was (1) to use matrix population models (Caswell, 2001) for each species to calculate stable age proportions (ages 0–39+), and (2) to use sexual maturity schedules reported in the literature to convert stable age proportions to stable stage proportions.

In order to conduct these analyses, we first compiled data on survival, female reproduction, and sexual maturity from the literature to help calculate stable stage proportions for bearded, ribbon, ringed, and spotted seals. For survival, we used results from a hierarchical meta-analysis previously fit to a variety of phocid mortality data sets (Trukhanova et al., 2018) to produce annual survival estimates for the four species of interest. In particular, we used the same methods and data reported in Trukhanova et al. (2018), using their ribbon seal example template, to refit models and produce posterior predictions of survival for each of the four species. These models specify a U-shaped mortality curve (Choquet et al., 2011), with typically high mortality at the beginning of life, followed by a period of low mortality, and finally increasing mortality at older ages corresponding to senescence. We conducted analysis with JAGS 4.2.0 (Plummer, 2003), using the highest-ranked DIC model from Trukhanova et al. (2018) which included effects of subfamily, species, and data set.

For female fecundity, we used a combination of different data sources depending on species and the amount of data available, with preference towards data collected in the BCB (where we collect aerial survey and satellite telemetry data) and to data that were recently collected. We favored recent data since there is some indication that pregnancy rates have increased and age at sexual maturity has decreased in recent decades (Alaska Department of Fish & Game, 2020; Krafft et al., 2006; Quakenbush et al., 2020). For ringed and spotted seals, we based female reproductive maturity on data that the Alaska Department of Fish and Game (ADFG) gathered from Alaska subsistence hunters between 2010 and 2019 (Quakenbush et al., 2020 and Alaska Department of Fish and Game, 2020, respectively). Fetal reproductive assessments were limited to specimens gathered between November and April, when seals were reliably pregnant or had just given birth. For bearded seals, ADFG data were limited, so we widened the years considered to 1964–2020 and combined them with Russian data from the Bering Sea gathered in the 1980s (Fedoseev, 2000, table 47). Russian harvest records were from early summer after the mating season and thus represent early pregnancy rates. For ribbon seals, we based female fecundity entirely on Russian records from the Bering Sea gathered in the 1980s (Fedoseev, 2000, table 24).

From these data, we summarized the number of specimens (n_{ia}) for each species (i) and age class (a), and the number of these which were pregnant or had given birth in the year they were examined (y_{ia}), as well as the number that were sexually mature (z_{ia}). We truncated ages 9 and greater into a single 9+ group to reduce the likelihood of aging errors. Raw proportions by age did not necessarily increase in a smooth, monotonic fashion (particularly for ADFG data where sample sizes were small), a feature of the data that we ascribed to low sample size. In these cases, we used generalized additive models (GAMs) to smooth proportions of reproducing or mature females as a function of age. This was accomplished using the mgcv package (Wood, 2017) in the R programming environment (R Core Team, 2017), using a binomial error structure:

$$y_{ia} \sim \text{Binomial}(n_{ia}, p_{ia}),$$

where $p_{i,a}$, gives the proportion of females of species i and age class a that give birth in any particular year. Note that these species almost never give birth to more than a single pup per year, so p_{ia} is roughly synonymous with per capita fecundity. The GAMs incorporated smooth effects of age on the logit scale, and predictions from these models were incorporated into stable stage calculations (see below).

For female maturity-at-age, we used the same data sources as described above for fecundity, but based maturity determinations on developmental characteristics (such as condition of the uterus and number of corpora lutea present). For males, data on the proportion of sexually mature bearded, ribbon, and spotted seal males were taken from Tikhomirov (1966) from collections in the Bering Sea and Sea of Okhotsk. For male ringed seal maturity, we averaged proportions reported in Fedoseev (1965) and Tikhomirov (1966), weighting by sample size when they were available for both studies, and weighting each study equally when sample sizes were missing. Russian authors reported basing male maturity on presence of semen and on weight of the testis.

We used the notation $m_{i,s,a}$ to denote the proportion of species i, sex s, and age a that are reproductively mature. For females, we used the same GAM analysis procedures described above to estimate $m_{i,s,a}$ from n_{ia} and z_{ia}. For Russian data, sample sizes were large enough that we simply used raw data proportions (i.e., $m_{i,s,a} = z_{ia}/z_{ia}$).

We used survival and reproductive values to parameterize a Leslie matrix model (Caswell, 2001). Our matrix model was structured with a postbreeding census (so that fecundity represents the product of adult survival and reproduction) and was also parameterized entirely in terms of females:

$$\mathrm{A_i} = \begin{bmatrix} F_{i,0} & F_{i,1} & F_{i,2} & \cdots & F_{i,37} & F_{i,38} & F_{i,39} \\ S_{i,0} & 0 & 0 & \ddots & 0 & 0 & 0 \\ 0 & S_{i,1} & 0 & \ddots & 0 & 0 & 0 \\ 0 & 0 & S_{i,2} & \ddots & 0 & 0 & 0 \\ 0 & 0 & 0 & \ddots & 0 & 0 & 0 \\ 0 & 0 & 0 & \ddots & S_{i,37} & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & S_{i,38} & 0 \end{bmatrix}$$

Here, S_{ia} gives survival probability for an age a seal, and $F_{ia} = 0.5 p_{ia} S_{ia}$ gives per capita births of female offspring for an age a female alive at the start of the year (this assumes a sex ratio at birth of 0.5). Our model includes 40 ages (0–39), though in practice very few pinnipeds live to be >30. Using this framework, we computed stable age distributions for each species as the dominant eigenvector of that species' Leslie matrix (Caswell, 2001). All calculations were done in the R programming environment (R Core Team, 2017).

Letting v_{ia} denote the proportion of seals of species i that are age a (determined through Leslie matrix computations), our next task is to translate these into stable stage proportions (i.e., for pups, subadults, adult females, and adult males). This step is necessary because stage-class determinations are typically all that is available when analyzing seal haul-out records (i.e., numerical age is unknown for live animals). For purposes of this study, we define subadults as being ≥1 year of age and reproductively immature. Letting the subscript $s = M$ denote male and $s = F$ denote female, we have

$$\pi_{i,pup} = v_{i,0},$$

$$\pi_{i,sub} = 0.5 \sum_{a=1}^{39} (1 - m_{i,M,a}) v_{ia} + (1 - m_{i,F,a}) v_{ia}$$

$$\pi_{i,am} = 0.5 \sum_{a=1}^{39} m_{i,M,a} v_{ia}$$

and

$$\pi_{i,a,f} = 0.5 \sum_{a=1}^{39} m_{i,F,a} v_{ia}$$

Note that these calculations implicitly assume that males and females have the same survival rates.

2.3 | Ribbon and spotted seal analysis

Having described a procedure for computing approximate stage frequencies for several Arctic phocids, we now turn our attention to analyzing possible impacts of age-sex structure on aerial survey correction factors. In particular, we reexamined haul-out behavior of 115 ribbon seals and 104 spotted seals initially analyzed by London et al. (2022). In addition to examining time-of-day and weather effects, London et al. (2022) estimated age-sex effects on haul-out probabilities and interactions between age-sex class (pup, subadult, adult female, and adult male) and day of year while controlling for heterogeneity among seals using individual-level random effects. In this study, we used their data and a GLMM modeling framework on the logit scale (1) to predict $\widetilde{\mathbf{a}}$ as in Equation 1 using a model with an age-sex effect, and (2) to predict $\mathbf{a}_0^*$ using a model without stable stage adjustments (we ran models for each species separately). To mimic aerial survey conditions during spring in the Arctic, we generated one availability prediction per day for Julian days 91–151 (April 1 to May 30 in nonleap years), at solar noon. To aid in interpretation, we omitted weather effects from GLMMs and only produced predictions for nonpups (availability of pups during Arctic spring is further complicated by the birthing process).

To see how differences in these estimates might influence abundance estimates from aerial surveys, we calculated potential relative bias as

$$\mathrm{Bias}\left(\widehat{N}\right) = \widetilde{\mathbf{a}}/\mathbf{a}_0^* - 1 \tag{2}$$

This formulation is motivated by assuming that $\widetilde{a}$ is an unbiased estimate of availability, and that abundance can be reasonably calculated using a Horvitz-Thompson-like estimator (cf., Cochran 2007), i.e., $\widehat{N} = C/\widehat{a}$ (C being a hypothetical aerial survey count).

2.4 | Data and software

TDR data and haul-out predictions are currently available at https://github.com/jmlondon/berchukFits; Survival and reproductive schedules, and R code to perform stable stage estimation are currently available at https://github.com/pconn/StableStagePhocid. Both repositories have been permanently and publicly archived on Zenodo (see London, 2022 and Conn, 2022, respectively).

3 | RESULTS

3.1 | Stable stage distributions

Hierarchical meta-analysis models for mortality produced estimates of annual survival for bearded, ribbon, ringed, and spotted seals that increased with age before declining due to senescence (Figure 2a), as expected given the functional form employed (Trukhanova et al., 2018). Reproductive and sexual maturity schedules differed substantially among species (Figure 2b–d), with ribbon seals maturing the fastest and bearded and ringed seals maturing the slowest. These translate into different expected age- and stage-proportions (Figures 3 and 4). In particular, ribbon seal populations should primarily be composed of adults owing to early maturation, whereas bearded and ringed seals should have a much higher proportion of subadults. For reference, finite rates of population growth (as determined by the dominant eigenvalue of the associated Leslie matrices) were 1.04 (bearded seals), 1.06 (ribbon seals), 1.08 (ringed seals), and 1.01 (spotted seals).

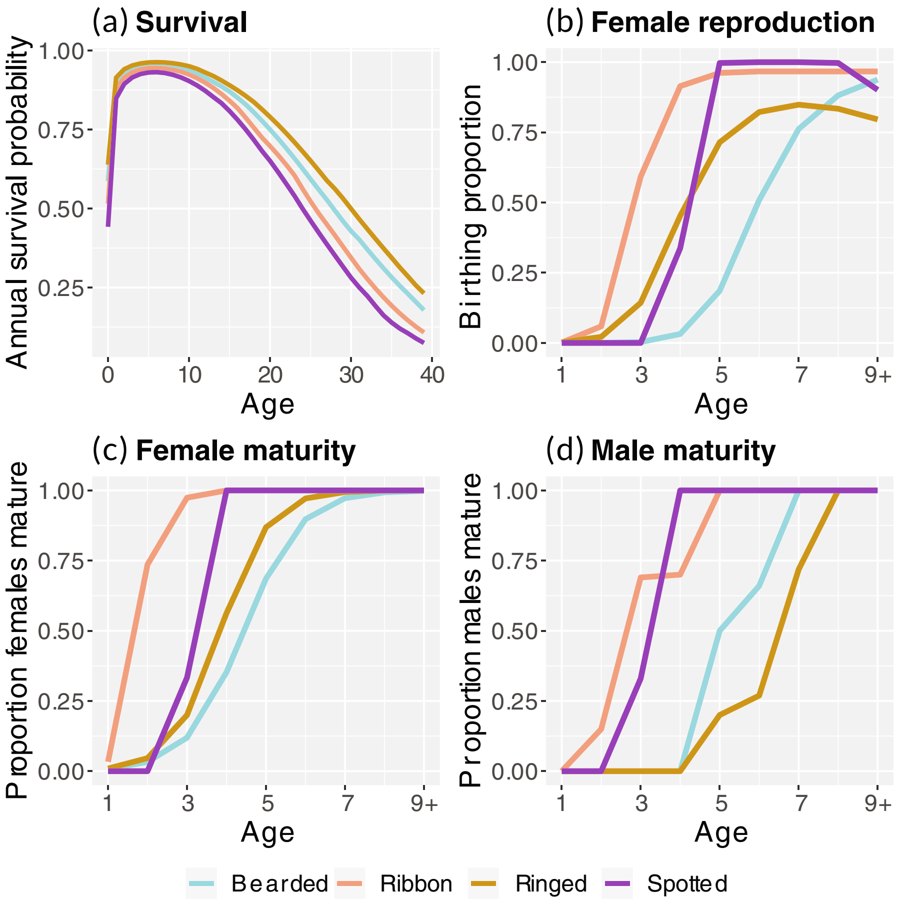


FIGURE 2 Annual survival probability, proportion of reproducing females, and proportion of sexually mature seals as a function of age for four species of ice-associated phocids in the Bering, Chukchi, and Beaufort Seas. We used survival and female reproduction to parameterize Leslie matrix models, and maturity values to convert stable age proportions to stable stage proportions.

3.2 | Aerial survey correction factors for ribbon and spotted seals

Estimates of haul-out probabilities for spotted and ribbon seals differed depending on whether age-sex class was ignored (treating the marked sample as representative of the population) versus accounted for in predictions using stable stage weighting (Figure 5). For spotted seals, weighted predictions were always higher than model predictions ignoring age-sex class. This is largely because samples of satellite tagged seals comprised higher proportions of subadults than expected for the population based on stable stage proportions. For spotted seals, 41% of nonpup telemetry observations were from subadults, whereas stable stage proportions suggested that 28% of nonpups should be subadults. Depending on the day of the survey, omitting stable-stage weighting adjustments could be expected to bias aerial survey abundance estimates of nonpups by −16% to 0% for ribbon seals (mean − 5%), and by 10%–20% (mean 13%) for spotted seals (Figure 5).

4 | DISCUSSION

In this paper, we showed that estimates of availability needed for aerial survey correction factors can be biased when the age-sex composition of satellite tagged seals differs from the population and when age-aggregated availability

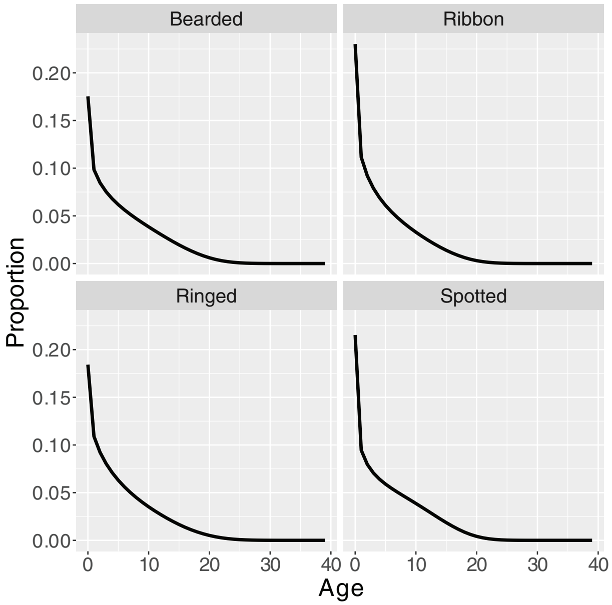


FIGURE 3 Stable age proportions as determined from the dominant eigenvectors of associated Leslie matrices for four species of ice-associated seals in the Bering-Chukchi-Beaufort region.

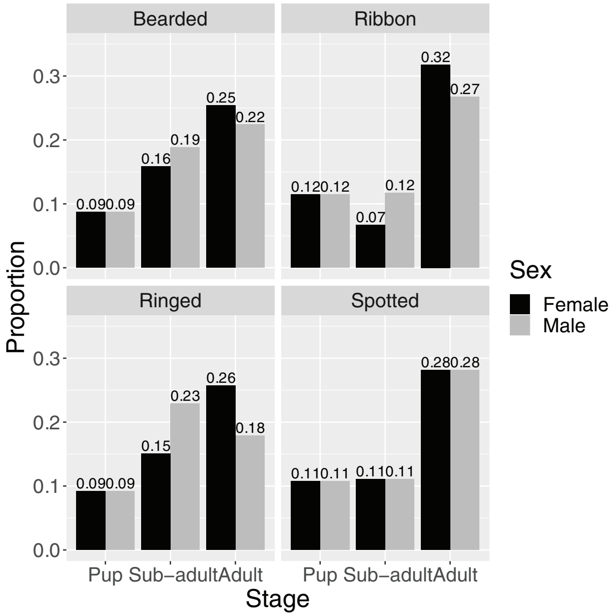
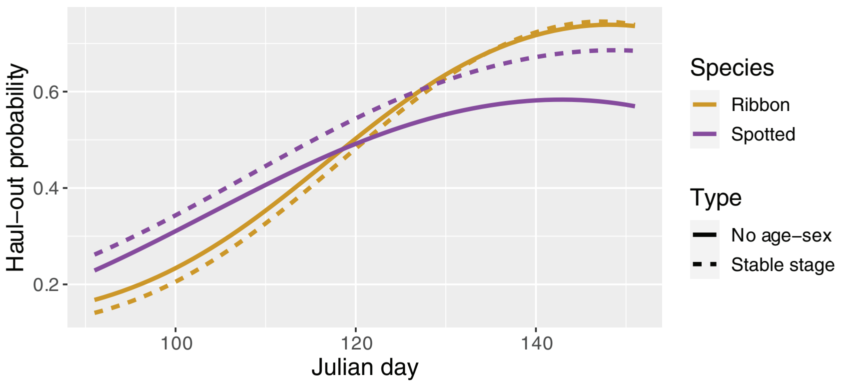


FIGURE 4 Stable stage proportions estimated from matrix population models and age-specific sexual maturity schedules for four phocid species.

estimates are used. We also illustrated how matrix population models and estimates of stable stage composition can be used to adjust estimates to remove these biases. Use of matrix population models and stable stage composition implicitly involves another set of assumptions – namely that life history schedules are accurate and that there have

(a) Modeled availability



(b) Expected bias in abundance

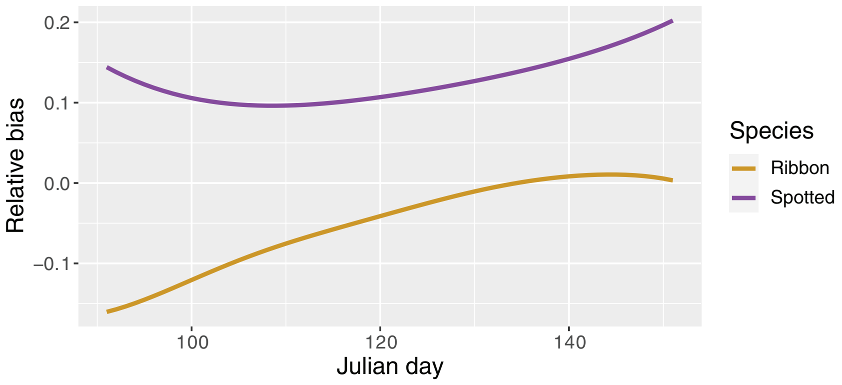


FIGURE 5 Availability and expected bias in abundance for models that do and do not adjust for age-sex effects. Panel (a) gives a comparison of predicted haul-out probabilities for subadult and adult ribbon and spotted seals for models ignoring age-sex structure (solid lines) with models that account for age-sex structure and adjust predicted haul-out behavior by stable age proportions (dashed lines). Panel (b) summarizes the expected bias in abundance estimates when age-aggregated availability estimates are used (assuming that the age- and sex-adjustment model is true).

not been any major perturbations to the system (e.g., wide scale recruitment failures, extreme stochasticity in vital rates). Nevertheless, we believe stable stage proportions obtained in this manner are an improvement over the raw age proportions obtained via opportunistic sampling that might favor capture of the most vulnerable (and often younger) individuals. When assumptions underlying matrix population models are in doubt, researchers may want to conduct analyses that allow for changes in age structure or sensitivity analyses to investigate the effects of alternative age- and sex-class proportions on resultant availability estimates. This is particularly the case for populations experiencing changes in reproduction or survival or reproductive failures, which will often be accompanied by changes in age and stage structure.

Although our analysis used ice-associated seals as an example, our methods could be applied to other taxa as well (e.g., cetaceans, sirenians, and other pinnipeds). However, additional modeling would likely be needed in many situations, including (1) when inference focuses on the number of offspring that are produced (e.g., pup production; Hammond et al., 2021), (2) when shipboard surveys are conducted (to account for changing availability while the ship traverses a study area; Langrock et al., 2013), or (3) when animals exhibit behavioral synchrony that cannot be explained by quantifiable covariates. Synchrony may only serve to introduce overdispersion, but may also induce bias, especially in colonial breeders like walruses (*Odobenus* sp.; Lydersen et al., 2008).

Differences in availability schedules between the naïve and stage-structured corrected versions were relatively minor for ribbon seals but larger for spotted seals (Figure 5a). Although it is tempting to speculate on drivers of availability differences (e.g., as a function of life history characteristics), we did not attempt to study them systematically. Ultimately, differences in availability schedules are likely a function of several factors, including (1) vulnerability of different age- and sex-classes to TDR capture efforts, (2) the proportions of animals in different stage-classes (themselves a function of life history parameters), and (3) differences in availability among stage classes (presumably a function of animal behavior and physiological constraints).

Assuming that a Horvitz-Thompson-like formulation for abundance estimates is reasonable and that the stage-structured availability estimates reflected truth, differences in availability schedules drive implied biases in abundance estimates (Equation 2). In particular, implied biases in abundance estimates for ribbon seals were predicted to be relatively minor later in the aerial survey window, but were quite large and pervasive for spotted seals (Figure 5b). This finding emphasizes the need to correct for age- and sex-related availability differences when estimating abundance for these populations.

For this analysis, we did not attempt to estimate uncertainty in stable stage proportions or propagate such uncertainty into availability predictions. Ultimately, this is an important component of variance that ideally would be accounted for when conducting abundance estimation with stage-structure corrected availability predictions. If point estimates are used, variance in final abundance estimates will be underestimated.

Where possible, our stable stage estimates relied on reproductive schedules developed from recent harvest collections (i.e., Alaska Department of Fish and Game, 2020; Quakenbush et al., 2020). However, ribbon seal and bearded seal reproductive schedules (and ages of male sexual maturity) relied on dated estimates from the Russian literature (i.e., Fedoseev, 1965, 2000; Tikhomirov, 1966). Although these schedules work to illustrate our modeling approach, they may need to be updated for specific locations and time periods where surveys are conducted. For example, there is considerable reason to believe that the age structure of ice-associated seals is changing under a warming climate. For instance, the age of ringed seal sexual maturity may have decreased in the last several decades in both Norway and Alaska (Krafft et al., 2006; Quakenbush et al., 2020), and there is evidence of reduced pup production under increasing temperatures in the Canadian Arctic (Ferguson et al. 2017; Harwood et al., 2020; Stirling & Smith, 2004). To address temporal changes in age structure, it would thus be useful to continue (and perhaps expand) sampling of Alaska Native subsistence harvests to update our analysis with more recent data. For ringed seals, there is also some thought that mature, sexually reproducing seals preferentially select landfast ice in the Chukchi Sea, and that immature seals preferentially select pack ice habitat in the Bering Sea (Crawford et al., 2019; but see Kelly, 2022). This raises an interesting question about habitat partitioning and the potential for spatial heterogeneity in age structure. If younger individuals select different habitats than older individuals, and if haul-out probabilities differ between the two groups, there is an argument that one should use an adult-biased correction factor in one area, and an immature-biased correction factor in the other. Although bias in overall abundance may actually be negligible if both areas were analyzed together and a single correction factor were used, maps generated with density surface models (Miller et al., 2013) could still have systematic bias. To make such regionally different availability predictions, researchers would need spatially explicit information on population age-sex composition, which may be difficult to collect. Nevertheless, researchers should be aware of the potential for temporal or spatial changes in age structure to affect availability, and therefore abundance estimates, if such changes are not explicitly controlled for.

Although we believe the stable stage proportions obtained here will be useful for developing aerial survey correction factors in Alaska, there are several possible sources of bias in life history parameters that are worth addressing. First, the use of the pregnancy data to determine fecundity rates does not account for possible losses due to abortion or early pup loss. For these reasons, our fecundity-at-age estimates are likely biased high. Similarly, our survival estimates were based on a meta-analysis of phocid seals (Trukhanova et al., 2018), where senescent effects were presumably driven by other species (e.g., elephant seals, *Mirounga* sp.). A cursory check of predicted stable stage age structure with the age composition of bearded seal harvests (ADFG, unpublished data) suggests that we may be underpredicting the proportion of old (e.g., >20) seals. Although this is a small proportion of the population and not likely to greatly bias stable stage proportions, it is worth noting for researchers studying phocid age structure.

Our finding that age-sex variation in seal behavior can bias availability and abundance estimators mirrors previous findings in the literature. For instance, Härkönen et al. (1999) showed that skewed sampling of age-sex classes can result in biased estimates of population growth, survival, and fecundity in harbor seals (*Phoca vitulina*). Similarly, Lonergan et al. (2013) illustrate how temporal variability in sex-ratios (with different haul-out probabilities for each sex) might confound inference about abundance and trend at a harbor seal haul-out site. When sample sizes allow, it thus seems prudent to account for age- and sex-based variation in behavior when applying population corrections based on biased samples of tagged seals. Our proposed method illustrates one possible approach for doing so. In cases where sample sizes do not allow for robust characterization of age-sex effects on availability, we advise increased caution when interpreting abundance estimates from aerial surveys of marine mammals.

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AUTHOR CONTRIBUTIONS

Paul Conn: Conceptualization; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing – original draft; writing – review and editing. **Irina Trukhanova:** Data curation; formal analysis; software; writing – review and editing.

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