VARIATION OF LIFE-HISTORY STRATEGIES IN PINNIPEDS WITH AN EMPHASIS ON SURVIVAL RATES AND SPATIAL DISTRIBUTION OF MALE WEDDELL SEALS IN EREBUS BAY, ANTARTICA

by

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ABSTRACT

This dissertation explores various components of male life-history theory using a species-specific approach focusing on Weddell seals (chapters 2 and 4) and a comparative approach focusing on pinniped (seal and sea lion) species (chapter 3). To better understand how marine mammal populations can function and to gain insight about the evolution of male Weddell seal fitness, my coauthors and I estimated the age-specific survival rates of male Weddell seals living in Erebus Bay, Antarctica. Actuarial senescence (decreasing age-specific survival with increasing age) has been documented for several wildlife species. However, contrary to females, little information exists regarding age-specific patterns of survival, including actuarial senescence, for males. We used 35 years of mark-recapture data to estimate age-specific survival rates in male Weddell seals using a hierarchical model approach in a Bayesian framework. We found that male survival estimates were moderate for pups and yearlings, highest for 2-year-olds, and gradually declined with age thereafter such that the oldest animals observed had the lowest survival rates of any age, illustrating that male Weddell seals in this population exhibit actuarial senescence. We further investigated male Weddell seal ecology by describing the spatial patterns of male Weddell seals in Erebus Bay using regression modeling and kernel density methods. The intermediately aged males tended to have the most reproductive-age female neighbors, but individual heterogeneity played a stronger role than age. We found that younger males tended to settle in more offshore and less crowded areas of the habitat relative to older males. From a comparative approach, we assessed the patterns of tradeoffs among various fitness traits in male pinnipeds by examining the relationships between stage-specific survival rates and body size, baculum size, mating strategies, and delayed social maturity. Comparative studies similar to ours have tended to focus on females of avian and some terrestrial species and have mostly addressed reproductive traits. However, we lack information about males and connections between survival rates and other life-history traits. We found evidence for a relationship between precopulatory, rather than postcopulatory, traits and survival rates. We highlight the need for more empirical survival rate data and robust comparative methods.

CHAPTER ONE

GENERAL INTRODUCTION

Identifying and monitoring life-history traits and habitat usage of a population can yield important insights about its ecological function and play an integral role in the preservation and management of an ecosystem. Organisms have finite resources that they can allocate to growth, survival, and reproduction (Cody 1966), which can lead to variation in life-history strategies. Ecological and evolutionary processes have shaped life history traits such that they occur in specific combinations, preventing a "Darwinian demon", i.e., a species that frequently produces high-quality offspring, reaches sexual maturity early in life, and has a long lifespan (Law 1979). For example, investing strongly in reproduction generally comes at the cost of inhibited survival (Gadgil and Bossert 1970). Evolution has produced a diversity of life-history strategies to maximize fitness from different combinations of life-history trait tradeoffs (Bonsall et al. 2004). Studying the survival rates of wildlife populations provides important insights about their general fitness, life-history strategies, and longevity (Lebreton et al. 1992, 1993; Caswell 2001; Rotella et al. 2012).

Physiology and behavior tend to shape life-history strategies. Whereas resource acquisition often determines fitness in females, male fitness tends to vary based on the current distribution of reproductive traits associated with male-male competition in the population (Maynard Smith 1979; Parker et al. 2012), which can lead males to take more risks than females. Males more often than females invest in traits subject to sexual selection, such as body size, baculum size, or ornaments. Males also tend to engage in

risky behaviors, such as male-male contests (Kraus et al. 2008). Variation among males in reproductive success and phenotypes for traits associated with male-male contests creates selection for certain phenotypes (Emlen and Oring 1977). However, many phenotypes associated with reproductive success are coupled with the cost of investing in somatic maintenance, resulting in a decrease in the probability of future reproduction events, survival rates, or both either immediately or at older ages (Bonduriansky et al. 2008; Festa-Bianchet 2012).

Survival rates often vary among different demographic groups, and these groups could contribute to the overall survival rate of the population disproportionately. For example, survival rates can vary among groups of individuals in a population with regard to sex, age, and geographic location within the habitat (Eberhardt 1985; Gerber and White 2014; Moorad et al. 2019). Including additional information, such as age and sex, into capture-recapture models increases the accuracy of and information provided by survival estimates (Lebreton et al. 1992). Accounting for non-specific phenotypic differences among individuals (i.e., individual heterogeneity) can also increase the accuracy of estimated demographic parameters while providing additional biological information (Vaupel and Yashin 1985; Chambert et al. 2013, 2014).

The habitat a population occupies can also influence the life-history traits of the population and the behavior of individuals (Simpson and Boutin 1993; Chambert et al. 2012; Sol et al. 2018). Similar to many other ecological characteristics of a population, habitat usage can vary according to age, sex, and individual (Wolf et al. 2005; Crawford et al. 2012; Sprogis et al. 2018). In territorial species, older territorial males can displace

younger males from preferred habitat areas (Sherry and Holmes 1989). Resulting in part from intense male-male competition in territorial males, younger, inferior, or both younger and inferior males often establish themselves in peripheral or less crowded areas of breeding habitat (Le Boeuf 1974a; Kiyota 2005; Crawford et al. 2012). This behavior can lead to seasonal heterogeneity in the age composition of animals occupying heterogenous habitats of varying quality, which can have important conservation implications.

Both empirical and comparative analyses have essential roles in testing various hypotheses of life-history theory and exploring the variation in life-history traits, and this dissertation employs both techniques. Comparative analyses have proven useful in ecology by revealing patterns that would otherwise be lost at smaller scales of inference (Arnqvist and Wooster 1995). Pinnipedia (seals, sea lions, and walruses) is an excellent suborder to test life-history hypotheses because pinniped species exhibit great diversity in geographic location, body size, and mating strategies. Three families and 34 extant species comprise Pinnipedia, all of which exhibit an amphibious lifestyle in which they feed aquatically but give birth terrestrially (Berta et al. 2018). Pinnipeds first evolved about 35 MYA, and the divergence between the Phocidae (true seals) and Otarioidea (fur seals, sea lions, and walruses) occurred about 23 MYA (Higdon et al. 2007). Pinnipeds originated in polar regions, and ancestral states for pinnipeds include a promiscuous mating system with equal probability that males or females would mate with multiple partners, aquatic mating, and short nursing periods on the ice (Krüger et al. 2014).

The Weddell seal (*Leptonychotes weddellii*), the southernmost breeding mammal (Dearborn 1965), has a circumpolar distribution in the Southern Ocean and relies on landfast ice for hauling out (Stirling 1969). With an adult diet mostly consisting of Antarctic silverfish (*Pleuragramma antarcticum*) and Antarctic toothfish (*Dissostichus mawsoni*) Weddell seals feed at a high trophic level and serve as an important mesopredator in the Ross Sea food web, which lacks apex predator fishes common to most marine systems (Smith et al. 2007). The relative lack of human-related disturbances in these remote southern areas of the world presents an ideal opportunity to study the population dynamics and animal behavior of long-lived marine mammals. The population of Weddell seals living in Erebus Bay, Antarctica has been studied extensively since 1969 as part of a long-term mark-recapture study (Siniff et al. 1977). Over the past two decades, a great depth of research emerged about the population ecology of the Erebus Bay population including survival, reproduction, and breeding colony attendance (e.g., Cameron et al. 2007; Hadley et al. 2007; Proffitt et al. 2007; Hadley et al. 2008; Garrott et al. 2012; Rotella et al. 2012; Chambert et al. 2013; Stauffer et al. 2013b; Chambert et al. 2015; Paterson et al. 2018). However, much of this effort has focused on questions pertaining to the females. This dissertation exclusively focuses on males to assess broad hypotheses in population and behavioral ecology in the areas of population dynamics, spatial structures, and apparent social associations.

This dissertation includes three main investigations to better understand life-history strategies in male pinnipeds with a focus on Weddell seals. The first investigation focuses on the age-specific survival rates of male Weddell seals living in Erebus Bay,

Antarctica. The second investigation uses a comparative approach to assess patterns of tradeoffs among various fitness traits in male pinnipeds by examining the relationships between stage-specific survival rates and body size, baculum size, mating strategies, and age at social maturity (i.e., the mean age at which males begin to engage in reproductive behaviors). The third investigation centers around the age-specific variation in spatial use of the Erebus Bay study site by male Weddell seals.

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CHAPTER TWO

VARIATION OF ANNUAL APPARENT SURVIVAL AND DETECTION RATES WITH AGE, YEAR, AND INDIVIDUAL IDENTITIY IN MALE WEDDELL SEAL (*LEPTONYCHOTES WEDDELLII*) FROM LONG-TERM MARK-RECAPTURE DATA

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Abstract

Exploring age- and sex-specific survival rates provides insight regarding population behavior and life-history trait evolution. However, our understanding of how age-specific patterns of survival, including actuarial senescence, compare between the sexes remains inadequate. Using 36 years of mark-recapture data for 7,516 male Weddell seals (*Leptonychotes weddellii)* born in Erebus Bay, Antarctica, we estimated age-specific annual survival rates using a hierarchical model for mark-recapture data in a Bayesian framework. Our male survival estimates were moderate for pups and yearlings, highest for 2-year-olds, and gradually declined with age thereafter such that the oldest animals observed had the lowest rates of any age. Reports of senescence in other wildlife populations of species with similar longevity occurred at older ages than those presented here. When compared to recently published estimates for reproductive Weddell seal females, we found that peak survival rates were similar (males: 0.94, 95% CI = 0.92-0.96; females: 0.92, 95% CI = 0.93-0.95), but survival rates at older ages were lower in males. Age-specific male Weddell seal survival rates varied across years and individuals, with greater variation occurring across years. Similar studies on a broad range of species are needed to contextualize these results for a better understanding of the variation in senescence patterns between the sexes of the same species, but our study adds information for a marine mammal species to a research topic dominated by avian and ungulate species.

Key Words: actuarial senescence, life history, mark-recapture, survival rates, Weddell seal

Introduction

Understanding the demographic behavior of populations reveals insight as to their persistence. However, populations are composed of individuals that represent a diversity of allelic combinations and behaviors that can affect fitness (Vaupel and Yashin 1985; Chambert et al. 2013; Gimenez et al. 2017). Grouping individuals (e.g., by age or sex) accounts for some of the variation among individuals and can also provide information regarding life-history trait evolution (Eberhardt 1985; Gerber and White 2014; Moorad et al. 2019). However, such groupings cannot account for all variation among individuals, and this latent variation potentially encompasses several phenotypic traits; it is frequently accounted for in statistical models by treating it as a fixed characteristic of an individual and measured by an associated variance parameter to reduce bias in inferring population-level trends (Gimenez et al. 2017). Studying life-history traits in long-lived vertebrate populations comes with several challenges because accounting for the variation among individuals imposes intense data-collection efforts and analytical requirements (Lebreton et al. 1992; Gaillard et al. 1994; Loison et al. 1999). When possible, including survival data for both sexes and multiple ages of a population can reveal pertinent information regarding fluctuations in population growth because males, females, juveniles, and adults can respond differently to extrinsic factors, such as density or weather (Coulson et al. 2001). As vital rates of males can differ from those of females, especially in polygamous species, results of population analyses can depend on whether one or both sexes are considered (Gerber and White 2014).

Actuarial senescence (i.e., the decrease in age-specific survival rates with increasing age) is a topic that has received much attention in the ecological literature. The main theories describing senescence predict that senescence would commence coincident with the onset of sexual maturity or immediately following first breeding (Williams 1957; Kirkwood 1977; Kirkwood and Rose 1991). However, available data indicate that the onset of senescence, at least at a detectable level, varies across species with senescence commencing immediately following first breeding in some species but delayed to an intermediate reproductive age (at which survival peaks) in other species (Berger et al., 2016; Catchpole, Fan, Morgan, Clutton-Brock, & Coulson, 2004; Ericsson, Wallin, Ball, & Broberg, 2001; Jones et al., 2008; Loison et al., 1999; Nussey, Coulson, Festa-Bianchet, & Gaillard, 2008). Data requirements and analytical challenges can make detecting senescence difficult, and, for many vertebrate species, senescence can easily go undetected without long-term data (Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013). Analytically, accounting for age and individual heterogeneity can improve inference on population-level vital rates (Beauplet, Barbraud, Dabin, Küssener, & Guinet, 2006; Cam, Link, Cooch, Monnat, & Danchin, 2002; Clutton-Brock & Sheldon, 2010; Service, 2000; Vaupel & Yashin, 1985). Fortunately, advances in computational power, the development of hierarchical modeling, and the emergence of long-term datasets with individually marked animals have allowed for describing or estimating population processes that occur over long periods of time and can be affected by individual heterogeneity (Clutton-Brock & Sheldon, 2010). In recent decades, actuarial senescence has been reported in many wild populations in diverse taxa (e.g., Ricklefs 1998, Loison et

al. 1999, Bonduriansky and Brassil 2002, Pardo et al. 2013, Hastings et al. 2018). Both the rate and age at onset of actuarial senescence in vertebrate populations can differ between males and females and likely stems from differential costs associated with reproductive activities (Boonekamp, Salomons, Bouwhuis, Dijkstra, & Verhulst, 2014; Clutton-Brock & Isvaran, 2007; Gaillard, Viallefont, Loison, & Festa-Bianchet, 2004; Gamelon et al., 2014; Kraus, Eberle, & Kappeler, 2008; Lemaître et al., 2015; Promislow, 1992) . For example, for feral horses, in which females expend considerable energy on reproductive effort but males do not, senescence commenced earlier in females than males (Garrott, 1991). In contrast, in species for which males expend substantial energy on reproduction through activities, such as fasting and male-male competition to obtain mating opportunities, senescence has been reported to occur earlier in life or to have a more rapid rate in males than in females (Catchpole et al. 2004; Lemaître and Gaillard 2012; Hastings et al. 2018). High reproductive effort by males intuitively correlates with higher age-specific mortality rates.

From empirical and comparative studies of several long-lived vertebrate species, male life spans are at least 20% shorter, and can be up to 52% shorter, than those of females (Clutton-Brock & Isvaran, 2007; Litzgus, 2006; Loison et al., 1999). For polygynous, long-lived, mammal species with aggressive male-male competition, many have hypothesized that males will tend to experience relaxed selection pressure for longevity in favor of sexually selected traits such that males are expected to have age-specific survival rates that are lower than those for females of the species, and data from wild populations usually, but do not always (Réale et al. 1996; Toïgo and Gaillard 2003),

support this supposition (Clinton & Le Boeuf, 1993; Clutton-Brock & Isvaran, 2007; Festa-Bianchet, 2012; Lemaître & Gaillard, 2012; Maklakov & Lummaa, 2013; Promislow, 1992). For example, males of some species with aggressive male-male competition can benefit from attaining larger body size, which could favor rapid growth rates. Although rapid growth rates might enhance an individual's fighting ability, larger body size could also reduce juvenile and adult male survival rates relative to females when food availability is limited because larger body sizes require greater energy requirements (Clutton-Brock, Albon, & Guinness, 1985; Toïgo & Gaillard, 2003). Behavioral differences between the sexes can also cause male survival rates to be lower than survival rates for females in species in which males tend to engage in risky behaviors related to reproduction, such as reduced predator vigilance in males searching for receptive females or engaging in male-male aggression (Clutton-Brock & Isvaran, 2007; Festa-Bianchet, 2012; Kraus et al., 2008).

Although there are demonstrated survival costs associated with aggressive male-male competition, the costs might not exceed costs of reproduction to survival and future reproduction incurred by females. Although the allocation principle (Cody 1966) and general framework of the disposable soma theory describe allocation of resources to reproduction, growth, or longevity (Kirkwood & Rose, 1991), allocating energy to any one of these three is not necessarily exclusive to allocating energy to the others. For example, the Y-model describes how individuals of a population can vary in their metabolic efficiency of energy allocation and/or acquisition of resources, which can result in individuals with both higher reproductive effort and survival relative to

individuals with lower metabolic efficiency or lower resource acquisition (van Noordwijk and de Jong 1986). Selection for some traits that favor male-male competition can also facilitate longevity, such as selection for larger body sizes coupled with delayed maturity (Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008; Clinton & Le Boeuf, 1993). Further, empirical estimates of survival for some species, including several polygynous mammals, provide evidence that males have survival rates greater than or equal to those of females (Clutton-Brock & Isvaran, 2007; Loison et al., 1999; Manske, Stobo, & Schwarz, 2002; Réale et al., 1996; Schwarz & Stobo, 2000; Toïgo, Gaillard, & Michallet, 1997). Polygynous males typically play no role in parental care, which can involve substantial energy expenditures (Bowen, Oftedal, & Boness, 1992; Clutton-Brock, Albon, & Guinness, 1989; Clutton-Brock, Guinness, & Albon, 1983; Noren, 2008). Additionally, females can experience unique survival risks associated with sexual coercion and harassment from aggressive males (Trillmich and Trillmich 1984; Réale et al. 1996; Ophir and Galef 2003; Scott et al. 2005). Given the lack of clarity regarding when males may have lower survival rates than females or when they may have higher survival rates as well as the presence of a limited number of studies comparing survival rates between the sexes, additional empirical work is needed.

Here, we take advantage of long-term data for individually marked Weddell seals (*Leptonychotes weddellii*), to estimate age-specific survival rates for males and to compare them to recently published survival rates for females in the same population. Survival rates of female Weddell seals are moderate for pups and yearlings and quite high for older animals (> 0.90); adult females endure costs to survival from pup production

and rearing (Hadley et al. 2007; Chambert et al. 2013, 2015; Paterson et al. 2018). Additionally, actuarial senescence that commences immediately after age at first reproduction, which typically occurs at eight years of age, was recently detected in female Weddell seals (Paterson et al. 2018). Unique reproductive costs might cause differences in age-specific survival rates and senescence patterns between male and female Weddell seals. Weddell seals exhibit female-biased sexual size dimorphism. Although Promislow (1992) found that sexual size dimorphism to generally correlate with relative survival between the sexes across several species of mammals, others (Toïgo and Gaillard 2003; Kraus et al. 2008) have found evidence that sexual size dimorphism might not drive sexually biased survival rates. Male Weddell seals engage in male-male competition in the form of underwater territory defense and exhibit a moderately strong polygynous mating system (Stirling 1983). In any given year, some males sire as many as eight pups, and about half of the males fail to sire any pups (Gelatt 2001; Harcourt et al. 2007a; b). Reproductive activity causes both male and female Weddell seals to incur loss of mass. In a single pupping/breeding season, females can lose up to 48% of their body mass during lactation (Macdonald 2018), and males can lose up to 24% of their body mass during underwater territory defense (Harcourt et al. 2007b). Reproductively active females incur an additional handicap during pregnancy. Vasoconstriction during diving of a non-pregnant female prevents blood from circulating in the uterus (Liggins et al. 1980), but pregnant females allocate blood flow to the uterus (Zapol et al. 1979), which would afford diving pregnant females less time for underwater activities, such as foraging.

Previous studies of female Weddell seals have indicated that adult survival rates had lower temporal variance than did rates for juveniles (Cameron and Siniff 2004, Hadley et al. 2006), a pattern that has been reported for a number of other long-lived vertebrates for both sexes (e.g., Tavecchia et al. 2001, Langtimm et al. 2004, Goodrich et al. 2008, Hyslop et al. 2012). Selection can act to reduce variation in adult survival in long-lived vertebrates (Crone 2001; Littles et al. 2016). Consequently, adult survival rates in large mammals tend to vary little across time (Fowler 1981). However, large disturbance events in variable environments can affect life-history processes (Moreno and Møller 2011; Fire et al. 2015). Recent studies reported little annual variation in survival rates for adult female Weddell seals across years that encompassed diverse environmental conditions, including a major iceberg event that led to a decrease in primary productivity (Arrigo et al. 2002; Chambert et al. 2012; Rotella et al. 2012). Female Weddell seals seem to breed each year but exhibit delayed implantation of the fertilized egg one to two months after breeding (Lake et al. 2008; Salas et al. 2017), and implantation seems to not occur during years with challenging environmental conditions (Chambert et al. 2012). This strategy would enable the females to avoid excessive energy expenditure associated with reproduction (i.e., gestation and lactation) and avoid augmented survival risks. Under the assumption that breeding occurs each year, males endure male-male contests every year, which might result in very little temporal variation in male survival because their activity remains consistent from year to year. On the other hand, this consistent energetically expensive activity might instead increase temporal variation in male

survival because it would cause individuals to become more susceptible to environmental harshness.

From analyses of 36 years of mark-recapture data collected on known-age male Weddell seals, we describe the age-related and temporal patterns of survival. Three major life stages are often observed in large mammals: young, prime age (period of intermediate adult ages characterized by high survival), and senescent (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000). First, we considered the following three alternate predictions related to the presence and timing of senescence: 1) male Weddell seals do not experience senescence (e.g., they might not survive to an old enough age to measure actuarial senescence), 2) adult males experience an age-related increase in adult annual survival rates until an intermediate (prime) age after which rates senesce, or 3) male Weddell seals experience senescence in early adulthood, immediately following the age of first reproduction. For male Weddell seals, senescence commencing immediately following first breeding would be the survival period from 3 to 4 years of age for the youngest breeders (Harcourt et al. 2007a), and onset of senescence following intermediate reproductive ages (ten to sixteen years of age, (Gelatt 2001) would be at seventeen years of age. Although some Weddell seals have sired pups at 4 years of age, copulations have more frequently been reported for older males, i.e., 5 to 10 years of age (Bartsh et al. 1992; Gelatt 2001). Onset of senescence occurring between 5 and 10 years would likely indicate that senescence commences with the onset of social maturity (i.e., becoming territorial, Bartsh et al., 1992) rather than sexual maturity and would also suggest that most seals start reproducing at an age older than 3 years of age. In one

geographic subset of our study population, most males reached social maturity by 11 years of age (Bartsh et al. 1992). Second, we tested for differences in ageing between male and female Weddell seals by comparing the age at onset of senescence and compared rates of senescence between the sexes. Finally, we estimated the amount of temporal variation in annual survival rates for male Weddell seals to better understand how environmental changes might affect male survival. A high degree of temporal variation in adult males would suggest that male-male contests impose a survival cost that intensifies with more difficult environmental conditions.

Methods

Study Site

All fieldwork occurred in Erebus Bay, Antarctica at 77.7° S and 166.5° E, adjacent to Ross Island, and covering about 420 km^2 (Figure 1). Commencing in late March or early April and continuing throughout the winter months, McMurdo Sound, including the more nearshore area of Erebus Bay, freezes to form land-fast ice, which gradually breaks out to varying degrees from the shore during late February to early March (Heine 1963; Jeffries et al. 1993). This fast ice averages about 1.3 – 2.0 m in thickness (Jeffries et al. 1993; Atkins and Dunbar 2009). The steep continental shelf of the eastern coast of Ross Island reaches nearshore depths of 900 m (de Jong et al. 2013). The tidally influenced nearshore waters of western Ross Island are fed by warm and saline water, relative to farther offshore locations, flowing under the land-fast ice (Heath 1971).

Mark-Recapture Efforts

During the spring (late September through November), Weddell seals haul out onto the ice to form pupping colonies in consistent areas associated with perennial tidal cracks in the land-fast ice (Figure 1), at which time gravid females give birth and nurse their pups (Cameron and Siniff 2004, Siniff et al. 2008), and sexually mature males compete to form and defend underwater territories (Siniff, DeMaster, Hofman, & Eberhardt, 1977). Pups are weaned six to seven weeks following birth, and adults copulate, presumably underwater, following this nursing period (Lindsey, 1937; Siniff et al., 2008). Males in the study area have sired offspring from ages 4 to 20 years old (Harcourt et al. 2007a) but might continue to reproduce at ages older than 20 years. Inferring from siring age, some males begin to engage in acquiring and defending underwater territories and experience successful copulation at 3 years of age.

Through extensive and frequent tagging efforts since the 1970s, all pups born in Erebus Bay are believed to have been tagged within one to two days following birth, and both male and female Weddell seals demonstrate strong site fidelity to Erebus Bay, which increases with age (Cameron, Siniff, Proffitt, & Garrott, 2007). Rubber or plastic livestock tags with unique number and tag color combinations for each animal were applied to the interdigital webbing of each of the rear flippers of pups, and tags were replaced in subsequent years if missing or broken (Siniff et al. 1977, Cameron and Siniff 2004). In addition to tagging young of the year, these tagging efforts also included the tagging of any untagged adult animal. Safety and ethics of all animal handling were approved by the Institutional Animal Care and Use Committee of Montana State

University (permit number 2011-38), and permission to conduct level A harassment of Weddell seals was approved under NOAA National Marine Fisheries Service (permit number17326). Following the birthing pulse, six to eight surveys were conducted each year from early November through early December with three to five days of no survey effort between consecutive surveys. During surveys, researchers visited each major colony for recapture events and approached seals on foot to read and record tag numbers; unless tags needed to be replaced, no animal handling occurred during recapture events. These recapture events mainly occurred at pupping colonies, but observers also recorded any seals that they observed while they travelled from one colony to the next. Mark-recapture data were used to determine the year each male was born (year of initial tagging), its age in every subsequent year (years after initial tagging), and whether it was seen or not in each year after its birth.

Model Construction and Analyses

We constructed hierarchical model extensions of Cormack-Jolly-Seber models using a Bayesian framework to estimate apparent survival (φ) and detection probability (p) of male Weddell seals from 1980 – 2015 (n = 7,516). We followed the method described by Link and Barker (2009) to use Markov Chain Monte Carlo (MCMC) based on the observed data likelihoods (ODL) to approximate the posterior distributions of our model parameters. We built models using the R package `NIMBLE` version 0.6-10 (de Valpine et al. 2017) in R version 3.5 (R Core Team 2018). As previous studies have suggested that age and year affect φ and p of Weddell seals (Cameron and Siniff 2004, Stauffer et al. 2013), and we had data from a large number of years for which at least

some female vital rates have been shown to vary (Cameron and Siniff 2004, Hadley et al. 2006, Stauffer et al. 2013b, Paterson et al. 2018), we structured our *a priori* candidate models for males such that temporal variation was allowed for both φ ($\hat{\sigma}_{yr}^{\varphi}$) and p ($\hat{\sigma}_{yr}^{p}$) by including random effects of year for each parameter that were normally distributed with a mean of zero. To evaluate support in the data for alternative predictions of how φ might change with age, we used five different model structures for the log-odds of φ. Three of the models considered functional forms of a continuous version of an individual's age: linear and quadratic forms of age and a third version that considered the natural logarithm of age. Two additional models treated age as a factor and used age classes that were found useful in previous work (see below). The three factor levels for the fourth model included ages 2 years through 9 years, 10 years through 16 years, and ages 17 years through 28 years. These ages were selected to test if survival rates remained constant for ages thought to represent different reproductive stages: early adult ages (4 through 9 years of age) with a low proportion of reproductive individuals (2 through 9 years of age), individuals at an intermediate reproductive age (10 through 16 years of age) with a high proportion of reproductive individuals, and older individuals (17 through 28 years of age) with a low proportion (Bartsh et al. 1992; Gelatt 2001; Harcourt et al. 2007a). The four factor levels for the fifth model included ages 2 years through 3 years, 4 years through 9 years, 10 years through 16 years, and 17 years through 28 years. This additional breakdown of ages was selected to test if survival rates of juveniles, (2 through 3 years of age), differed from early adult ages (4 through 9 years of age) with a low proportion of reproductive individuals. For models of the log-odds of p, we used the

same three functional forms that were used to model φ, and we used a fourth model structure that worked with age as a factor (see below). The four factor levels for the fourth model included ages 2 years through 3 years, 4 years through 9 years, 10 years through 16 years, and 17 years through 28 years. Thus, we had 20 model structures (5 structures for φ × 4 structures for p). To evaluate the effect of variation among individuals on survival and detection, we fit each of those 20 models with and without individual random effects for φ ($\hat{\sigma}^{\varphi}_{ind}$) and p ($\hat{\sigma}^{p}_{ind}$), which yielded a total of 40 candidate models (Table 1). We designed our models to investigate potential improvements or declines in apparent survival with aging, potential variation in detection with age, and variation among individuals and years in apparent survival and availability for detection. These functional forms allowed us to assess the age-related patterns of variation in survival, including the presence of an intermediately aged prime age group as well as senescence, age at onset of senescence if present, and how the rate of senescence varied with age if present. For all models, parameters for pups and yearlings were estimated independently from older individuals because previous studies have indicated that φ is lower for such animals and because yearlings typically do not attend pupping colonies such that they have very low p (Cameron & Siniff, 2004; Hadley et al., 2006). The functional forms of age effects we considered only describe older individuals. The age variable was rescaled and centered at 12 years of age to provide a baseline intercept value of a median-aged seal for improved interpretability of our results and to minimize the correlations between coefficients in our quadratic model (Hocking 2013). To fully explore age-specific apparent survival rates, we ran a full age-as-factor model to

separately estimate φ for each age. As this model was very computationally intensive, we only paired this model for φ with the best-performing model for p.

To obtain samples from the posterior distribution, we used an MCMC approach (Gelfand and Smith 1990; Casella and George 1992; Geman and Geman 1993). Given our large dataset and interest in obtaining posterior distributions based on this large dataset, we used uninformative priors for both φ and p on regression coefficients. For each candidate model, the MCMC ran with three chains for 20,000 iterations for each chain depending on model convergence with a burn-in of an additional 10,000 iterations. To reduce storage demands, we retained every tenth sample from each chain for a final sample size of 6,000 from the posterior distribution. We checked for MCMC convergence using the following techniques to compare the within and between variances of the three chains: viewing the trace plots of each monitored parameter and using the Gelman-Rubin statistic ($\widehat{R}$, Gelman and Rubin 1992) to ensure that $\widehat{R}$ values were < 1.1 and Geweke convergence diagnostics (Geweke 1991) using the R packages, `coda` (Plummer et al. 2006) and `ggmcmc` (Fernández-i-Marín 2016). We used Watanabe-Akaike Information Criterion (WAIC) scores for model selection (Watanabe 2010). We assessed model fit by comparing key features of our observed datasets to capture histories simulated from our best-supported model (see below). Using our estimates of φ and a life-table strategy similar to Clutton-Brock and Isvaran (2007), we estimated the life expectancy for an average individual in an average year.

We tested for individual heterogeneity in annual apparent survival and/or detection rates by constructing two versions of each model: one that included a random

effect of individual for both φ and p and one that did not. Including individual heterogeneity in demographic models increases the accuracy of the model by accounting for unmeasured differences among individuals in demographic groups and better meets the assumption that all individuals have the same probability of survival and detection to the next capture occasion (Gimenez et al. 2017). We assessed the relative importance of individual heterogeneity on the survival of male Weddell seals by running each age-specific model without including random effects of individual and the same model but including random effects of individual. In males, individual heterogeneity in detection might relate directly to reproductive status and behavior. There is some evidence that certain Weddell seal males spend more time in the water, e.g., those that are more successful at defending underwater territories (Bartsh et al. 1992), than others and might have different values of age-specific p. However, we collapsed information from multiple surveys down to a simple 0-1 (not seen or seen) record for each year, which could reduce heterogeneity in p that exists in how many times an individual was detected (Craig and Ragen 1999).

To minimize the opportunity for a seal to lose its tags, each animal received two tag sets with four total identification tags. Animals with damaged, unreadable, or broken tags received a new set of tags. We adjusted our survival estimates ($\hat{\varphi}$) to account for tag loss using the tag retention rates for retaining at least one tag ($\hat{\theta}$) as adjustment factors of 0.997 for pups surviving their first year of life, 0.990 for yearlings surviving to their second year of life, and 0.982 for all older seals (Cameron, 2001) and the equation, $\hat{\varphi}_{adj} = \frac{\hat{\varphi}}{\hat{\theta}}$ (Arnason and Mills 1981). The adjusted rates are presented in Results.

We performed goodness-of-fit tests on results from our best-supported model using the R software platform (R Core Team 2019) and the `furrr` (Vaughan and Dancho 2018), `purrr` (Henry and Wickham 2019), and `future` (Bengtsson 2019) packages. To do so, we simulated capture histories for the specific 7,516 individuals and 36 years in our study using 5,000 random iterations from the posterior distribution for the best-supported model. Specifically, we used the estimated parameters in the 5,000 chosen iterations to produce individual- and year-specific values for φ and p that were then used to conduct binomial trials to simulate whether each animal survived from one year to the next and whether it was captured. We then summarized how many simulated individuals were seen alive at various ages from 1 year of age to 26 years of age across the 5,000 simulated datasets, focusing our checks on the first six ages after release – early life 0-6 years – and last five ages after release – late life, 21 to 26 years – and compared the distribution of age-specific values to the numbers in the actual data for the same ages. We then used Bayesian *P*-values to assess model fit by calculating the mean of the number of simulated individuals detected at the given age that is greater than the actual number of individuals detected at the same age in the observed dataset (Meng 1994; Gelman 2013). When presenting results, we provide 95% credible intervals (95% CI).

Results

We analyzed mark-recapture data from 7,516 male Weddell seals tagged as pups between 1980 and 2014 and monitored through 2015 with a total of 13,693 recaptures (See Appendix Figure S1). Most individuals (n = 5,837; 78% of individuals) were never encountered again after the year in which they were first tagged as a pup. Of the seals

that were recaptured at least once, the number of individual recaptures ranged from 1 to 19 recaptures with a median of 3 recaptures and an interquartile range between 1 and 5 recaptures throughout the 35-year recapture period. The longest time period between recaptures was 13 years, which occurred for two seals that were born in 2000 and 2001. Estimated recapture rates for reproductively aged males were relatively high even though these males were presumably spending much of their time underwater. The oldest male seal recaptured in the Erebus Bay study area from 1980 – 2015 was 28 years old and was last recaptured in 2015. Few animals might have survived to reach 20 years of age or older. Only 86 individuals (1.1% of all pups tagged and 5.1% of all individuals with at least one recapture) were recaptured at 20 years of age or older, but 3,051 males could have reached age 20 during the study period. The age at which most recaptured males in the dataset were last recaptured was four years (n = 134), which is the youngest age that any male in this population is known to have sired a pup (Harcourt et al. 2007a).

The best-supported model included a quadratic functional form of age for φ and a logarithmic functional form of age for p, and individual random effects for both φ and p (models 2 and 3 for φ and p, respectively, from Table 1). The best-supported model received considerably more support than any other model (WAIC weight = 0.9998). All other models had WAIC scores that were >18.46 units higher than the score for the best model. Thus, we focus our inference on results from the best model. From our goodness-of-fit-tests, we did not detect any obvious issues, and visual inspection yielded similar results for simulated compared to actual data (Bayesian P-values ranged from

0.12 to 0.96 and averaged 0.55), suggesting that the predicted number of individuals detected at each age was similar to the observed number of individuals detected.

Our best-supported model suggested that both annual apparent survival and detection rates varied with age (Figure 2). Estimates of φ for pups and yearlings were modest: 0.55 (95% CI = 0.47 – 0.63) and 0.60 (95% CI = 0.51 – 0.68) respectively, for an individual with a random effect of 0 in a year with a random effect of 0 (i.e., an average individual in an average year). As pup apparent survival was estimated at 0.55 but only 78% of pups were recaptured during the study period, it is possible that some individuals have dispersed out of the Erebus Bay study area. Alternatively, many of these animals might not have reached breeding age and, therefore, have little reason to attend a breeding colony. Some individuals in the dataset remained juveniles throughout the study period; 301 individuals tagged as pups in 2014 and 261 individuals tagged as pups in 2013 were not recaptured in 2015, our final year recapture year in the dataset. Of the individuals that were tagged in 1980 and recaptured at least once, 68% were first recaptured at 3 years of age or older. However, of the pups tagged in 1980, only 26% were ever recaptured by 2015. Therefore, our data might suggest that some animals permanently emigrate from the study site; this group of animals might represent non-breeding individuals. Alternatively, we might not detect an animal for a given year if it was in the water during all 6-8 surveys. Age-specific estimates of φ peaked during the period from two to three years of age when the estimate for an average individual in an average year was 0.94 (95% CI = 0.92 – 0.96). Although receiving substantially less support, the age-as-factor models for φ also estimated φ to peak during young adult years

and decline with older adult ages. The best-supported model suggests that only 31% of tagged pups survived to the first known age at which male Weddell seals can begin reproductive activity, 3 years of age.

We found clear evidence for actuarial senescence but did not find any indication that adult survival increased and remained high for any set of adult ages before declining. Specifically, models that allowed survival to be constant across a set of ages that were previously defined as prime ages (10 – 16 years of age) were not supported by the data. Instead, and aligning with predictions that species with polygynous mating system would begin senescence at first reproduction, we found evidence that survival rates peaked during the survival period from 2 to 3 years of age with declines commencing thereafter and strengthening with advancing age. Accordingly, 26-year-olds (one of the oldest ages for any male ever observed in the study) had a lower estimated φ than did seals of any other age (mean estimate in an average year = 0.51, 95% CI = 0.31 – 0.66). All candidate models indicated similar patterns of decreasing annual apparent survival with increasing adult age. For example, in the second-most supported model, which modeled φ as age factors of pup, yearling, 2-3 years of age, 4-9 years of age, 10-16 years of age, and 17-28 years of age, the highest estimate of φ was for 2-3 years of age and declined to the lowest estimate of φ for 17-28 years of age (Figure S3).

We found evidence that male survival rates varied more across years ($\hat{\sigma}^{\varphi}_{yr}$ = 0.37, SE = 0.001) than among individuals ($\hat{\sigma}^{\varphi}_{ind}$ = 0.19, SE = 0.02) (Table 2, Figure 3). When translated to the real parameter scale, φ for a 10-year-old is predicted to be 0.83 (95% CI = 0.74 – 0.87) in a poor year (based on mean – 2 $\hat{\sigma}^{\varphi}_{yr}$), 0.92 (95% CI = 0.87 – 0.94) in an

average year, and 0.97 (95% CI = 0.94 – 0.98) in a good year (based on mean + 2 $\hat{\sigma}_{yr}^{\varphi}$). In contrast, φ for a 10-year-old is predicted to be 0.87 (95% CI = 0.60 – 0.93) for a frail individual (based on mean – 2 $\hat{\sigma}_{ind}^{\varphi}$), 0.92 (95% CI = 0.87 – 0.94) for an average individual, and 0.95 (95% CI = 0.92 – 0.98) for a robust individual (based on mean + 2 $\hat{\sigma}_{ind}^{\varphi}$).

We found some similarities and differences in patterns of φ between male and female Weddell seals. Although comparing age-specific survival rates between males and females for all ages would be the most accurate, we did not have comparable data for females to make such comparisons. Comparable analytical methods for female Weddell seals in Erebus Bay were used to estimate only the survival rates of reproductive females, and estimates were presented for 7 years of age and older (Paterson et al. 2018). The average total life expectancy, given that the individual survived to 7 years of age, for males (14.6, 95% CI = 13.4 – 15.7) and females (15.6, 95% CI = 14.9 – 16.4) was similar (Table S1), as average life spans of males were only 6% shorter than for females. Similarly, the estimates of φ for an average 10-year-old female and male were the same (0.92). However, annual variation in male survival ($\hat{\sigma}_{yr}^{\varphi}$ for males = 0.37) was nearly double the value estimated for adult females ($\hat{\sigma}_{yr}^{\varphi}$ for females = 0.19, Paterson et al. 2018). As predicted for species with polygynous mating systems, onset of actuarial senescence for male Weddell seals has potentially occurred at a younger age than what has been reported for females (Figure 4).

Discussion

We used long-term mark-recapture data to estimate the relationships between the age of male Weddell seals and annual apparent survival and detection rates. We used this information to evaluate the presence and the timing of actuarial senescence and compare with the pattern of actuarial senescence in female Weddell seals of the same population. Our best-supported model of age-specific survival rates for males had a quadratic functional form of age that indicated that survival peaked early in male life before undergoing actuarial senescence. The onset of senescence occurred during early adulthood and likely immediately followed the earliest reported ages of first reproduction for males (Harcourt et al. 2007a). We found no support for models that contained a well-defined prime age group of 10-16 years of age whereby survival rates increased over a number of young ages, plateaued and remained high for the previously suggested prime ages of 10-16 years, and then decreased at later ages. Our data suggest that reproductive activity comes at an immediate and higher survival cost to males relative to females because although adult male and female Weddell seals in Erebus Bay experienced similar peak survival rates, males incurred earlier and more drastic actuarial senescence than reported by Paterson et al. (2018) for breeding females in this population. Similar to the observations made previously for females (Cameron and Siniff 2004, Hadley et al. 2006, Rotella et al. 2012), the apparent annual survival rates of the males estimated in the current study were lowest for the pups and yearlings but increased rapidly between 2 and 3 years of age. Juvenile Weddell seals endure unique survival challenges, such as predator avoidance and relatively inefficient foraging as a result of physiological

constraints related to diving ability (Burns 1999). Additionally, the youngest age classes would presumably have a higher proportion of lower quality individuals because they would have had exposure to selection pressures for less time (Cam et al. 2002). However, annual apparent survival rates for males aged 24 years and older were estimated to be similar to or lower than the survival estimates for pups surviving to their first and second years of life (the ages with the next lowest survival rate estimates), further demonstrating the effects of actuarial senescence in male Weddell seals. It seems likely that engaging in territory acquisition and defense has an immediate trade-off with survival in male Weddell seals, and this tradeoff might increase with age.

Similar to our results, reproductively active female Weddell seals in the Erebus Bay population also experience actuarial senescence early in their reproductive lives (Paterson et al. 2018). Although, Paterson et al. (2018) only presented a survival curve for ages starting with the median age at primiparity (7 years of age), survival rates began to decrease immediately. It is difficult to directly compare our results to those of Paterson et al. (2018) because the male survival data includes all males recaptured, but only known breeders were included in the survival estimates for females. It is possible that by excluding non-breeding females from the survival analyses, a lower proportion of lower quality individuals were included in these estimates. Survival data from our study of male Weddell seals provide little support for the evolutionary theory of senescence (Williams 1957) because senescence appears to start prior to the age of first reproduction. Although the magnitudes of peak annual age-specific survival rates were similar for males (3 years of age, 0.94, 95% credible interval 0.92-0.96) and females (7 years of age,

0.92, 95% credible interval 0.93-0.95), males tended to have lower estimated survival rates than females for 20 years of age (males: 0.75, 95% credible interval 0.64-0.81, females: 0.85, 95% credible interval 0.83-0.87) and older. Senescence appears to commence at an earlier age in males than breeding females, but age-specific annual survival rates were not presented by Paterson et al. (2018) for individuals younger than 7 years of age. It is possible that senescence also starts at 3 years of age in females, such that survival for females at 3 years of age is higher than those at 7 years of age. The findings of an early onset of senescence detected for the males in our study population join a limited number of accounts of detecting actuarial senescence in pinniped species. Actuarial senescence has also been observed in both males and females in Steller sea lions (*Eumetopias jubatus*) and Hawaiian monk seals (*Monachus schuinsladi*) and in females in subantarctic fur seals (*Arctocephalus tropicalis*), California sea lions, northern elephant seals (*Mirounga angustirostris*), and New Zealand sea lions (*Phocarctos hookeri*) (Hastings et al. 2018).

The maximum survival rates of both sexes (females: 0.90 – 0.93 for experienced breeders and 0.92 – 0.95 for skip breeders (Paterson et al. 2018), males: 0.92 – 0.95), maximum observed life span for the oldest recorded female (31 years of age (Paterson et al. 2018) and male (28 years of age), and mean life expectancy from 7 years of age for females (15.6 years) and males (14.6 years) were similar. We attribute these findings to three possible characteristics of Weddell seal ecology. First, male Weddell seals likely engage in less risky behavior than some other species with polygynous mating systems. Most male Weddell seals sire 0 to 2 offspring per season, but almost 90% of seals studied

at one colony in Erebus Bay sired at least one pup in a five-year period (Harcourt et al. 2007a). This mating strategy is likely coupled with a lower cost of reproductive effort than species in which only a few males sire all offspring and typically only reproduce for one or two years (e.g., southern elephant seals, Le Boeuf 1974), and it might explain the similar life spans between the sexes in Weddell seals.

Environmental variation can also play a role in reproductive behavior. Whereas females of multiple polygynous species tend to restrict reproductive effort in favor of survival when resources are limited (Trillmich and Limberger 1985; Pitcher et al. 1998), males typically continue focusing their efforts on reproductive attempts (Trillmich and Limberger 1985; Hogg and Forbes 1997). Evidence of restricted reproduction in female Weddell seals during environmental hardship from 2000 to 2005 has been reported for the Erebus Bay population (Chambert et al. 2012). Although, any changes in male reproductive effort are unknown, detection of males at pupping colonies strongly decreased during this time, suggesting that fewer males maintained their usual territorial defense behavior in Erebus Bay since they were not seen at pupping/breeding colonies. Survival rates did not have any notable decrease during those years, which indicates that males might have been able to avoid risky behavior in favor of survival (i.e., demographically buffer their survival) during that time. Rotella et al. (2012) reported demographic buffering in females.

Finally, the life-history strategy of rapid growth that polygynous males with aggressive male-male competition often demonstrate seems absent in Weddell seals (Bryden et al. 1984). Unlike many other pinniped species that have sexual size

dimorphism with males as the larger sex, Weddell seals have a slight sexual size dimorphism with females as the larger sex. Additionally, pups and juveniles of both sexes have similar annual apparent survival rates, which suggest that males are not suffering a survival cost to rapid growth during these young years (Proffitt et al. 2008). However, weaning mass has been shown to affect male juvenile survival but not that of females (Proffitt et al. 2008), which might indicate that males require more resources than females for potential faster physiological maturing. If males grow and mature faster than females, it might explain their faster rate of senescence through possible antagonistic pleiotropy effects.

Although several recent studies of long-lived vertebrates have found the onset of senescence to occur in post-prime ages rather than immediately following first reproduction (e.g., Chantepie et al. 2016; Berger et al. 2016), these studies failed to account for individual heterogeneity. Including individual heterogeneity enables detection of senescence with greater sensitivity because it can separately account for the decrease in abundance of frail individuals with increasing age (Vaupel et al. 1979; Cam et al. 2002). By accounting for individual heterogeneity, our tests were more sensitive to detecting senescence. Cameron and Siniff (2004) estimated survival rates for males in the same population but did not detect senescence. However, they had a smaller dataset (data collected from 1983 – 2000 and recaptured individuals aged from pup to 17 years), especially with regard to the number of individuals recaptured in the oldest ages, which can pose challenges for detecting actuarial senescence in long-lived animals (Nussey et al., 2008). Additionally, they did not account for individual heterogeneity. Similar to the

females in this population (Paterson et al. 2018), individual heterogeneity plays an important role in the survival of male Weddell seals. It is possible that higher quality individuals might engage in territorial defense more frequently (e.g., in consecutive years) than frail individuals, which would provide robust individuals a disproportionately high contribution of offspring to the population.

Adults of long-lived large mammals typically demonstrate relatively constant survival rates among years because stochastic changes in adult survival could devastate stability in population vital rates (Langtimm et al. 1998; Gaillard and Yoccoz 2003; Rotella et al. 2012). Despite the limited annual variation in survival rates for male Weddell seals, the temporal variation in male survival rates was almost double the temporal variation in adult female survival rates (Paterson et al. 2018). The large difference in temporal variance between males and females indicates that male annual apparent survival seems more sensitive to changes in the environment. Consistent reproductive effort each year serves as a plausible explanation of their greater temporal variance in annual apparent survival compared to the females. Early life conditions could also impact temporal variation in survival among individuals. Males born during a year with favorable environmental conditions might have better survival prospects than those born in more challenging conditions. Females in this population have a higher probability of recruiting to the pup-producing portion of the population by 10 years of age if they experienced favorable environmental conditions while in utero (Garrott et al. 2012). Future analyses that try to explain temporal variation in male survival using

environmental covariates are needed to learn if adult survival rates for males also vary according to the environmental conditions that occurred while the males were in utero.

The fluctuations in annual detection rates were far more dramatic than those in annual apparent survival rates and likely reflected changes in male Weddell seal behavior (Figure S2). Pup production was reduced from 2000 to 2005 and was associated with challenging environmental conditions associated with the presence of mega-icebergs in the area (Chambert et al. 2012). We hypothesize that during the iceberg event, male Weddell seals had notably lower detection rates for two possible reasons. They might have had lower attendance rates at pupping colonies due to decreased reproductive effort in Erebus Bay but might have temporarily emigrated to colonies outside of the study area to either attempt breeding in a less harsh environment or to forgo breeding opportunities and spend the season in better hunting grounds. Alternatively, they were present but more difficult to detect because they spent more time in the water to compete harder for the more limited breeding opportunities given the lower abundance of reproductively active females. The highest detection rates occurred in 2010 and 2012-2015, which were all years with above-average pup production, and therefore, large numbers of adult females attended the colonies.

Our study adds to a small but growing number of studies comparing the patterns of actuarial senescence between males and females. Our results from a long-term mark-recapture dataset of male Weddell seals in Erebus Bay, Antarctica from 1980 to 2015 indicate that male Weddell seals possibly experience actuarial senescence at an earlier age than females. Although we lack data for exact causes of increased mortality rates

with increasing age, our results provide an interesting foundation for a multitude of future studies. As male Weddell seal apparent annual survival rates were strongly tied to age and individual heterogeneity, we postulate that male-male contests in the form of aquatic territory defense might contribute to a survival tradeoff in this species. However, it is also possible that males experience higher mortality rates than females at older ages resulting from activities possibly related to but not directly caused by male-male contests, such as increased susceptibility to disease (Zuk and McKean 1996; Moore and Wilson 2002). Our study is among few reports investigating the variation in actuarial senescence between the sexes of the same species. Additional studies of other taxa are necessary for a better understanding of sex-specific patterns of senescence and life-history tradeoffs. By analyzing year as a random effect, our results provide additional evidence that survival in adult long-lived mammals varies little with time, but we have pinpointed specific years that have resulted in relatively low apparent survival rates consistent across multiple ages. We expect that further investigation of these year effects would further explain the factors affecting survival in male Weddell seals in Erebus Bay.

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Tables and Figures

Table 1. List of candidate models for each parameter, (a) apparent survival (φ) and (b) detection (p), with the number of fixed effects (K) included in each model.

We used all possible combinations of the first five model structures for φ and the four model structures for p to yield 20 candidate models that also included random effects of individual and those same combinations of fixed effects for 20 candidate models that did not include random effects of individual. Year was included in each model as a random effect. We ran one final model using model 6 for φ and model 3 for p. For each model, A represents age and Y represents year.

(a)

Model number	**Model φ**	**K**
1	$\text{Logit}(\varphi) = \beta_0 A_0 + \beta_1 A_1 + \beta_{2\ldots28}(A_2 + \ldots + A_{28}) + \beta_Y Y$	3
2	$\text{Logit}(\varphi) = \beta_0 A_0 + \beta_1 A_1 + \beta_{2\ldots28}(A_2 + \ldots + A_{28}) + \beta_{2\ldots28}(A_2 + \ldots + A_{28})^2 + \beta_Y Y$	4
3	$\text{Logit}(\varphi) = \beta_0 A_0 + \beta_1 A_1 + \beta_{2\ldots28}\ln(A_2 + \ldots + A_{28}) + \beta_Y Y$	3
4	$\text{Logit}(\varphi) = \beta_0 A_0 + \beta_1 A_1 + \beta_{2\text{-}9} A_{2\text{-}9} + \beta_{10\text{-}16} A_{10\text{-}16} + \beta_{17\text{-}28} A_{17\text{-}28} + \beta_Y Y$	5
5	$\text{Logit}(\varphi) = \beta_0 A_0 + \beta_1 A_1 + \beta_{2\text{-}3} A_{2\text{-}3} + \beta_{4\text{-}9} A_{4\text{-}9} + \beta_{10\text{-}16} A_{10\text{-}16} + \beta_{17\text{-}28} A_{17\text{-}28} + \beta_Y Y$	6
6	$\text{Logit}(\varphi) = \beta_0 A_0 + \beta_1 A_1 + \beta_2 A_2 + \beta_3 A_3 + \beta_4 A_4 + \beta_5 A_5 + \beta_6 A_6 + \beta_7 A_7 + \beta_8 A_8 + \beta_9 A_9 + \beta_{10} A_{10} + \beta_{11} A_{11} + \beta_{12} A_{12} + \beta_{13} A_{13} + \beta_{14} A_{14} + \beta_{15} A_{15} + \beta_{16} A_{16} + \beta_{17} A_{17} + \beta_{18} A_{18} + \beta_{19} A_{19} + \beta_{20} A_{20} + \beta_{21} A_{21} + \beta_{22} A_{22} + \beta_{23} A_{23} + \beta_{24} A_{24} + \beta_{25} A_{25} + \beta_{26} A_{26} + \beta_{27} A_{27} + \beta_{28} A_{28} + \beta_Y Y$	29

(b)

Model number	**Model p**	**K**
1	$\text{Logit}(p) = \beta_1 A_1 + \beta_{2\ldots28}(A_2 + \ldots + A_{28}) + \beta_Y Y$	2
2	$\text{Logit}(p) = \beta_1 A_1 + \beta_{2\ldots28}(A_2 + \ldots + A_{28}) + \beta_{2\ldots28}(A_2 + \ldots + A_{28})^2 + \beta_Y Y$	3
3	$\text{Logit}(p) = \beta_1 A_1 + \beta_{2\ldots28}\ln(A_2 + \ldots + A_{28}) + \beta_Y Y$	2
4	$\text{Logit}(p) = \beta_1 A_1 + \beta_{2\text{-}3} A_{2\text{-}3} + \beta_{4\text{-}9} A_{4\text{-}9} + \beta_{10\text{-}16} A_{10\text{-}16} + \beta_{17\text{-}28} A_{17\text{-}28} + \beta_Y Y$	5

Table 2. Effects of temporal and individual variation on annual apparent survival.

We illustrate the effect of variation among years and individuals on survival rates for male Weddell seals with 10 years of age. Poor and frail estimates were calculated as 2 standard deviations below the mean random effect for year and individual, respectively. Good and robust estimates were calculated as 2 standard deviations above the mean random effect for year and individual, respectively. 95% upper and lower credible intervals are provided in parentheses. All estimates have been adjusted for tag loss.

	Effect of Individual		
Effect of Year	**Frail**	**Average**	**Robust**
Poor	0.758 (0.404, 0.860)	0.830 (0.739, 0.872)	0.880 (0.818, 0.940)
Average	0.867 (0.603, 0.928)	0.917 (0.872, 0.935)	0.946 (0.919, 0.980)
Good	0.954 (0.849, 0.986)	0.966 (0.942, 0.982)	0.981 (0.963, 1.00)

Figure 1. Map of Erebus Bay study site depicting the breeding/pupping colonies (a), the full continent (b), and Ross Ice Shelf (c) for reference. Gray points designate perennial breeding/pupping colonies.

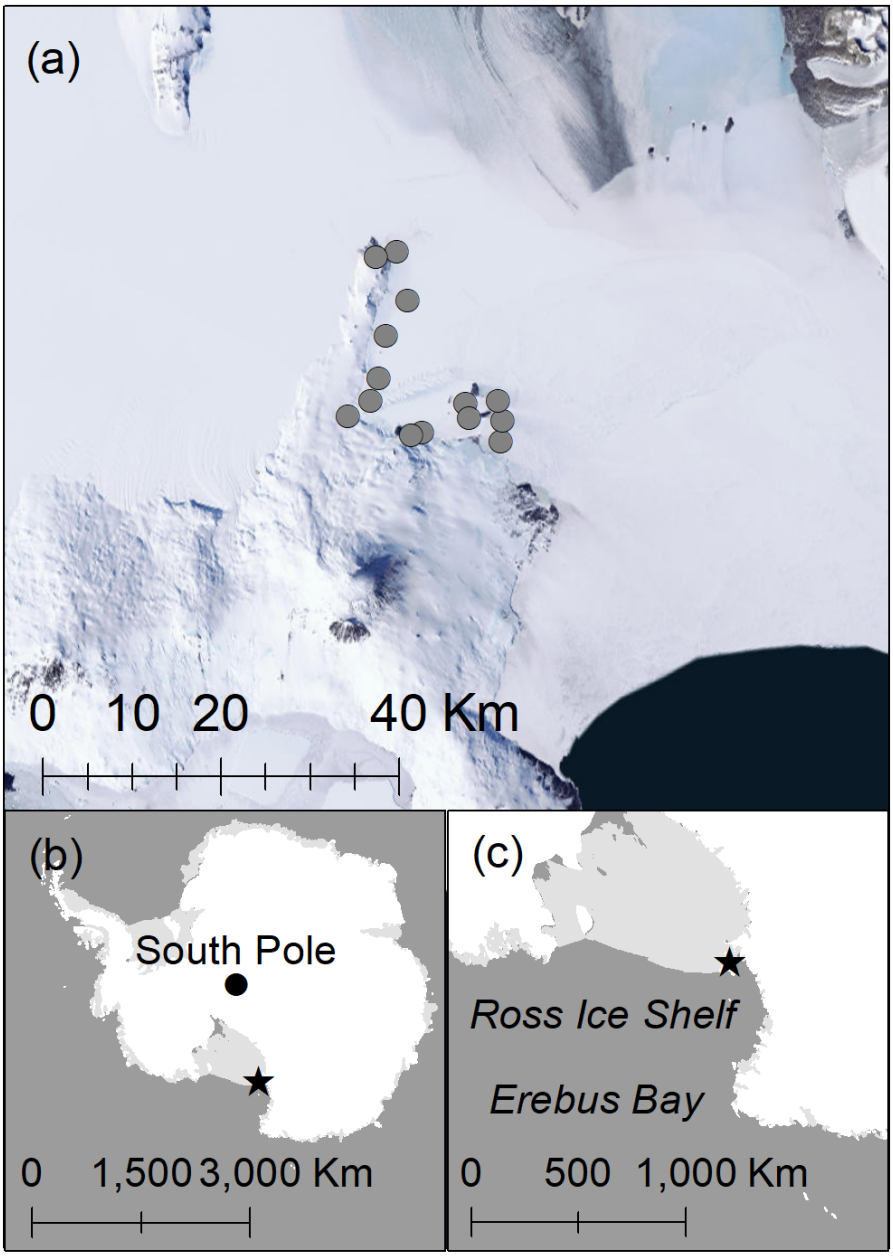


Figure 2. Apparent annual survival and annual detection by age of male Weddell seals. Apparent annual survival (a) and annual detection (b) rates were estimated by our best-supported model (lowest Watanabe-Akaike information criterion score), Logit(φ) = $\beta_{age\ 0} \times age_0 + \beta_{age\ 1} \times age_1 + \beta_{age} \times$ (age 2…age 28) + $\beta_{age}^2 \times$ (age 2…age 28) + $\beta_{year} \times$ year, Logit(p) = $\beta_{age\ 1} \times age_1 + \beta_{ln(age)} \times$ (age 2…age 28) + $\beta_{year} \times$ year, for each age for an average individual during an average year. Error bars show the 95% credible interval.

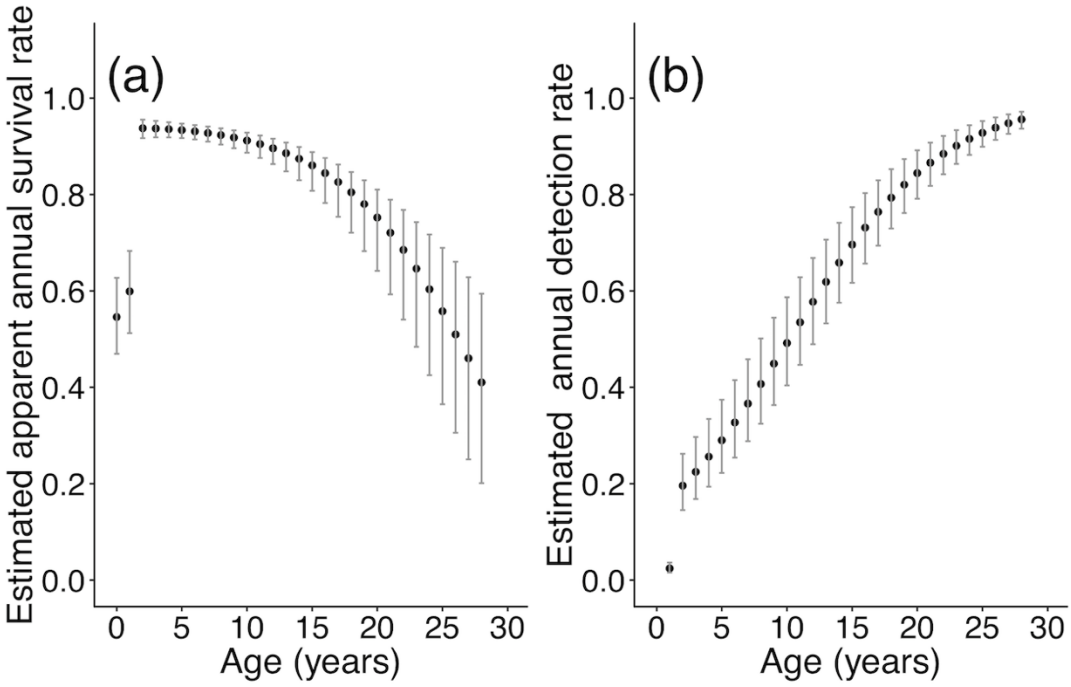


Figure 3. Apparent survival by year of male Weddell seals. Apparent survival rates as estimated by our best-supported model (lowest Watanabe-Akaike information criterion score), Logit(φ) = $\beta_{age\ 0} \times age_0 + \beta_{age\ 1} \times age_1 + \beta_{age} \times$ (age 2…age 28) + $\beta_{age}^2 \times$ (age 2…age 28) + $\beta_{year} \times$ year, for an individual with a random effect of surviving from 0 to 1 year of age (a), surviving from 2 to 3 years of age (b), and surviving from 19 to 20 years of age (c). Error bars show the 95% credible interval.

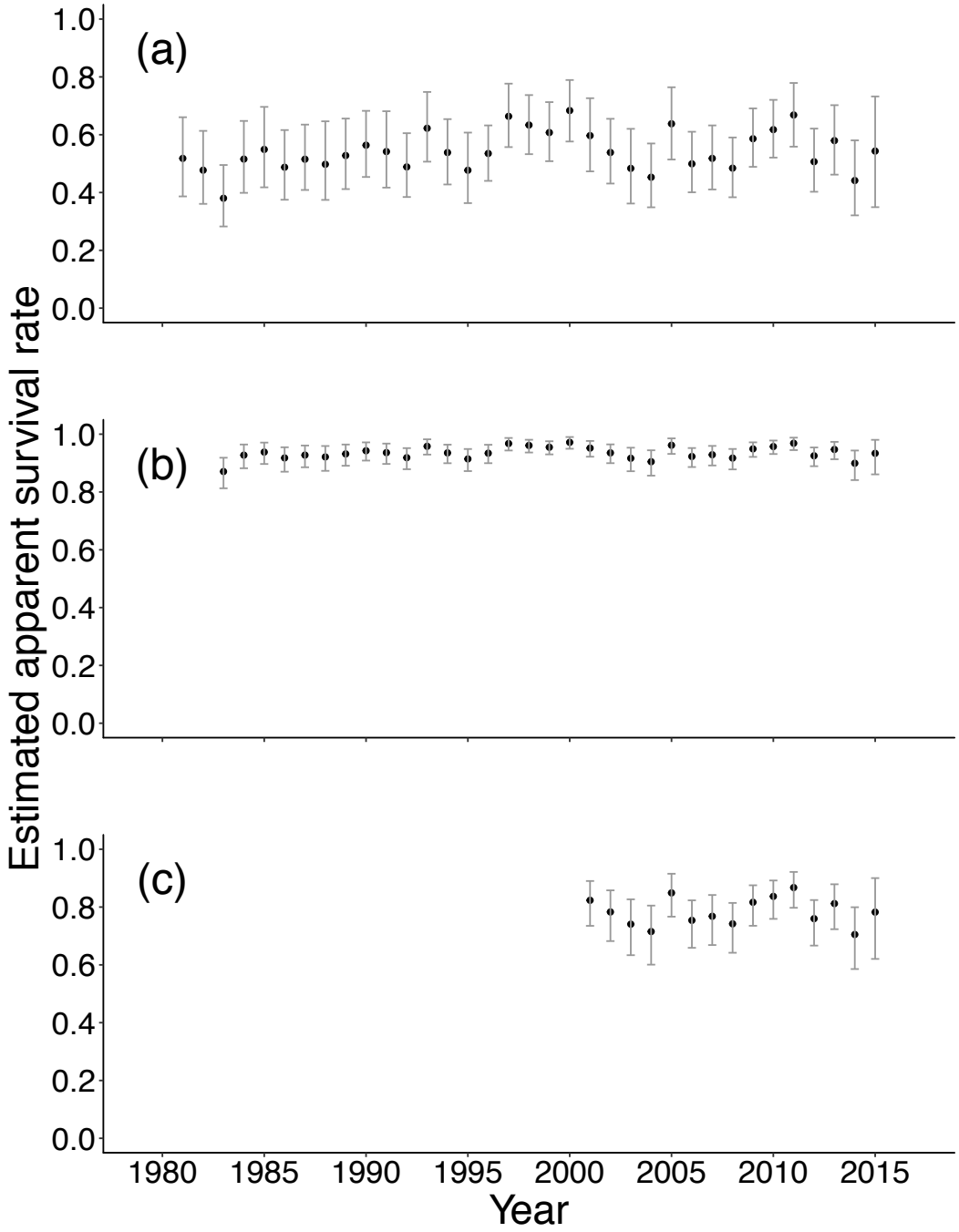
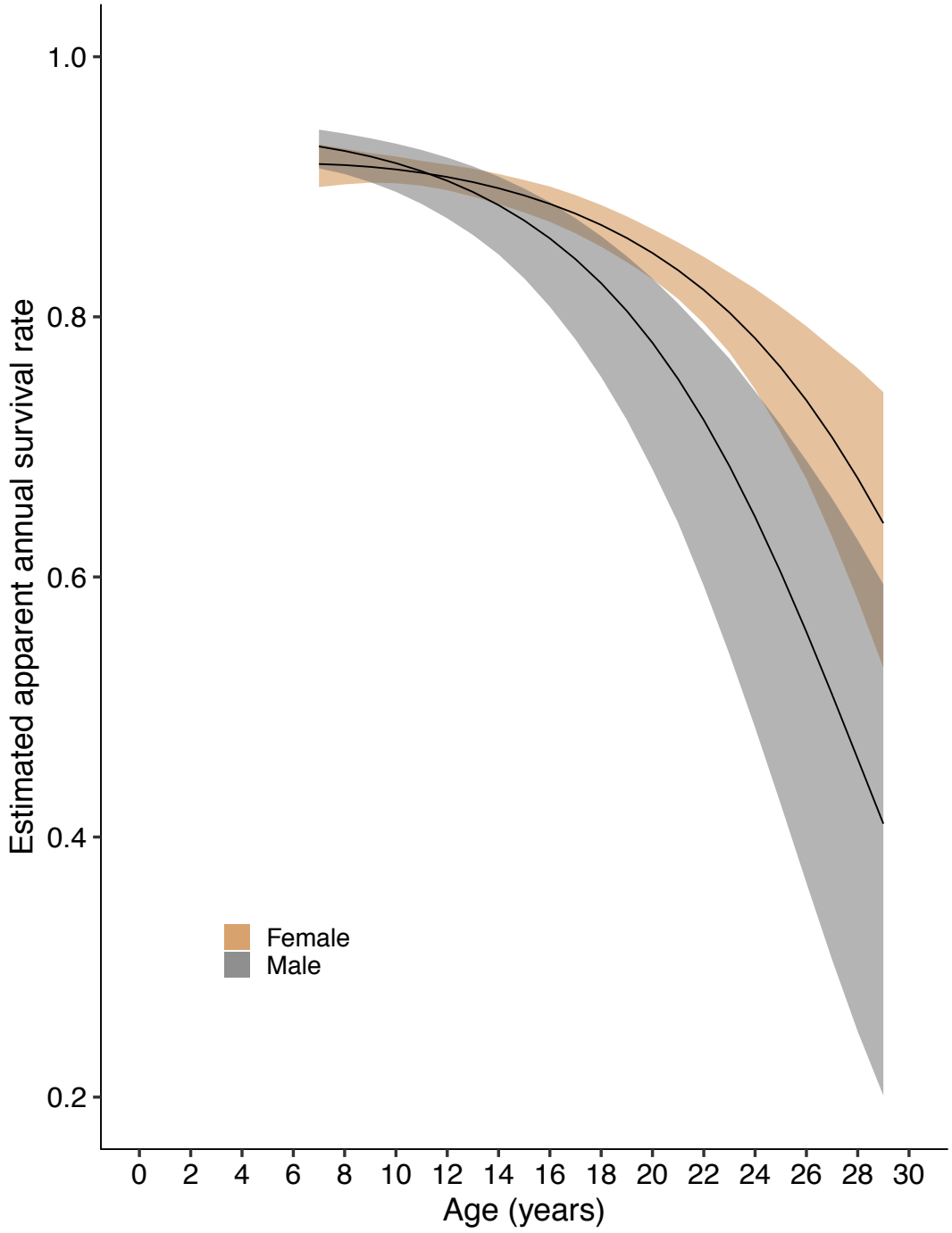


Figure 4. Senescence rates of male and female Weddell seals. The 95% credible interval of annual apparent survival rates are shown for males (gray) and females (beige) starting with the youngest common measured age (7 years) and ending with the oldest common measured age (28 years). Female data use to create this figure are from Paterson et al. (2018).



CHAPTER THREE

A COMPARATIVE STUDY EVALUATING HOW STAGE-SPECIFIC SURVIVAL RATES VARY WITH LIFE-HISTORY TRAITS IN MALE PINNIPEDS

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Contributions: Contributed to data analyses, helped design the quantitative portions of the study, contributed to writing, and approved of the final manuscript

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Manuscript Information

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Abstract

Survival rates are a central component of life-history strategies of large vertebrate species. However, comparative studies seldom investigate variation in survival rates with respect to other life-history traits, especially for males. Further, the relationship between male survival rates and precopulatory versus postcopulatory investment has received little attention. We used graphical analyses to examine the relationship between estimated stage-specific survival rates and other life-history traits for male pinnipeds that met the inclusion criteria of our study (13 species). We also present a quantitative approach using Bayesian phylogenetically controlled regression with the flexibility to incorporate uncertainty in the estimated survival rates and quantitative life-history traits as well as genetic similarity among species (with uncertainty). However, as with any comparative analysis, this approach makes several assumptions regarding the generalizability and comparability of empirical data from separate studies. From our graphical analysis, only mating system, a proxy for precopulatory traits, varied with survival rates, which provided modest evidence that investment in precopulatory traits, but not postcopulatory traits, was associated with reductions in adult survival. Our work elucidates the challenges associated with addressing important questions related to broader ecological life-history patterns and how survival-reproduction tradeoffs shape evolutionary histories of extant taxa. Specifically, we highlight the importance of generating high-quality estimates of age-specific survival rates and information on other life-history traits that reasonably characterize a species as a whole.

Key Words: life-history evolution, pinnipeds, survival rates, phylogenetic uncertainty, comparative analysis

Introduction

Survival rates for juveniles and adults are fundamental characteristics of fitness and influence the diversity of life-history strategies observed across iteroparous vertebrate species (Eberhardt 1985; Promislow and Harvey 1990; Langtimm et al. 1998; Gaillard and Yoccoz 2003; Toïgo and Gaillard 2003; Lemaître et al. 2015; Berta et al. 2018). Although several factors can affect the evolutionary underpinnings of life-history traits, ancestral traits can be maintained through several recent nodes of a phylogeny from phylogenetic inertia (Pagel 1999). Studying the variation in life-history traits of species within a monophyletic group can provide a unique opportunity to illustrate ecological and evolutionary characteristics related to this variation (Martin 1996; Balasubramaniam and Rotenberry 2016; Arlettaz et al. 2017). Focusing only on species of a monophyletic group can capture important ecological details because it is easier to control for phylogenetic effects when studying closely related species (Lanyon 1994). However, few studies have investigated the connection between various life-history strategies and survival rates in monophyletic groups, especially in long-lived vertebrates (Sacher 1978; Young and Keith 2011), and the relationships among life-history traits seem to be better understood in females than males (Festa-Bianchet 2012).

Sexual selection for precopulatory or postcopulatory traits can indirectly affect survival rates in males. Theoretically, males would maximize their reproductive output by reproducing early, often, and for several years, but strong competition for mating

opportunities often constrains male life histories, especially in species with polygynous mating systems (Mysterud *et al.*, 2003; Festa-Bianchet, 2012). Male-male competition for mating opportunities can lead to sexual selection for precopulatory, postcopulatory or both precopulatory and postcopulatory traits (Emlen & Oring, 1977). As both precopulatory and postcopulatory traits require energy investment (Dewsbury, 1982), they can impose a survival-reproduction tradeoff (Stevenson & Bancroft, 1995; McElligott *et al.*, 2002).

Greater selection for longevity is expected to occur when traits are differentially expressed at sexual maturity and social maturity – defined here as the mean age at which males begin to successfully engage in reproductive activity and/or sire offspring (Bonduriansky *et al.*, 2008). For example, longevity might be favored in Cape fur seals (*Arctocephalus pusillus*) and polar bears (*Ursus maritimus*) because the baculum undergoes a growth spurt at sexual maturity and again at social maturity (Oosthuizen & Miller, 2000; Dyck *et al.*, 2004). Similarly, Stewart et al. (2000) reported that moose (*Alces alces*) invest less in antler growth at younger ages compared to fully mature moose. However, an increase in reproductive trait expression with older ages might not favor selection for longevity in populations with a high degree of polygyny because a few high-quality males can potentially fertilize all reproductively active females in a population (Le Boeuf, 1974; Clinton & Le Boeuf, 1993; Graves, 2007; Bergeron *et al.*, 2008). Therefore, populations with extreme polygyny might not experience high average survival rates for juveniles and young adults relative to populations with lesser degrees of polygyny.

The power of basic science lies in the comparison of similar empirical studies, and the comparative method is useful for contextualizing broad hypotheses and identifying patterns (Stearns, 1983; Adams, 2008; Freckleton, 2009). Ecological and evolutionary meta-analyses make several assumptions about data mined from empirical studies, such as independence of data, incomplete data reporting, comparability of data across studies, that data availability across a taxonomic group are representative of the taxonomic group, and that available data are representative of a population (Gurevitch & Hedges, 1999; Pagel, 1999; Adams, 2008; Freckleton, 2009; Nakagawa *et al.*, 2017; Noble *et al.*, 2017). Comparative analyses are similar to meta-analyses but do not adhere to the requirement of comparing effect sizes of a variable across studies (Felsenstein, 1985; Vetter *et al.*, 2013; Koricheva & Gurevitch, 2014), and, as such, comparative studies rely more heavily on the assumption that available data are generalizable for an entire species. Additionally, they often assume that values gleaned from empirical studies are known without measurement error (Ives *et al.*, 2007). Incorporating variances, and/or standard errors can better reflect this source of uncertainty in comparative data, and hierarchical models or models that incorporate phylogeny (when non-independence issues are caused by species relatedness) can address issues of non-independence (Freckleton *et al.*, 2002; Adams, 2008; Nakagawa *et al.*, 2017). Further, ecologists have recently started incorporating measurement error (Hansen & Bartoszek, 2012) and phylogenetic uncertainty (de Villemereuil *et al.*, 2012) into comparative studies.

Comparative studies investigating tradeoffs between age- or stage-specific survival rates and reproductive traits in male mammals are not common in the literature. Because it is challenging to obtain sex- and age-specific survival data in long-lived vertebrate species (Lebreton *et al.*, 1992; Hupman *et al.*, 2018; Kanive *et al.*, 2019), empirical data on survival rates for multiple species in a monophyletic group are limited. For groups with adequate data, information is also needed on measurement errors in life-history traits and evolutionary pathways so that uncertainties in these measurements are incorporated into the comparative analyses (Ives *et al.*, 2007; de Villemereuil *et al.*, 2012; Revell & Reynolds, 2012). Most comparative studies investigating reproductive life-history trait tradeoffs do not include both precopulatory and postcopulatory traits (Festa-Bianchet, 2012; Lemaître & Gaillard, 2012; Dines *et al.*, 2015).

The suborder and monophyletic group, Pinnipedia, serves as an interesting taxonomic group to investigate various relationships between age-specific survival and reproductive traits. Pinniped species have a cosmopolitan distribution, represent a wide range of polygynous mating strategies, and exhibit diverse sexual selection in the form of body size (Stirling, 1983; Le Boeuf, 1991; Ferguson & Higdon, 2006; Krüger *et al.*, 2014). Furthermore, Fitzpatrick et al. (2012) recently found that pinniped species tend to invest either in body mass, a precopulatory trait, or testes mass and baculum length, postcopulatory traits. We initially, set out to ask the following research questions about pinnipeds, 1) how does investment in precopulatory traits relate to survival rates of yearlings and survival rates at the ages of sexual and social maturity? 2) how does investment in postcopulatory traits relate to survival rates of yearlings and survival rates

at the ages of sexual and social maturity? 3) how does the age at social maturity relate to survival rates of yearlings and at the ages of sexual and social maturity? 4) how does body length relate to survival rates of yearlings and at the ages of sexual and social maturity? and 5) how do the relationships between the life-history traits mentioned in questions 1 – 4 compare with each other? However, our literature search revealed that survival rate data for male pinnipeds were only available for 13 species. Therefore, we used available data for age-specific survival rates for males of pinniped species to provide an organized compilation of life-history trait data for male pinniped species, preliminarily investigate questions 1 – 4 about male pinnipeds using a graphical approach, and lay the foundation for more intricate quantitative analysis for when survival rate data become available for additional species. Additionally, we highlight the importance of high-quality empirical trait data for comparative studies in evolutionary ecology.

Methods

Life-History Traits Considered

We set out to identify possible life-history-trait tradeoffs and describe the diversity of life-history strategies in male pinniped species by investigating the relationships between survival rates and the following life-history characteristics. In the following sub-sections, we provide the biological motivation for the traits we analyzed.

Body Size Both body mass and length vary greatly across pinniped species and do not necessarily reflect reproductive investment. In mammalian species, body mass can

fluctuate to a great extent throughout the year, among years, with age, and among individuals of a species (Gaillard et al. 2003). Additionally, blubber concentrations can vary with season in pinnipeds (McLaren 1993), and body mass metrics for all pinniped species are not prevalent enough for standardization to account for the variation associated with season, year, age, and individual. For these reasons, comparing body mass among pinniped species is inappropriate, but comparisons of body length can be informative (McLaren 1993). Body mass typically serves as a useful indicator for the slow – fast life-history continuum because larger body sizes tend to correlate with longer lifespans and higher survival rates (Promislow and Harvey 1990; Gaillard et al. 2003), and achieving larger bodies can prove useful when living off of energy reserves when fasting during the mating season (Bartholomew 1970; Le Boeuf 1991). However, acquiring and maintaining energy sufficient for large bodies can become challenging in times of limited resources (Toïgo and Gaillard 2003).

Mating System and male-male contest behavior We considered mating system and male-male contest behavior as a proxy for precopulatory traits. Pinniped species demonstrate a diversity of mating strategies, but most species participate in some degree of polygyny. The range in the degree of polygyny across pinniped species exceeds that for most other taxonomic groups of birds or mammals and extends from a single mate during the breeding season to harems reaching as many as 100 females per male (Bartholomew 1970; Stirling 1983; Promislow 1992; Liker and Székely 2005; Bleu et al. 2016). A high degree of male-male competition that accompanies extreme polygyny often results in lower longevity relative to species with lesser degrees of polygyny or

monogamy (Clutton-Brock and Isvaran 2007; Tidière et al. 2015). However, Gaillard et al. (2003) found that the ratio of male mortalities to female mortalities was higher for populations with weak polygyny than strong polygyny in ungulates, which suggests that a high degree of polygyny is not a prerequisite substantial tradeoff for survival. Intense male-male contest behavior can also correlate with delayed social maturity (e.g., Clinton and Le Boeuf 1993). An important correlate of survival rate across mammal species is age at maturity (Promislow and Harvey 1990), and species that mature at older ages might have higher juvenile survival rates and greater longevity than species that mature at younger ages.

Sperm Competition We evaluated baculum length as a proxy for sperm competition. Baculum length has been found to vary independently of body length (Ramm 2007). A larger baculum likely evolved to facilitate sperm competition in response to females mating with multiple males in a single breeding season (Miller et al. 2000). However, baculum size also correlates with the copulation environment (terrestrial with dry bodies or aquatic or ice with wet bodies, Scheffer and Kenyon 1963), and logistical properties for successful copulation might have also helped drive selection for baculum size. Given that females choose the frequency with which they mate, males with sperm that can move through the female reproductive tract with greater efficiency would have an advantage (Parker et al. 2012). The size and shape of the baculum in pinnipeds is also likely important for stimulating the female reproductive tract (Miller et al. 1998), which can add further selection pressure for a larger baculum.

As allocation of energy to sperm competition decreases the available energy for both precopulatory trait investment (e.g., large body size, weaponry) and somatic maintenance, greater investment in sperm competition might come with reduced investment in precopulatory traits and/or a cost to survival (Parker et al. 2012). Investing in both precopulatory and postcopulatory traits can increase the reproductive competitiveness of males in species that do not monopolize access to females, but exclusive investment in precopulatory traits in lieu of postcopulatory investment seems common for species in which males can restrict their competitor's access to females (Lüpold et al. 2014). Pinnipeds illustrate this pattern in that species that form harems have smaller bacula than species that do not form harems (Fitzpatrick et al. 2012).

Data Collection

In an effort to obtain life-history trait estimates for our comparative analysis that best represent each pinniped species as a whole, we employed the following selection criteria. We acknowledge that our decisions and the availability of information largely restrict our scope of inference to published literature that made it into our analysis, and we re-visit this important limitation in the Discussion section.

Selection criteria

To find peer-reviewed published studies (published up through June 2019) that provided age-specific survival rate data, we searched the Google Scholar database using the common and Latin names for each pinniped species and any and all combinations of the following search terms – "survival", "survival rate", "Cormack-Jolly-Seber", "mark-recapture", "capture-recapture", and "mortality." We used Google Scholar to maximize

our opportunity to find usable studies, as it tends to return more results than other databases, such as Web of Science. We included survival data from all pinniped species for which we found reported survival or mortality data from non-lethal methods for at least one of the following stages: yearling (i.e., the survival interval between 1 year of age and 2 years of age), age at sexual maturity, age at social maturity (Table 1). Studies varied in duration, models used to estimate survival (i.e., model type and its included covariates), methods of marking individuals, and sample size. For studies using tagging techniques, many accounted for possible tag loss, but not all studies reported this adjustment to survival rate estimates. We limited our data to only studies that also included an uncertainty estimate associated with the estimated age- and sex-specific survival rates (e.g., standard error or confidence interval) to allow us to reflect uncertainty in our analysis.

For each species, we also searched the literature for species-specific information on body size, age at sexual maturity and at social maturity, type of male-male contest, baculum length, and specific type of mating system (Table 1). For most species, data for each of the life-history traits were compiled from different populations (i.e., from different studies), but data for multiple life-history traits from the same population (study) were used whenever possible. We summarized quantitative life-history traits using averages and by sex when appropriate, including an associated uncertainty measurement (e.g., a standard error for an average) when possible. Mating system was determined by the estimated total offspring sired by the most competitive males in a single breeding season. Following the guidelines of Le Boeuf (1991), we defined mild

polygyny as males siring 2-5 offspring per breeding season, moderate polygyny as males siring 6-15 offspring per breeding season, and extreme polygyny with males siring 16 or more offspring per breeding season. If available evidence suggested that a male mated with no more than a single female in a breeding season, we labeled the species as reproducing by seasonal monogamy. Baculum size data were often limited to very small sample sizes. Although not all baculum measurements were from animals of the same age, we only included baculum size from adult animals. When age was reported, we selected a baculum size from the age at social maturity.

We categorized our data collection into two main tiers of age-specific annual survival rates based on available information for each species. The first tier, species for which we have the most complete data, included age-specific survival with associated measurement error from all ages throughout the known life span for each species from a single population. Some studies grouped multiple ages (e.g., 1 year of age, 2-3 years of age, 3-7 years of age), and we used these age groupings as our second tier of sex- and age-specific data collection. Depending on available survival data for each age, species were included in the analyses of survival rates for the following ages: yearling, age at sexual maturity, and/or age at social maturity. When multiple papers reported survival rates for the same species, we selected papers that presented age-specific results with the smallest age ranges (e.g., a paper with survival rate data for "2 to 3 and 4 to 7 years of age" was used instead of one with survival rate data for "adults ≥ 3 years of age"). Given that survival rate estimates for some species included in our analyses were not specific to a single age but were estimated from an age range that included either the age at sexual

maturity or the age at social maturity (tier 2 species), we assume that the survival rate estimated for the age range that includes sexual or social maturity is representative of the single age at sexual or social maturity. If multiple papers presented age-specific survival rate data for each age, we selected the study that provided the most complete methods (e.g., accounting for individual heterogeneity). We used this method to maximize the comparability and generalizability of empirical data for our comparative analysis. For one of the second-tier species (*Arctocephalus tropicalis*, age at sexual maturity), the authors reported that there was no significant difference in annual survival rates between males and females and presented survival rates from male and female grouped data.

After our literature search, we only had survival rate data for 8 species at 2 years of age (yearling), 11 species at the age of sexual maturity, and 12 species at the age of social maturity. However, our full model to identify life-history trait tradeoffs and evaluate the relationships between survival rates and other life-history traits was to include 6 parameters – reducing the sample size within mating system to 4 species at most (because mating system is a categorical variable). Given this limitation, we limit our analysis to graphical techniques to evaluate how the age at social maturity and investment in precopulatory or postcopulatory traits relate to survival rates of yearlings and at the ages of sexual and social maturity. We follow our graphical analyses by presenting a method that could address these questions of interest and provides an approach that could be adjusted for use with other comparative studies. Specifically, we present a Bayesian phylogenetic generalized least squares (BPGLS) model that addresses non-independence of species and phylogenetic uncertainty, incorporates uncertainties in

point estimates from separate studies, and provides a framework for future analyses if data for more species were available.

Graphical analyses

We began by plotting the age-specific survival rates for all species with survival rate data for all ages. To gain insight about the relationships between stage-specific survival rates and other life-history traits of interest, we also plotted the reported life-history trait data we obtained from our literature search against the log-odds of survival. We present the relationship between mating system and the log-odds of survival from our graphical analysis because this life-history trait seemed to vary the most with survival rates.

BPGLS model for future work with example

We used R Statistical Software version 3.5 (R Core Team 2018) for all of our analyses. To provide a framework for investigating the relationships between stage-specific survival rates and other life-history traits in future work and other comparative studies, we present a phylogenetically controlled linear regression model in a Bayesian framework that can be written in the JAGS language (Plummer, 2003). We executed the BPGLS model using the packages `rjags` (Plummer *et al.*, 2016) and `runjags` (Denwood & Plummer, 2016). Our BPGLS model incorporates one source of uncertainty in survival estimates (i.e., standard error) with male survival rates at the age at social maturity (n = 12) as the response variable and standard body length as a covariate. We first inspected a plot of the relationship between standard lengths of our 12 species and

their respective log-odds of survival at the age of social maturity to assess a reasonable functional form (e.g., approximately linear).

Incorporating measurement error in comparative phylogenetic analyses is rare even though it can yield better parameter estimates and better detect phylogenetic signal (Ives *et al.*, 2007). We adjusted the methodology presented by de Villemereuil *et al.* (2012) to include measurement error in survival rates when standard errors are only reported on the probability scale (i.e., SE on the logit scale was unavailable), and there is only one observation representing each species. Specifically, we used the beta distribution parameterized for regression (Ferrari & Cribari-Neto, 2004) to assume the observed survival rate for a particular species was a random variable with a beta distribution with mean equal to the true (unknown) survival probability and standard deviation close to the estimated standard error for that species. That is, the data were used to help specify the one unknown parameter in the species-specific prior distribution for the observed survival rate, where the mean is assumed to be the true survival probability. We assumed classical additive Berkson measurement error (Berkson, 1950) for average standard body length and used a normal distribution for the general species-wide standard body length estimate. Specifically, the estimated/observed average standard body length for a species was assumed to be a normal random variable with mean equal to true standard body length for that species and standard deviation equal to the standard error that came from the empirical study estimating standard body length for that species.

To specify the model, let Y_i be the true logit-transformed overall survival rate for species i ($i = 1,2,\ldots,n_i$ and n_i is the number of species in the j^{th} stage, j = yearling, sexual maturity, social maturity), Wi be the *observed* average standard body length, and X_i be the true average standard body length of species i. Then, the logit-linear regression model can be written as $Y_{n_j \times 1} \sim \mathcal{MVN}_{n_j \times 1}\left(\alpha + \beta X_{n_j \times 1}, \sigma_\epsilon^2 \Sigma_k\right)$, where Σ_κ is the $n_j \times n_j$ scaled variance-covariance matrix (or correlation matrix) calculated from the kth ($k = 1,2,\ldots,100$) phylogenetic tree as described by de Villemereuil *et al.* (2012), and a uniform categorical prior was used to provide equal prior probability to each candidate correlation matrix Σ_κ. Weakly-informative Normal(0, 0.1) priors were used on the partial regression coefficients (α and β) to constrain the estimates within a reasonable range on the logit-scale (i.e., between -10, 10), and a vague gamma (1, 1) prior was used for the residual precision, σ_ϵ^{-2}. The Berkson measurement error on the average body lengths was incorporated assuming $W_i|X_i \sim N(X_i, \sigma_{ui}^2)$ and that the true average species lengths can be assumed to have come from a normal population distribution (i.e., assumes exchangeability), $X \sim \mathcal{MVN}_{n_j}(\mu_x, \sigma_x \Sigma_k)$, with a uniform prior on the population mean between 100 and 700, $\mu_x \sim Uniform(100, 700)$; correlation structure equal to that specified by the phylogenetic tree, Σ_κ; and a vague prior on the common variance $\sigma_x^{-2} \sim gamma(1, 1)$. We selected the prior for the standard length based on the mean standard lengths observed across species; the shortest species in our dataset was 144 cm, and the longest species was 540 cm. As such, we deem standard body lengths shorter than 100 cm or longer than 700 cm to be very unlikely. We chose a uniform prior because this distribution made biological sense and would restricts the MCMC sampling

to only reasonable values for our specific variable of standard length. For future use of our BPGLS model, researchers should select the distribution that best fits their covariates with regard to the question they are investigating. For our study, the joint distribution for the average standard body length might be improved by setting each species to its own prior with an appropriate distribution to match standard body lengths specific to that species and allowing each species to have its own posterior distribution that would better reflect the variation present in each species rather than including the variation across species. However, the standard body lengths of the different pinniped species might be related from phylogenetic inertia, which could influence the range of standard body lengths found across individuals for each species, with all pinniped species potentially coming from a common distribution. Measuring the phylogenetic influence of standard body length can help elucidate the potential of the standard body lengths of pinnipeds coming from a common distribution by ruling out the possibility if there is no phylogenetic influence on standard body length. The measurement-error variance for the i^{th} species (σ_{ui}^2) must be provided as data (or could be estimated from the data if more than one observation per species is taken into account), and it was assumed to be equal to the squared standard error estimate for species *i*.

Measurement error information was not available for the logit survival rates. It was induced on the probability scale by letting $p_i = logit^{-1}(Y_i)$, and assuming $D_i \sim \text{Beta}(p_i\phi_i, p_i(1 - p_i)\ \phi_i)$. That is, we let p_i be the true, unknown survival rate for species *i* and specify ϕ_i, a function of the typical Beta distribution parameters ($\phi_i = \alpha_i + \beta_i$), where α and β were set to reflect a Beta(α_i, β_i) distribution with mean and standard

deviation similar to the observed survival rates and standard errors for species *i* (see Supplement S1 for details and model code).

We constructed phylogenetic trees for the species we included in our analyses and incorporated uncertainty in branch lengths (de Villemereuil *et al.*, 2012) to account for any lack of independence in life-history traits from shared ancestry (Felsenstein, 1985; Adams, 2008; Chamberlain *et al.*, 2012). Nucleotide sequences were retrieved from the NCBI nucleotide database using the `rentrez` package for R version 3.6 (R core Team 2019). Up to, but no more than, the first 50 records for each of the 33 mitochondrial genes for each pinniped species in the BPGLS model were retrieved. Species representation within each gene varied between 0 and 50 individual records (Table S1). Sequences were aligned with ClustalW using the `msa` package for R (Bodenhofer *et al.*, 2015), and the most likely nucleotide substitution model for each gene was determined with the *modelTest* function of the `phangorn` package (Schliep, 2011). Internal and terminal gaps were both represented with a dashed line. Phylogenetic species supertrees were generated using the *BEAST method (Heled & Drummond, 2010). Briefly, BEAUti version 2.6.1 was used to create input files for all genes and species where nucleotide substitution models were assigned for each gene according to the *modelTest* output. An estimated random local clock was set as the evolutionary rate prior for all genes, and an estimated Yule model was used as the tree prior. Species for which there were no representative sequences for a gene were simply entered in the alignment series as "N" ambiguities to satisfy the requirements of the BEAST program. BEAST version 2.6.1 was used to create two Markov Chain Monte Carlo (MCMC) chains sampled every

1×10^4 generations for 1.74×10^8 generations. Convergence and chain diagnostics were visualized and assessed with the `rwty` package (Warren *et al.*, 2017). The average standard deviation of split frequencies was 0.003 (95% CI = 0.000, 0.020). Using the *vcv* function of the `ape` package (Paradis & Schliep, 2019), variance-covariance matrices were generated from the last 1000 trees sampled from the posterior distribution of each of the two MCMC runs. The pseudo estimated sample size (pseudo-ESS, Lanfear *et al.*, 2016) of the tree topology from these 1000 trees was 176 (95% CI = 138, 340), and we selected 100 random trees from this sample to reduce computational demands. Using at least 100 trees with associated uncertainty estimates can provide regression parameter estimates for life-history trait models with greater precision as well as reduce the frequency of making a Type I error (de Villemereuil *et al.*, 2012).

For our BPGLS example, we incorporated the phylogenetic information into the BPGLS model by using a known variance-covariance structure for the survival probabilities and standard body length by assuming it is equal to the corresponding particular phylogenetic tree. To incorporate uncertainty in the tree, we allowed the sampler to explore multiple trees (each with equal prior probability of being the "true tree", i.e., we introduced a discrete uniform prior on Σ_κ with probability 1/100). We adjusted for phylogenetic influence of standard body length by incorporating Pagel's λ; a λ value of 0 indicates phylogenetic independence, and a λ value of 1 indicates strong phylogenetic dependence assuming Brownian motion (Pagel, 1999; Freckleton *et al.*, 2002). We specified an uninformative uniform prior on λ.

We ran an MCMC with 3 chains, a burn-in of 10,000 iterations, and retained every 5th sample to reduce computational demands for a final sample of 300,000 MCMC iterations used to fit the model. We inspected MCMC convergence using the coda package (Plummer et al. 2006) and ggmcmc package (Fernández-i-Marín 2016) to observe Geweke convergence diagnostics (Geweke 1991), trace plots, and calculate the Gelman-Rubin statistic ($\widehat{R}$, Gelman and Rubin 1992) for each monitored parameter. To assess the goodness of fit for our model, we created residual plots and plots to compare the observed data values and values predicted from the models (Conn *et al.*, 2018). Additional goodness-of-fit testing can be performed following the guidelines by de Villemereuil *et al.*, 2012. We present 90% credible intervals for all analyses we conducted (90% CrI). When describing reported data from empirical studies we present 95% confidence/credible intervals for survival rates provided by the empirical studies, as they provided 95% confidence/credible intervals but not enough essential information to transform these values to 90% confidence/credible intervals.

Results

Summary of survival rate data

We were able to compile survival data for 13 species (Table 1) and additional life-history trait data for 23 species (Table 1). We found complete age-specific male survival data for five species (first tier, see Methods) and data for an additional eight species for which some ages were combined (second tier). Similar to many other life-history traits, survival rates of male pinnipeds vary substantially across species. Of the five species with full age-specific male survival estimates, peak survival rates ranged from 0.72 (95%

CI = 0.45, 0.95) for northern elephant seals to 0.94 (95% CI = 0.92, 0.96) for Weddell seals (Figure 1). However, the age at which peak survival rates were reached varied considerably among species, and uncertainty associated with age-specific estimates also varied among species.

Relationships between life-history traits

Our results provide modest support for the hypothesis that investment in precopulatory traits imposes a survival tradeoff. Our graphical analyses indicated that mating system might be related to survival rates for yearlings and at the ages of sexual and social maturity (Figure 2). Pinniped species with the most extreme forms of polygyny had lower survival rates at the ages of sexual and social maturity than did species that exhibit a lesser degree of polygyny (Figure 2). However, we were unable to visually detect a pattern between baculum length and stage-specific survival rates (Figure S2).

BPGLS model example with
standard body length data

Visual inspection of model diagnostics revealed abundant mixing of chains and all $\hat{R}$ values lower than 1.1, which indicated model convergence. Our goodness of fit testing demonstrated the lack of statistical power with small sample sizes in that uncertainty associated with point estimates was large. However, the goodness of fit testing also suggested that our models would perform adequately with larger sample sizes to shrink the uncertainty associated with point estimates (Figure S3, S4).

In the results of our BPGLS, the 90% CrI for the coefficient associated with standard body length overlapped zero (mean = -0.83, 90% CrI = -2.36, 0.73), which provides further evidence of the necessity to increase the number of species with male survival rate data. Additionally, we observed large uncertainty in the posterior for λ (mean = 0.92, 90% CrI = 0.80, 0.99), which is to be expected with a sample size of fewer than 20 species (Münkemüller *et al.*, 2013) and can influence the relationship between covariates analyzed and the response variable (Chamberlain *et al.*, 2012).

Discussion

Comparative analyses provide an opportunity to make higher-order conclusions than afforded by the empirical studies upon which they are based (Arnqvist & Wooster, 1995), but they require assumptions that can be unrealistic. For example, comparable data for multiple characteristics of species and that represent a taxonomic group of species can be difficult to acquire (Freckleton, 2009; Gerstner *et al.*, 2017). Additionally, narrowing the scope of inference to a single monophyletic group can reduce sample size. This study underscores the paucity of data on male survival rates for many pinniped species and the importance of high-quality and long-term data collection for survival rates. To gain better insight of the mechanisms related to variation in male survival rates among pinniped species, we explored possible connections between survival rates and body size, baculum size, delayed maturity, and mating system. Age- and stage-specific survival rates of male pinnipeds varied widely across species. Mating system appears to be related to inter-specific variation in annual survival rates of male pinnipeds for each stage. Mating system served as a proxy for various precopulatory traits, such as sexual

size dimorphism and aggressive behavior. However, our graphical analyses did not reveal any visual evidence of a relationship between stage-specific survival rates and baculum length, a postcopulatory trait. As such, we recommend further investigation into the relationships between survival rates and precopulatory and postcopulatory traits.

For nearly all species evaluated, the survival rate at the age of sexual (n = 7) and social maturity (n = 8) exceeded the survival rate for yearlings. However, yearlings had higher survival rate estimates than adults reaching sexual or social maturity in southern elephant seals, a species that engages in extreme polygyny. Pistorius *et al.* (1999) suggested that the relatively low male adult survival rate for male southern elephant seals might be the result of stress from male-male contests and the inability of males to meet increased nutritional demands coincident with the breeding season and growth spurts following sexual maturity.

Although baculum length can be a useful proxy for sperm competition (Ferguson *et al.*, 1996) and can vary greatly across species (Scheffer & Kenyon, 1963), this life-history trait needs further study in pinnipeds. Males of pinniped species that invest in the precopulatory traits of large body mass and holding harems tend to not invest in the postcopulatory trait of baculum length (Fitzpatrick *et al.*, 2012). However, our data collection revealed the scarcity of quality data for baculum length in many pinniped species. Although some studies reported values and associated variance of baculum length for a population (Miller *et al.*, 1998, 2000; Oosthuizen & Miller, 2000), other studies present a single value believed to be representative of a "typical full-grown baculum of a typical full-grown male body" and did not provide any associated variation

with presented values (Scheffer & Kenyon, 1963). Finally, it is possible that the lack of a difference in baculum length among mating systems could indicate that a larger baculum facilitates copulation for reasons other than sperm competition, such as maintaining a lock-and-key mechanism for aquatic copulations (Scheffer & Kenyon, 1963).

High-quality survival data for many long-lived vertebrate species are absent because many logistical and temporal challenges often accompany the collection of survival data for these species (Hiby & Mullen, 1980; Lebreton *et al.*, 1992, 1993; Gaillard *et al.*, 1993). Wickens and York (1997) initially brought this issue to attention for pinniped species, specifically for fur seals, and recent studies focusing on survival rates in pinnipeds have emerged. To increase the abundance of high-quality data for comparative studies of survival rates in pinniped species, data from live animals, such as mark-recapture or telemetry methods, are necessary (Loison et al. 1999). There is high potential for increasing the number of demographic studies on additional pinniped species because their amphibious behavior, annual reproductive pulse found in most species, and predictable aggregation patterns facilitate mark-recapture techniques.

Male pinnipeds exhibit diverse life-history strategies and appear to experience survival tradeoffs from investing in precopulatory but not necessarily postcopulatory traits. Our results from graphical analysis suggest that mating system, in particular, was related to survival rates for adult pinnipeds. However, age-specific male survival data for several more pinniped species would enable us to fully explore the relationships between age- or stage-specific survival rates in pinnipeds, particularly with the BPGLS method we presented. We exemplify the importance and relative ease of incorporating uncertainty

into a comparative analysis using a BPGLS model when empirical data are presented with estimates of uncertainty. Our comparative study illustrates the importance of high-quality survival estimates, and advances in quantitative population biology have provided avenues for acquiring these estimates (Clutton-Brock & Sheldon, 2010). We provide a foundation for understanding the complexities of the relationships between survival rates and other life-history traits in male pinnipeds. Although graphical analyses revealed some information about life-history strategies in male pinnipeds, a more formal analysis with additional species would provide more concrete answers to our research questions posed in the Introduction. Therefore, we presented a BPGLS model that would better address these questions for pinnipeds or other taxa in future studies.

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Tables and Figures

Table 1. Male survival rates and other life-history traits of pinniped species. Male-specific survival data from live, free-ranging animals were available for 13 pinniped species (a). Survival rates are provided for as many ages of each species as were made available from studies with empirical data for annual survival rates. Covariates reported here are in addition to age and time that were used in the presented estimated survival rates. Additional life-history trait data are presented for 23 pinniped species (b). The standard length of a species indicates the mean or asymptotic length of an adult. All estimates of life-history traits are single estimates from one representative publication for the species; in many cases, the information was only available from a single publication. In instances when multiple studies were found that provided information about the same life-history trait, the study that met all model assumptions and had the greatest sample size was selected. Standard errors/standard deviations and sample sizes are presented when available.

(a)

Species	Latitude and Location Name	Ages measured (years of age)	Time Period	Survival Rate (SE, 95% confidence interval) *N* *Modeling method (closed or open population assumed) and covariates included*	References
Gray seal *Halichoerus grypus*	Sable Island, 43.93°[2]	5-16	1969-1994	Sexual maturity: 0.98 (0.003, 35) Social maturity: 0.98 (0.003, 2,765) N_{sexual} = 18, N_{social} = 48 *Jolly-Seber (open)l, cohort*	Manske *et al.* 2002
Harbor seal *Phoca vitulina*	Tugidak Island, 56.48°[1]; Moray Firth, 58.64°[2]	1, 2-3, 4-7	2006-2011	Yearling: 0.78 (0.03, 0.71 – 0.84) Sexual maturity: 0.88 (0.03, 0.78 – 0.94) Social maturity: 0.88 (0.03, 0.78 – 0.94) $N_{marked\ as\ pups}$ = 181 *Cormack-Jolly-Seber (closed)*	Hastings *et al*. 2012

Weddell seal *Leptonychotes weddellii*	Erebus Bay, -77.7°	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28	1980-2015	Yearling: 0.60 (0.03, 0.51 – 0.75) Sexual maturity: 0.94 (0.02, 0.92 – 0.96) Social maturity: 0.93 (0.02, 0.91 – 0.94) $N_{yearling}$ = 106, N_{sexual} = 101, N_{social} = 102 *Hierarchical model extensions of Cormack-Jolly-Seber in a Bayesian framework (closed), individual heterogeneity*	Brusa *et al.*, 2020
Southern elephant seal *Mirounga leonina*	Marion Island, -46.91°	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	1983-1997	Yearling: 0.75 (0.051) Sexual maturity: 0.74 (0.062) Social maturity: 0.65 (0.128) $N_{marked\ as\ pups}$ = 3,695 (assuming 50% sex ratio of marked individuals) *Cormack-Jolly-Seber (closed)*	Pistorius *et al*. 1999
Northern elephant seal *Mirounga angustirostris*	Año Nuevo State Park, Santa Cruz, California, USA 37.11°	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15	1985-2008	Yearling: 0.68 (0.62 – 0.74) Sexual maturity: 0.68 (0.62 – 0.75) Social maturity: 0.69 (0.53 – 0.82) $N_{yearling}$ = 84, N_{sexual} = 17, N_{social} = 4 *Model extensions of Cormack-Jolly-Seber in a Bayesian framework (closed)*	Condit *et al.* 2014
Mediterranean monk seal *Monachus monachus*	Cabo Blanco, Mauritania-Morocco, 20.93°	4+	2004-2007	Social maturity: 0.87 (0.81 – 0.94) N_{social} = 57 *Jolly-Seber (open)*	Martinez-Jauregui *et al*. 2012
Hawaiian monk seal *Monachus schauinslandi*	French Frigate Shoals, 23.75°	1-2, 3-4, 5-17	1984-2003	Yearling: 0.56 (0.06, 0.43 – 0.68)[§] Sexual maturity: 0.72 (0.09, 0.65 – 0.80)[§] Social maturity: 0.89 (0.03, 0.83 – 0.93)[§] $N_{marked\ as\ pups}$ = 1,710 (assuming a 50% sex ratio of marked individuals) *Cormack-Jolly-Seber (closed)*	Baker & Thompson 2007

Steller sea lion *Eumetopias jubatus*	Forrester Island, 54.8°	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16	2001-2009	Yearling: 0.69 (0.02, 0.65 – 0.72) Sexual maturity: 0.80 (0.02, 0.76 – 0.83) Social maturity: 0.73 (0.03, 0.68 – 0.78) $N_{\text{marked as pups}}$ = 897 (assuming a 50% sex ratio of marked individuals) $N_{\text{territorial}}$ = 53 *Cormack-Jolly-Seber (closed), Multi-state (closed), natal rookery, cohort, territoriality*	Hastings *et al.* 2018
Australian sea lion *Neophoca cinerea*	Seal Bay, -35.98°	1.5-3, 3-14	1991-2002	Yearling: 0.88 (0.02, 0.83 – 0.92), Sexual maturity: 0.89 (0.03, 0.82 – 0.94) Social maturity: 0.89 (0.03, 0.82 – 0.94) $N_{\text{marked as pups}}$ = 209 *Cormack-Jolly-Seber (closed), cohort*	McIntosh *et al*. 2013
New Zealand sea lion *Phocarctos hookeri*	Sandy Bay, Enderby Island, -50.5°	1, 2, 3, 4-15	1989-2005	Yearling: 0.60 – 0.70, Sexual maturity: 0.98 (0.9 – 0.99) Social maturity (0.98 (0.9 – 0.99) $N_{\text{marked as pups}}$ = mean of 845 per year (assuming a 50% sex ratio of marked individuals) *Multi-state (closed), tag type*	Chilvers & MacKenzie 2010
California sea lion *Zalophus californianus*	San Miguel Island, 34.03°	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19	1987-2015	Yearling: 0.76 (0.71 – 0.80) Sexual maturity: 0.93 (0.91 – 0.94) Social maturity: 0.89 (0.89 – 0.87) N_{yearling} = 1,047, N_{sexual} = 613 *Burnham extension of Cormack-Jolly-Seber (closed), sea surface temperature, yearling weight, disease*	DeLong *et al*. 2017
New Zealand fur seal *Arctocephalus forsteri*	Cape Gantheaume, Kangaroo Island, -36.07°	7-15	1992-1998	Social maturity: 0.76 (0.66 – 0.82) N_{social} = 34 *Kaplan Meier estimate (closed), mass*	Troy *et al.* 1999

Subantarctic fur seal *Arctocephalus tropicalis*	Amsterdam Island, -37.9°	pup, 1-2, 3-5	1995-2004	Yearling: 0.61 Sexual maturity: 0.96 (0.02)* $N_{\text{marked as pups}}$ = 365 *Cormack-Jolly-Seber (closed), cohort*	Beauple *et al*. 2005

(b)

Species	Standard Length in cm (SE, *N*)	Baculum size at maturity in cm (SD, *N*)	Mating Strategy	Age at Sexual Maturity (years)	Age at Social Maturity (years)	References
Gray seal *Halichoerus grypus*	230.7 (3.65, *244*)	14.8 (2.36, *96*)	Mild polygyny, aquatic and terrestrial dominance hierarchies, female defense	5	6	Hewer 1964‡; McLaren 1993†; Hammill & Gosselin 1995‡; Twiss *et al*. 1998‡; Wilmer *et al.* 1999‡
Harbor seal *Phoca vitulina*	157.5 (1.42, *262*)	13.7	Mild polygyny, aquatic and terrestrial lekking, display behavior	6	6	Scheffer & Kenyon 1963‡; McLaren 1993†; *Coltman et al.* 1998‡; Boness *et al*. 2006‡; Hammill *et al*. 2010‡
Weddell seal *Leptonychotes weddellii*	239.7 (3.90, *38*)	19.8 (*1*)	Moderate polygyny, aquatic resource defense and display	3	5-11	Bartsh *et al*. 1992‡; McLaren 1993†; Gelatt 2001‡; Morejohn 2001‡; Harcourt *et al.*, 2007‡
Southern elephant seal *Mirounga leonina*	540.9 (38.8, *139*)	33.10	Extreme polygyny, terrestrial female defense	3	9-10	Laws 1956‡; Stirling 1983‡; McLaren 1993†; Galimberti *et al.* 2007‡
Northern elephant seal *Mirounga angustirostris*	448.6 (14.64, *162*)	27.4 (*1*)	Extreme polygyny, terrestrial female defense	5	9-10	Scheffer & Kenyon 1963‡; Le Boeuf 1974‡; Stirling 1983‡; McLaren 1993†

Mediterranean monk seal *Monachus monachus*	251.9 (11.1, *37*)	21.5	Mild polygyny, aquatic resource defense	4	7	Stirling 1983‡; Samaranch & González 2000†; Gucu *et al*. 2004‡; Pastor *et al*. 2011‡; Fitzpatrick *et al*. 2012‡; Murphy *et al*. 2012‡
Hawaiian monk seal *Monachus schauinslandi*	198.4 (2.30, *51*)	18.3 (*1*)	Seasonal monogamy, aquatic female defense	4	8-9	Kenyon & Rice 1959‡; Scheffer & Kenyon 1963‡; Stirling 1983‡; Reif *et al*. 2004†; Harting *et al*. 2007‡
Steller sea lion *Eumetopias jubatus*	310.2 (1.85, *101*)	18.1 (1.02, *22*)	Extreme polygyny, terrestrial resource defense	3	9-13	Pitcher & Calkins 1981‡; McLaren 1993†; Miller *et al*. 2000‡; Parker & Maniscalco 2014‡
Australian sea lion *Neophoca cinerea*	192.2 (0.25, *35*)	NA	Moderate polygyny, terrestrial female defense	3	3	McIntosh, 2007†; Higgins 1990‡; McIntosh 2007†
New Zealand sea lion *Phocarctos hookeri*	220 (1.7, *20*)	17.5 (2.59)	Moderate polygyny, terrestrial resource defense	4	7-9	Bartholomew 1970‡; McConkey *et al*. 2002†; Campbell *et al*. 2006‡; Robertson *et al*. 2006‡; Duignan & Jones 2007‡; Childerhouse *et al.* 2010†; Foote 2018‡
California sea lion *Zalophus californianus*	229.8 (4.4, *44*)	12.1	Mild polygyny, terrestrial resource defense	5	9-10	Scheffer & Kenyon 1963‡; Peterson & Bartholomew 1967‡; McLaren 1993†; Aurioles-Gamboa &

New Zealand fur seal *Arctocephalus forsteri*	144 (2.3, *39*)	9.6 (0.08, *2*)	Moderate polygyny, terrestrial resource defense	4	7	Zavala-González 1994‡; Flatz *et al*. 2012‡ Mattlin 1978‡; Carey 1991‡; Troy *et al*. 1999‡; Dickie & Dawson 2003†; Duignan & Jones 2007‡; McKenzie *et al.* 2007‡
Subantarctic fur seal *Arctocephalus tropicalis*	163.7 (5.8)	9.5 (*123*)	Mild polygyny, terrestrial female defense	4	8-9	Bester 1990‡; Bester & Jaarsveld 1994†
Harp seal, *Pagophilus groenlandicus*	172.2	17.4 (1.44, *706*)	Mild polygyny, aquatic social groups	4	4	Sergeant 1976‡; *Merdsoy et al.* 1978‡; Miller *et al*. 1998‡; Nordøy *et al.* 2008†
Leopard seal *Hydrurga leptonyx*	294 (19.0, *44*)	23.3 (*2*)	Mild polygyny, ice	4	4	Scheffer & Kenyon 1963‡; Stirling 1983‡; Rogers 2003‡; Rogers 2007‡; Gray *et al.* 2009†
Crabeater seal *Lobodon carcinophaga*	225.4 (1.39, *51*)	22.0 (*1*)	Seasonal Monogamy, defense of single female on ice	3	5	Scheffer & Kenyon 1963‡; Siniff *et al.* 1979‡; Bengtson & Siniff 1981‡; McLaren 1993†
South American sea lion *Otaria flavescens*	256.5 (*3*)	NA	Moderate polygyny, terrestrial resource defense	4	9	Campagna & Boeuf 1988‡; Rosas *et al.* 1993†; Grandi *et al.* 2010‡
Galapagos sea lion *Zalophus wollebaeki*	205	NA	Mild polygyny, semi-aquatic resource defense	4	5	Pörschmann *et al.* 2010‡; Trillmich *et al.* 2014†; Kalberer *et al*. 2018‡

Galapagos fur seal *Arctocephalus galapagoensis*	152	NA	Moderate polygyny, terrestrial resource defense	3	8-10	Trillmich 1984†; Trillmich 1987‡
Antarctic fur seal *Arctocephalus gazella*	212.2 (13.7, *78*)	11.3	Moderate polygyny, terrestrial resource defense	3	8	Bonner 1958‡; Rand 1967‡; Payne 1979‡; McLaren 1993†; Hoffman *et al*. 2003‡; Fitzpatrick *et al*. 2012‡
Cape fur seal *Arctocephalus pusillus*	220	12.0 (0.8, *20*)	Moderate polygyny, terrestrial female defense	3	9-10	Stirling 1983‡; Rand 1955‡; Oosthuizen & Miller 2000‡; Arnould & Warneke 2002†
Northern fur seal *Callorhinus ursinus*	189.3 (2.59, *291*)	13.0 (0.6, *4*)	Extreme polygyny, terrestrial female defense	3	7-10	Scheffer 1950‡; Bartholomew & Hoel 1953‡; Johnson 1968‡; York 1983‡; McLaren 1993†
Pacific walrus *Odobenus rosmarus*	310.1 (6.9, *168*)	NA	Moderate polygyny, terrestrial female defense	8	15	Fay 1982‡; McLaren 1993†; Sjare & Stirling 1996‡

*Survival estimates from pooled sexes, as no significant difference in survival was found between sexes

†Reference for standard length estimates, means from multiple populations provided for some species when available

‡Reference for mating strategy

§Age-specific estimates across all years of study were only presented in graphical format, and point estimate values were provided for each individual year of the study. We selected a year with point estimates that was representative of the average of estimates across all years that were presented in graphical format.

Figure 1. Age-specific male survival rates for 5 pinniped species. Error bars indicate either 95% confidence intervals or 95% credible intervals.

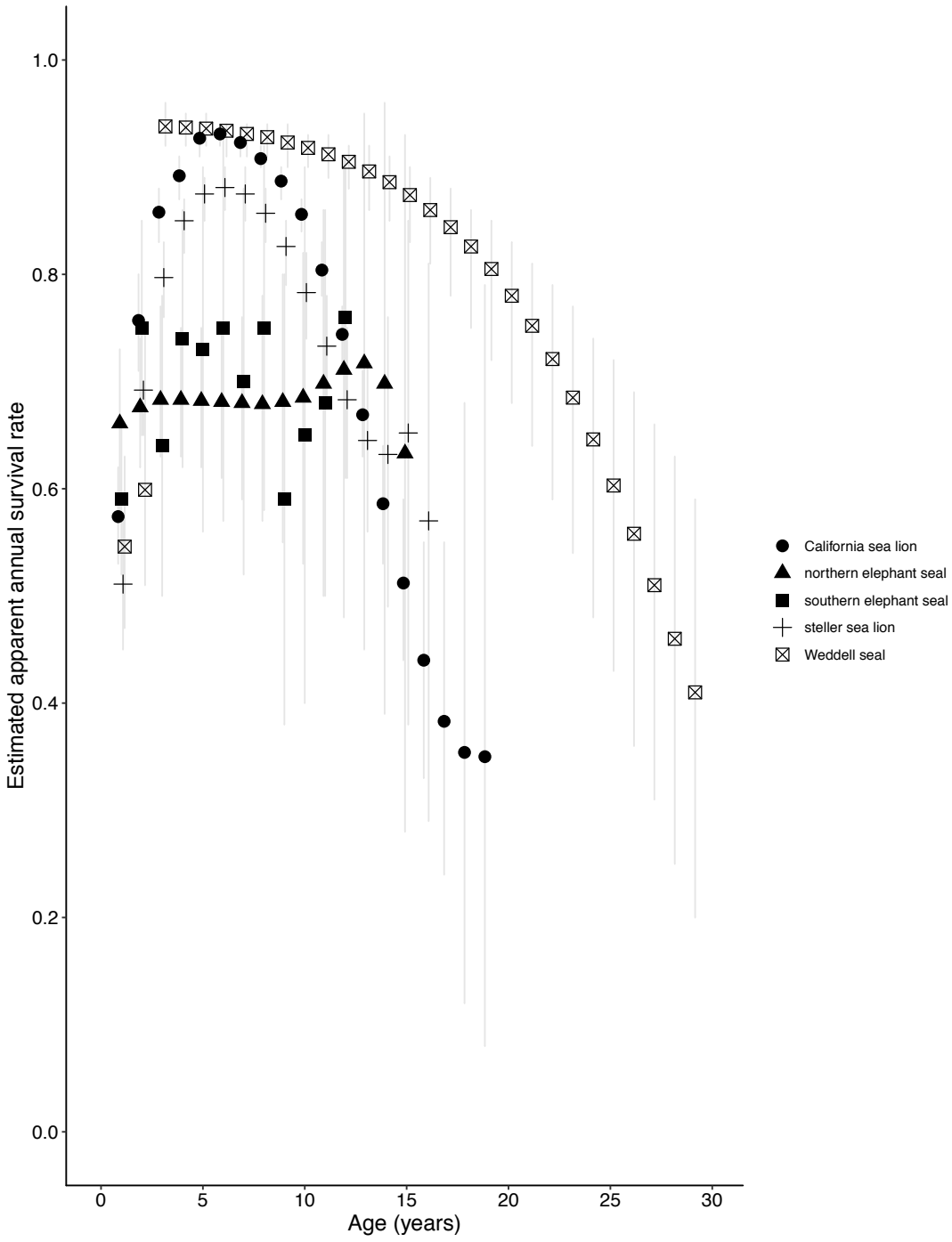
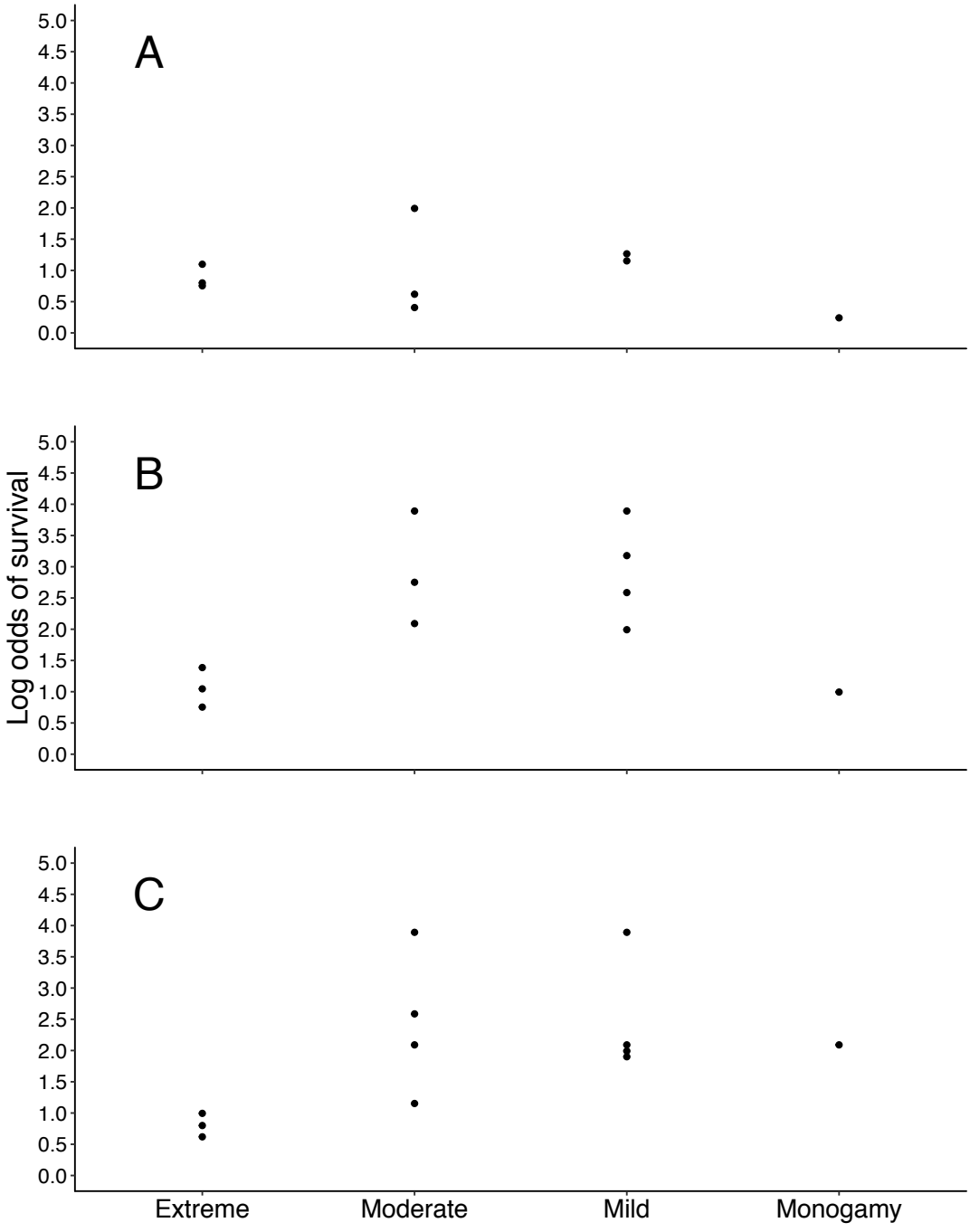


Figure 2. Empirical relationship between mating system, which is defined using the guidelines of Le Boeuf (1991) and inter-specific variation in survival rates for

pinnipeds at 2 years of age (A), age at sexual maturity (B), and age at social maturity (C). Survival rates are on the logit scale.



CHAPTER 4

INFLUENCE OF AGE AND INDIVIDUAL IDENTITY IN THE USE OF BREEDING COLONY HABITAT BY MALE WEDDELL SEALS (*LEPTONYCHOTES WEDDELLII*) IN EREBUS BAY, ANTARCTICA

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Abstract

Male-male contest behavior can contribute to spatial distributions of males during breeding seasons. To maximize breeding opportunities, the most competitive males would be expected to be surrounded by the highest abundances of reproductive-age females. Males of intermediate reproductive age might position themselves to compete the hardest in male-male contest behavior, with younger males suffering from smaller sizes and inexperience and older males suffering from senescent declines. Alternatively, the oldest males might invest the most energy into male-male contests and select locations with the greatest potential reproductive payoffs. We performed kernel density analyses to evaluate age-specific habitat use of male Weddell seals in Erebus Bay, Antarctica. Additionally, we investigated the relationship between age and number of surrounding reproductive-age females using a competing set of regression models in a Bayesian framework that considered different functional forms of age while incorporating individual heterogeneity. As male adult Weddell seals aged, to at least 20 years, they were more likely to be found in areas associated with the greatest densities of reproductive-age females, but individual heterogeneity strongly influenced the number of reproductive-age female neighbors. Our models suggest that a greater proportion of male Weddell seals aged 10 to 28 either are more competitive in male-male contests or are more willing to risk strong competition in favor of access to the most productive females in the population. Further analysis exploring age-specific paternities and underwater habitat use

would provide additional context for our findings in this preliminary investigation of fine-scale spatial use in Weddell seals.

Key words: spatial distribution, habitat usage, Weddell seal, *Leptonychotes weddellii*, age, individual heterogeneity

Introduction

Throughout the animal kingdom, many species migrate across the landscape or seascape to access different resources and partake in different life-history activities (e.g., reproduction, moulting) at varying times of the year (Alerstam et al. 2003). Suitable habitat for breeding might differ from other activities, which can lead to colony formation. For colonially breeding species, colonies subdivide the population into discrete geographic locations, and the decision an individual makes regarding where to settle can influence its reproductive success (Misenhelter and Rotenberry 2000). The spatial and temporal distribution of females in the habitat typically dictates the spatial configuration of males during the breeding season in polygynous species (Emlen and Oring 1977), and observations of some species have found that older male individuals have a tendency to obtain high-quality breeding sites (Coulson 1968, Pärt 2001). Individuals can differentially partition their habitat usage based on sex and age, but determining the sex and age of marine mammal species, as well as obtaining a sample of diverse ages, often poses challenges, therefore limiting the number of marine mammal studies investigating fine-scale habitat use by different demographic groups (Baker and Thompson 2007; Sprogis et al. 2018).

Both physical and biotic characteristics of a habitat can dictate spatial patterns of animals. For colonial species, spatial patterns of individuals, including colony formation, might be driven by physical features for suitable habitat, such as appropriate substrate type, abundant thermoregulation resources (e.g., shade), and large enough areas to accommodate adequate numbers of animals for social interactions. Habitats can include areas with greater exposure to harsh weather or predators, which tend to be occupied more often by younger and/or lower quality individuals (Carrete et al. 2006; Krafft et al. 2007). Under the assumption that natural selection drives habitat use, individuals should settle in the highest-quality habitat to maximize fitness (Fretwell 1969; Clark and Shutler 1999), but the overall quality of a section of habitat or colony encompasses several factors, such as food resources and potential mates. Resource distribution tends to play a key role in the spatial arrangement of individuals of wildlife populations (Lott 1984). In breeding grounds, reproductively active females serve as important resources for males (Trivers 1972). Spatial variation in reproductive potential tends to influence where individuals settle during the breeding season (Grant and Birney 1979; Krafft et al. 2007). From a theoretical perspective, several factors, including a negative experience in a previous territory, age, survival rate, and spatial variation in habitat characteristics, can influence the site fidelity of an animal to its breeding site (Switzer 1993). As some of these factors (e.g., age and experience in a previous area of the habitat) can vary during an animal's lifespan, movement among colonies might occur as an animal ages.

Sexual selection can also be related to where animals settle in the habitat during the breeding season. For example, the dominance status of males can dictate the spatial arrangement of display territories for male-male contest behavior (Le Boeuf 1974; Magaña et al. 2011), which might lead to age-specific spatial arrangements of territories. Territorial versus nonterritorial behavior can also influence spatial use of the habitat. In some species, such as canids and ungulates, younger and nonterritorial animals can be driven out of areas by territorial males (Wahlström 1994) or might elect to avoid areas of the habitat where territorial animals settle (Sacks et al. 1999). Therefore, in species with male-male contests, the age and quality of the individuals (e.g., physiological condition) at each colony contributes to the heterogeneity of habitat quality and can relate to where males position themselves in the habitat (Wolf et al. 2005).

As an animal reaches old age, it is expected to invest more effort into its final reproductive attempts, i.e., terminal investment (Williams 1966; Pianka and Parker 1975; Clutton-Brock 1984). For males, older individuals also tend to take greater risks for and/or have greater aggression and persistence in male-male contest behavior for current reproductive opportunities (Magnhagen 1990; Kemp 2006; Fischer et al. 2008; Ory et al. 2015). Although the oldest males might exert the most effort into current reproduction, their ability to compete in male-male contests might fall victim to senescent declines (Yoccoz et al. 2002; Piper et al. 2017, 2018). For example, in territorial species, the oldest males might elect to defend territory in a suboptimal location in favor of higher chances of winning contests, maintaining territory, and gaining copulations but at the cost of losing

the potential to mate with the most fit females and/or the most females. Reproductive effort can be measured behaviorally and might not reflect reproductive allocation because individuals can allocate resources to reproduction with varying efficiency (McElligott et al. 2003; Mysterud et al. 2004; Javoiš 2013). Thus, both reproductive allocation and effort can vary not only with age but can also vary with individual quality (McElligott et al. 2003; Mysterud et al. 2004; Pelletier et al. 2006; Mainguy and Côté 2008). Alternatively, the oldest age class would be expected to have a higher proportion of more robust individuals that were able to survive to the oldest ages (Vaupel et al. 1979; Vaupel and Yashin 1985; Cam et al. 2002). In some species, e.g., northern elephant seals, the males that survive to the oldest ages also are the ones with a much higher chance of reproducing (Clinton and Le Boeuf 1993). Therefore, older males might appear to exhibit greater reproductive success, but not necessarily effort, resulting from a lower proportion of frail individuals relative to younger age classes rather than terminal investment.

Data on the spatial arrangement of male Weddell seals (*Leptonychotes weddellii*) provides an opportunity to test the terminal-investment and individual quality-hypotheses. Weddell seals form breeding colonies on sea ice along perennial tidal cracks in Erebus Bay, Antarctica in late September to early October. Females arrive in late September and October to give birth to pups, and mothers and pups spend about two weeks constantly on the ice in these breeding colonies before taking intermittent swims throughout the rest of the 6- to 7-week nursing period (Stirling 1969; Siniff et al. 2008). During this time and through

December, males engage in underwater male-male contests in the form of underwater territorial defense and use visual and acoustic displays to attract females, but they take breaks from defending their underwater territory to haul-out on the ice in the breeding colonies among other males and females (Bartsh et al. 1992). Mating occurs in December after moms have weaned their pups. Hastings and Testa (1998) found that older female Weddell seals in Erebus Bay with more pupping experience tended to pup at the more crowded nearshore locations, whereas mothers in locations farther offshore tended to produce pups that exhibited lower survival rates relative to those living closer to shore. If the survival rates of pups are related to the quality of mothers, males would likely compete for access to females of the highest quality. Therefore, we predict that better male competitors are more likely to be observed in the nearshore areas of the habitat. In accordance with the terminal-investment hypothesis, the oldest male Weddell seals might establish themselves in the southern nearshore areas to gain access to the best females and surround themselves by the greatest number of reproductive-aged females. Alternatively, male Weddell seals of intermediate reproductive ages (10 – 16 years of age, Gelatt 2001) might be more competitive and be most likely to seek these optimal areas of the habitat and also surround themselves by the largest number of reproductive-age females.

The objectives of this study were to describe the spatial arrangement of male Weddell seals in Erebus Bay, Antarctica and to evaluate the hypotheses regarding how space use might vary with male age using data collected during 2014 through 2018. We specifically focused on how age might relate to variation

in relative densities of males throughout Erebus Bay and how age might relate to the number of surrounding reproductive-age female neighbors during the breeding season. Although the spatial patterns of Weddell seals on the ice surface might not relate to the spatial patterns in the water, where breeding occurs, we explore a few hypotheses related to reproductive activity to help contextualize our results.

Methods

Study Site

Data were collected in Erebus Bay, Antarctica (77.7° S and 166.5° E) from 2014 to 2018 from late September through early December when female Weddell seals aggregate around perennial tidal cracks to birth and nurse their pups and male Weddell seals establish and defend underwater territories. Female Weddell seals haul out across about 13 breeding colonies that form around perennial cracks in the land-fast sea ice along the west coast of and offshore islands near Ross Island (Figure 1). These colonies are located on the land-fast ice in the subtidal zone, which forms in March or April and breaks out in late February or March of the following year (Heine 1963; Jeffries et al. 1993). However, ice located in the coastal areas between Turk's Head and the Erebus Glacier Tongue as well as between the Erebus Glacier Tongue and Hutton Cliffs does not break out every year and might form multi-year ice, which can provide prolonged protection from the seal's primary predators, orca/killer whales (Stirling 1969). Both male and female Weddell seals demonstrate strong annual site fidelity to Erebus Bay (Stirling 1969; Cameron et al. 2007).

Mark-Recapture Techniques

From a long-term mark-recapture effort from 1980 to 2018, individually identifiable livestock tags were applied to the interdigital webbing of the rear flippers within 2 days following birth of all Weddell seal pups observed in Erebus Bay, which allowed us to determine the identity and age for all individuals that were born in the study area and subsequently observed later in the study. Each year from early November to early December, about 6 repeated surveys were conducted in which the identities of all previously tagged individuals hauled out and observable on the sea ice surface were recorded. Survey effort spanned either one full day or two consecutive days when two days were necessary to traverse the full study site (e.g., during years when seal abundance in the study site was particularly high, sea ice conditions complicated travel, or weather caused delays), and separate surveys occurred between 4 and 6 days apart from one another. From 2014 to 2018, latitude and longitude coordinates were obtained for a precise measurement (3 m) of spatial locations of seals using Trimble Ranger™ field computers (Trimble Navigation, Sunnyvale, CA, USA). As some adult Weddell seals in Erebus Bay were typically observed without tags during at least one survey each year (likely immigrants from animals not born in Erebus Bay), we did not know the age of every animal recorded during recapture surveys. For analyses in this study, we only included animals of known age.

Statistical Analyses

To investigate if the distribution of male Weddell seals in the Erebus Bay study site during the breeding season varied with age, we performed fixed-

bandwidth kernel density analysis. To compare where males of different age groups settled in the Erebus Bay study site to where females aged 12 to 20 years (see below), we also performed kernel density analysis for females aged 12 to 20 years. Females reach a peak in the probability of reproducing during intermediate reproductive ages centering around 16 years of age with a range of 12 to 20 years of age (Paterson et al. 2018), defined here as prime-aged females. Finally, to compare where males of different age groups settled in the Erebus Bay study site to the relative densities of pup production, we also performed kernel density analysis for pups. Visual depictions of spatial data were overlaid on imagery obtained from Google imagery©2020 using `ggmap` (Kahle et al. 2019) and the R software environment (R Development Core Team 2019).

Kernel density methods result in probability density functions that can estimate the utilization distribution of animals using non-parametric smoothing parameters to display the relative concentration of spatial points for an event per unit area (Worton 1989). In our case, each event represented the recapture of a Weddell seal during a survey, and we used kernel density estimation to identify high-use areas by Weddell seals of different ages. To compare the distribution and density of males of different ages, we partitioned the male recapture data into the following age groups: 2 – 4 years of age, which represents the pre-breeding through youngest known age (3 years) to engage in reproductive activity (Harcourt et al. 2007); 5 – 10 years of age, which represents the earliest known age of males exhibiting territoriality (5 years) through the age at which many males are territorial (Bartsh et al. 1992) but not as likely to sire offspring (Gelatt

2001); 11 – 19 years of age which represents the age by which almost all males become territorial (11 years, Bartsh et al. 1992) and are likely to sire offspring (Gelatt 2001); and 20 – 28 years of age, which represents the oldest known age of siring offspring (20 years, Harcourt et al. 2007) and older. Data were pooled across surveys and years. For kernel density plots, we used `sp` (Pebesma et al. 2019), `mass` (Ripley et al. 2019), `spatialEco` (Evans and Ram 2019), and `ggspatial` (Dunnington and Thorne 2018) packages in the R programming language (R Development Core Team 2019). As the bandwidth can bias the kernel density estimate, we selected a bandwidth using the plug-in method described by Sheather and Jones (1991). The Sheather-Jones plug-in method is optimal for large sample sizes (Harpole et al. 2014).

We conducted regression modeling in a Bayesian framework to evaluate competing hypotheses about the relationship between the number of reproductive-age female conspecifics within a 100-m radius of individual male Weddell seals as a function of male age. We used the mean age at first reproduction of 7 years of age for females (Paterson et al. 2018) to define our lower boundary of female reproductive age. As females are known to continue to produce pups at all ages > 5 years, we did not define an upper boundary of reproductive age. Therefore, reproductive-age females are defined here as females ≥ 7 years of age. Male Weddell seals vary in the age at which they become territorial (Bartsh et al. 1992) and might also vary in individual quality with regard to age-specific reproductive effort. Therefore, we predicted that individual heterogeneity would play a role in the number of reproductive-age female neighbors that were within 100 m of a

male. We selected a radius of 100 m because that seemed appropriate given that Weddell seals tend to space themselves about 5 m from their nearest neighbor during the breeding season (Stirling 1969), and Weddell seal breeding colonies in Erebus Bay tend to be several hundred meters long. Therefore, we selected a radius of 100 m to strike a balance between having a high enough probability that males will have female neighbors and not covering too much distance of a single breeding colony. As this is the first study to address fine-scale spatial arrangements in Weddell seals, we acknowledge that our work is exploratory, and encourage future work to explore if patterns noted here are robust to the choice of radius.

To test our competing hypotheses regarding the relationship between the number of reproductive-age females surrounding a male and the age of the male, we built five candidate models that each included (1) a random effect of the individual male (some males were observed multiple times within and among years) and (2) allowed the intercept to vary by year (year was treated as a factor coded such that the intercept represented the average value across years, i.e., sums contrasts were used). Our candidate models included an intercept-only model, a threshold model that combined age groups (treated as factors), and models for each of three different functional forms for age: linear, quadratic, and logarithmic. The age groups for the threshold model were the same four groups as described above for the kernel density analyses. We used the linear model to evaluate support for the idea that the number of reproductive-age females within 100 m of a male would steadily increase with male age such that the oldest males

would have the most female neighbors of reproductive age. The quadratic model allows the number of reproductive-age females near a male to increase with male age for younger males, to peak at some intermediate (prime) male age and to decline at older ages. The logarithmic model allows the number of reproductive-age females near a male to initially increase with male age but then to reach a pseudo-threshold at older ages. We standardized the male ages used in the models (age, age^2, or ln[age]) by centering them about the mean to reduce the correlation among coefficients in the quadratic model (Hocking 2013). The random effect of individual was included in each model as normally distributed with a mean of 0 and variance of $\sigma^2_{individual}$, ~$N(0, \sigma^2_{individual})$ and structured such that they allow different individuals to have different means.

We used the package `rstanarm` (Gabry et al. 2020) in R version 3.5 (R Core Team 2018) for all regression analyses. Based on preliminary investigations that used Poisson regression, it became apparent that our response data were overdispersed count data. Thus, we used a negative binomial model structure (Allison and Waterman 2002; Berk and MacDonald 2008). We specified our model as,

$Y_i \sim NB(\mu_i, k)$,

where Y_i is the number of reproductive-age female neighbors within a 100-m radius of a male for recapture i and follows a negative binomial distribution with mean μ_i and dispersion k.

The mean and variance of Y_i can be defined as,

$E(y_i) = \mu_i$ and $var(Y_i) = \mu_i + \mu^2 \times k$,

where k is the reciprocal of the dispersion parameter, and overdispersion is present when $\mu^2 \times k$ is > 0.

Our regression models were specified as,

$$Y[i,j] \sim NB(\beta_0 + \beta_1 \times A_i \ldots + \beta_j \times Y_j + \gamma_{ind} \times I),$$

where β_0 and β_1 are regression coefficients for the intercept and the age structure (A) for each specific functional form (i.e., age, age + age^2, or ln[age]) for each recapture, i, and each year (Y), j; and γ_{ind} is the random effect for each individual and is defined as,

$$\gamma_{ind} \sim N(0, \sigma^2_{ind}),$$

where σ^2_{ind} is the variance associated with the random effect of individual identity.

A Markov Chain Monte Carlo (MCMC) approach estimated the posterior distribution of our model parameters (Gelfand and Smith 1990; Casella and George 1992; Geman and Geman 1993) using 4 chains and vague priors for our all model parameters. We used independent, vague normal priors with a mean of 0 and standard deviation of 10 for the intercept and a mean of 0 and standard deviation of 2.5 for the coefficients; we used a vague exponential prior for the reciprocal dispersion with a rate of 1. Because some males were recorded multiple times within a year and/or in different years, we also included a random effect of male identity. Individual identity was included using a normal distribution with a mean of 0, and we monitored the variance as the random effect of individual identity, $\sim N(0, \sigma^2_{\text{individual}})$. We used an independent, vague normal prior with the mean set to 0 and variance $\sigma^2_{\text{individual}}$. After 1,000 burn-in iterations,

we ran an additional 1,000 iterations per chain, resulting in 4,000 total samples from the posterior distribution. We evaluated the extent to which individual heterogeneity related to the variation in the age-specific number of reproductive-age female neighbors across males by calculating the posterior estimates for the mean – 2 σ^2_{ind} (below-average individuals) and mean + 2 σ^2_{ind} (above-average individuals) and comparing these estimates to the posterior estimates for the mean (average individual random effects) for an average year.

Using the R packages, `coda` (Plummer et al. 2006) and `ggmcmc` (Fernández-i-Marín 2016), we assessed model convergence by inspecting the trace plots and Geweke diagnostics (Geweke 1991) and calculating the Gelman-Rubin statistic, $\hat{R}$, which indicates model convergence if values for all parameters are less than 1.1 (Gelman and Rubin 1992), for each monitored parameter. Once convergence was achieved, we calculated k-fold information criteria (kfoldic) values by partitioning the dataset into 10 folds and compared scores for each of our competing models using the R package `loo` (Vehtari et al. 2019). Finally, we evaluated the best-performing model's ability to predict data that compared well with observed data using posterior predictive checks and by creating residual plots and plots comparing simulated data from the best-performing model to the raw data (Conn et al. 2018). We present the uncertainty associated with our model estimates using 95% credible intervals (95% CI).

Results

From 2014 to 2018, 31 surveys were completed to record the fine-scale spatial location data of known-age male Weddell seals during the breeding season. From the 31 surveys occurring between 2014 and 2018, we had spatial data for a total of 3,954 observations of 638 individual males. On average, an individual male was observed approximately 10 times (SD = 5.25, range = 1 – 27 recaptures) during the five-year study period and approximately 4 times per year (SD = 1.59, range = 1 – 6). The average male was approximately 10 years of age (SD = 4.98, range = 1 – 28). The average individual male had approximately 4 females of reproductive age within 100 m of him on the sea-ice surface during a survey in which he was sighted (SD = 7.49, range = 0 – 48, Figure 2).

Although we observed large aggregations of seals associated with named breeding colony sites near perennial tidal cracks, some seals were recaptured in areas not associated with a referenced breeding colony. We found evidence that females aged 12 to 20 years (prime-aged) settled in the southern nearshore areas of the habitat generally associated with the Hutton Cliffs breeding colony, where the greatest number of pups tend to be born each year (Figure 3). The relative densities of males in different age groups supported our prediction that males of different ages used the Erebus Bay study site heterogeneously. As the age of males increased to an age by which most males engage in male-male contests to acquire and defend territory, 20 years of age (Bartsh et al. 1992; Gelatt 2001; Harcourt et al. 2007), a proportion of high usage areas were found in the more southern and nearshore locations of the habitat associated with the Hutton Cliffs

breeding colony. The youngest males tended to be more likely to be observed in the northern offshore areas of the habitat, and the oldest males were most likely to occupy the southern and nearshore areas of the habitat but were also present in relatively high densities in the northern and offshore areas of the habitat (Figure 4). The plots of relative densities of females aged 12 to 20 years and of males in different age groups provide evidence that males in the age class 11 – 19 years of age had higher densities in areas with more females aged 12 to 20 years whereas the youngest and oldest males tended to be found in areas with lower relative densities of females aged 12 to 20 years (Figures 3, 4).

In support of our prediction that the number of reproductive-age females (≥ 7 years of age) near a male would vary with male age, models that included age as a covariate outperformed the intercept-only model (Table 1). We could not clearly distinguish among our competing models that evaluated different functional forms of age, however, as each had relatively similar performance based on the k-fold cross validation, especially given the uncertainty in those scores (Table 1). It is notable that each of these models did provide similar inference in a general sense: the expected number of reproductive-age females within a 100-m radius of a male tended to increase with a male's age. However, the magnitude of the increases across ages and the predicted pattern in counts of reproductive-age females near males varied by model, especially for ages greater than 20 years of age, where the sample size was modest (n = 148). Accordingly, we can only make weak inferences about patterns for the oldest ages (see below).

Among the four models that contained male age, the model that used the quadratic functional form of age performed the best in k-fold cross-validation evaluations (Table 1). Posterior-predictive checks for the best-supported quadratic model indicated that our model was able to generate predicted values that largely resemble our observed data; although, it slightly over-predicted the variation in the number of reproductive-age female neighbors for some ages (Figures S1, S2, S3). The residuals were small, and the distributions of the observed number of reproductive-age female neighbors were similar to the predicted number of reproductive-age female neighbors. Further, the coefficients for age (1.12) and age-squared (-0.83) were estimated precisely such that the 95% CI's for those coefficients did not include 0 (0.73, 1.50 for age, -1.21, -0.46 for age-squared). Estimated coefficients for adjustments from our baseline yearly effect of 2018 (mean = 0.60, 95% CI = 0.47, 0.72) ranged from an adjustment of 0.002 (-0.16, 0.16) in 2016 to -0.20 (-0.32, -0.08) in 2014.

Our quadratic model suggested that the number of reproductive-age females within a 100-m radius of a male peaked at ages in the upper teens and early 20s, and our other age-specific models showed a similar pattern (Figure 5). The youngest reported age for a reproductively active male Weddell seal is 3 years (Harcourt et al. 2007), and our quadratic model predicts that an average 3-year-old male would have approximately 1 (95% CI = 0.75, 1.17) reproductive-age female within 100 m for an average individual. By 9 years of age, nearly all males attempt to engage in reproductive activity by becoming territorial (Bartsh et al. 1992), and the average 9-year-old male is predicted to have approximately 2

(95% CI = 1.43, 1.94) reproductive-age females within 100 m. Sixteen years of age is the upper end of the prime reproductive age range that Gelatt (2001) described for males, and the average 16-year-old is predicted to have approximately 2 (95% CI = 2.03, 2.80) reproductive-age females within 100 m. Finally, 20 years of age is the oldest known age at which males have reportedly sired offspring (Harcourt et al. 2007), and the average 20-year-old male is predicted to have approximately 3 (95% CI = 2.16, 2.94) reproductive-age females within 100 m.

For males > 20-years old, the quadratic model predicts a drop-off in the number of females within 100m. However, the uncertainty associated with the predicted number of reproductive-age female neighbors was higher for these older ages as a result of smaller sample sizes for the oldest ages (e.g., the average prediction for a 24-year-old male = 0.74, 95% CI = 0.28, 1.47). Further, other supported models indicated that the number of reproductive-age female neighbors continued to increase with age for all ages, and those models received similar amounts of support. Thus, given those results and the modest sample sizes for males over 20 years of age, we are unable to make any strong inferences about patterns at the oldest ages. However, we do note that there were four individual males older than 20 years that were observed with > 10 reproductive-age female neighbors within 100 m and that one male aged 23 years was repeatedly seen with > 20 females nearby. Such observations were characterized by individual random effects as described below.

Individual random effects suggest that some males are expected to be near quite a few more reproductive-age females than are other males of the same age (Table 2). Predicted values suggest some 20-year-old males are predicted to have fewer than 1 (mean = 0.2, 95% CI = 0.1, 0.3) reproductive-age female within 100 m, which is well below the mean for that age (2.5, 95% CI = 2.2, 3.0) The average values for the random effect of individual tended to be farther from 0 for very young and very old males. For example, the mean estimated random effect was -0.20 (95% CI = -1.42, 1.73) for a 2-year-old male and was -1.04 (95% CI = -1.71, -0.20) for a 24-year-old male. In contrast, for most other ages, the average values for random effects of individual were close to 0, e.g., 0.05 (95% CI = -1.83, 1.72) for a 15-year-old male. The negative, relatively large estimated random effects for males > 20 years of age appear to be crucial to how the quadratic model accommodates low observed values for many of the oldest males despite the fact that the model's age structure predicts that the average individuals at those oldest ages should have many female neighbors. Thus, we conclude that the current data do not allow for strong inference at the oldest ages but do show that at least a few old males are observed near many females.

Discussion

Our investigation of age-specific spatial patterns of male Weddell seals in Erebus Bay, Antarctica represents the first fine-scale spatial analysis of Weddell seals in Erebus Bay. Access to reproductive females and male-male contest behavior can affect the spatial distribution of males of several taxa during the

breeding season (Le Boeuf 1974; Post and Jeanne 1983; Sherry and Holmes 1989; Wahlström 1994; Sacks et al. 1999; Magaña et al. 2011). Younger males occupied the more offshore locations of the habitat that had lower abundances of reproductive-age females, and densities of males in the more southern and nearshore areas of habitat increased with increasing age up to about 20 years of age. Similarly, males with the greatest number of reproductive-age female neighbors within a 100-m radius tended to be older (≥ 10 years of age). It is possible that the oldest males are being driven out of the best locations (i.e., areas associated with the Hutton Cliffs breeding colony). Alternatively, the oldest males might select areas heavily occupied by younger (7 to 11 years of age) or older (≥ 21 years of age) females, which tend to have a lower probability of reproducing than females aged 12 to 20 years; the probability for a female Weddell seal to reproduce at 7 years of age is 0.68 (95% CI = 0.63, 0.72), at 16 years of age is 0.79 (95% CI = 0.76, 0.81), and at 31 years of age is 0.37 (95% CI = 0.23, 0.53, Paterson et al. 2018). However, it is also important to recognize that the oldest male age group (≥ 20 years of age) also had the smallest sample size with 148 recaptures (3.7% of all recaptures) of 39 individuals (6.1% of all individuals). Our results suggest that the variation in the number of reproductive-age female neighbors surrounding a male in Erebus Bay during the breeding season was greater across individuals than across ages. The young males that attended the larger and more productive colonies were likely either high-quality individuals and among the youngest of breeders or did not hold territory.

Even though many males ages 3 to 8 years old are not holding territory or reproducing (Bartsh et al. 1992; Gelatt 2001), they were still frequently recaptured in or around the breeding colonies in Erebus Bay. One possible reason for their attendance in breeding grounds when they are not participating in breeding is gaining knowledge of the breeding scene, which has a positive relationship with siring success (Harcourt et al. 2007a). Additionally, young male Weddell seals might use this area of Erebus Bay to escape predators, such as pack ice (i.e., Type B) killer whales, *Orcinus orca* (Pitman and Durban 2012), that are more of a threat to Weddell seals on the pack ice than the land-fast ice that is abundant in the breeding colonies. As few relatively young males occupied the southern nearshore areas of Erebus Bay, we further hypothesize that many younger males selected to attend northern offshore colonies to decrease the number of interactions with the most competitive territorial males and in favor of better access to prey. Additionally, access to these locations would be easier for younger animals, as younger Weddell seals have not yet developed the ability to dive as long as seals 6 years of age or older (Burns 1999). The offshore breeding colony locations are closer to the ice edge and, consequently, require less energy to attend a breeding colony. Similar to our findings, Crawford et al. (2012) reported that ringed seal subadults tended to occupy farther offshore areas of the habitat, which are associated with better foraging opportunities, and adults tended to stay more nearshore for better breeding prospects.

Although it seems apparent that old and prime-aged male Weddell seals (ages 11 to 28) have a greater likelihood of settling in areas of Erebus Bay

associated with the highest pup production and the largest abundances of females, the mechanism behind this relationship is less clear. Similar to many ungulate and other pinniped species, participation in male-male contest behavior in Weddell seals likely increases with age (Pitcher and Calkins 1981; Clinton and Le Boeuf 1993; Melis et al. 2005; Mainguy and Côté 2008). However, our quadratic model and kernel density estimates suggest that male Weddell seals might experience reproductive senescence. Evidence that male Weddell seals exhibit survival senescence (Brusa et al. 2020) and that females exhibit both survival and reproductive senescence (Paterson et al. 2018) recently emerged. Alternatively, despite physiological impairments related to senescence, a senescent animal might not demonstrate any decrease in reproductive effort. According to the terminal investment hypothesis, reproductive effort will increase near the end of the lifespan (Clutton-Brock 1984). For male Weddell seals, maximizing reproductive effort could include engaging in male-male contests in areas of the habitat with the greatest relative densities of reproductive-age females. Once a male Weddell seal reaches 20 years of age, his life expectancy is only about another 2 years compared to 4 or 5 additional years for younger males at ages associated with territorial behavior (Bartsh et al. 1992; Brusa et al. 2020). Because some individual males ≥ 20 years of age were observed in areas of the greatest relative densities, our results provide some support for male Weddell seals behaving in accordance with the terminal investment hypothesis.

However, because male Weddell seals exhibit large variation among individuals of the same age, we found greater support for the individual quality

hypothesis. Furthermore, a greater proportion of Weddell seals of more intermediate ages compared to ages ≥ 20 years were found to be associated with a greater relative density of reproductive-age females from the quadratic model. Greater support for the individual-quality hypothesis compared to the terminal-investment hypothesis was also reported for males of multiple ungulate species (McElligott et al. 2003; Mainguy and Côté 2008).

As the oldest males in a population have the least reason to reserve energy for future reproductive attempts, they are expected to exert the most energy into their current reproductive effort (Enquist and Leimar 1990; Kemp 2006). Even though our quadratic model provided some evidence that older male Weddell seals were less likely to be found near reproductive-age females than the more intermediately aged males, they might have exemplified terminal investment by fighting with greater aggression for territories. Alternatively, the oldest males might surround themselves by the most reproductive-age females, as suggested by our linear and logarithmic models, but it is difficult to estimate the spatial behaviors of these older-aged males because the sample size is small. Males at older ages might fare better in male-male competitions for social reasons. Surviving to older ages could provide enough time for males to attain a high social rank or build a social network of male alliances, both of which should aid in gaining access to females. In other marine mammal species, males fare better in gaining copulations from attaining a high social rank followed by posturing and winning contests (e.g., northern elephant seals, Le Boeuf 1974) or from developing a cooperative alliance with one or two other males (e.g., bottlenose

dolphins, Connor et al. 2001; Möller et al. 2001). Male Weddell seals might employ similar techniques. However, it is important to recognize that the spatial information gained from recapturing marked Weddell seals on the ice might serve as a poor proxy for the reproductive activity that occurs in the water. The number of reproductive-age female neighbors of males on the ice might not be related to the number of copulations the males gain, their territory-holding ability, or the number of females that visit the male territories. Thus, we need additional information about the relationship between the number of reproductive-age females observed nearby a male on the ice and male fitness or mating opportunities. Our study provides initial insight to the fine-scale spatial behaviors of male Weddell seals in Erebus Bay, a topic that not previously been explored for either sex. Further investigations, possibly using acoustic tags, would provide more information about the underwater behavior of Weddell seals.

Our results suggest that individual heterogeneity strongly influenced the number of reproductive-age female neighbors that were in the proximity of individual males. If the number of reproductive-age female neighbors is positively linked to a male's mating opportunities and his ability to sire young, then individual quality might play an integral role in shaping the reproductive abilities and efforts exerted by male Weddell seals. The fewest number of males survive to the oldest age groups and likely have the highest proportion of high-quality males because older individuals have been exposed to selection pressures for the longest time, and many lower-quality individuals are present at younger ages (Cam et al. 2002). Thus, it would be expected that the oldest ages would

have the highest proportion of the best competitors and should settle in the areas of the habitat with highest reproductive payoffs and the highest density of reproductive-age female neighbors. However, some males might survive to reach old age but never reach a high enough social dominance status to fare well in male-male contests, such as reported for male mountain goats, a species in which social rank functions independently of age (Mainguy and Côté 2008). Individual quality might also have a greater influence on social rank than age in male Weddell seals, and the phenotypes that benefit the reproductive potential might differ from phenotypes that benefit survival. For example growth to large body sizes would likely favor males competing in male-male contest behavior but could also pose a challenge to survival in times of limited food resources (Clutton-Brock et al. 1985; Toïgo and Gaillard 2003).

Individuals tend to select areas of the habitat and social interactions in a way to maximize their fitness (Hirth 1977). Male Weddell seals seem to follow this general pattern in that age and individual identity are related to habitat use. Areas of Erebus Bay with high food resource abundance (Testa et al. 1985) were most likely to be frequented by the youngest males, and older males, which are the most likely to be territorial (Bartsh et al. 1992), were most likely to be found in areas with the highest abundances of reproductive-age females. The age-specific distribution of male Weddell seals in Erebus Bay, Antarctica suggests that younger males are generally less competitive in areas of the habitat with the most pup production. However, the large variation in the number of reproductive-age female neighbors surrounding a male across individuals relative to across

ages implies that reproductive effort might have a strong relationship to individual identity. Although males can be driven into less desirable areas of the breeding grounds by older, more territorial males (e.g. Sherry and Holmes 1989), our results demonstrate that individual heterogeneity can also play an important role in the observed spatial patterns of polygynous species with male-male contest behavior during the breeding season. The male social hierarchy of the Erebus Bay population of Weddell seals might correlate with age but more likely correlates with individual quality. Our finding that older males are most likely to be found in the areas of the habitat with the greatest abundances of reproductive-age females suggests that older males might be better competitors or are more likely to engage in risky behavior for high reproductive payoffs. Age-specific paternity analyses to investigate the relative number of offspring sired for each age would provide greater insight into the age-specific reproductive behaviors of male Weddell seals. We anticipate that further age-specific behavioral and reproductive research focused on male Weddell seals will reveal the mechanisms behind this variation in relative densities of males with age in Erebus Bay.

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Tables and Figures

Table 1. Summary of relative model performance based on k-fold information criteria (kfoldic) scores. We present the change in expected log predictive density (ELPD) for a new dataset across candidate models. The ΔELPD shows the change in ELPD score from the model with the highest ELPD (and lowest kfoldic score). The large standard errors for the change in ELPD indicate that the age-structure models performed similarly. Y represents fixed effect of year as a factor variable, and I represents random effect of individual.

Model	ΔELPD (SE)
$Log(F) = \beta_0 + \beta_{2014} \times Y_{2014} + \beta_{2015} \times Y_{2015} + \beta_{2016} \times Y_{2016} + \beta_{2017} \times Y_{2017} + \beta_{2018} \times Y_{2018} + \gamma_{Ind} \times I$	-19.8 (9.1)
$Log(F) = \beta_0 + \beta_1 \times Age + \beta_{2014} \times Y_{2014} + \beta_{2015} \times Y_{2015} + \beta_{2016} \times Y_{2016} + \beta_{2017} \times Y_{2017} + \beta_{2018} \times Y_{2018} + \gamma_{Ind} \times I$	-8.7 (7.9)
$Log(F) = \beta_0 + \beta_1 \times Age + \beta_2 \times Age^2 + \beta_{2014} \times Y_{2014} + \beta_{2015} \times Y_{2015} + \beta_{2016} \times Y_{2016} + \beta_{2017} \times Y_{2017} + \beta_{2018} \times Y_{2018} + \gamma_{Ind} \times I$	0 (0.0)
$Log(F) = \beta_0 + \beta_1 \times \ln(Age) + \beta_{2014} \times Y_{2014} + \beta_{2014} \times Y_{2014} + \beta_{2015} \times Y_{2015} + \beta_{2016} \times Y_{2016} + \beta_{2017} \times Y_{2017} + \beta_{2018} \times Y_{2018} + \gamma_{Ind} \times I$	-7.6 (8.3)
$Log(F) = \beta_1 \times Ages_{1\text{-}4} + \beta_2 \times Ages_{5\text{-}10} + \beta_3 \times Ages_{11\text{-}19} + \beta_4 \times Ages_{20\text{-}28} + \beta_{2014} \times Y_{2014} + \beta_{2015} \times Y_{2015} + \beta_{2016} \times Y_{2016} + \beta_{2017} \times Y_{2017} + \beta_{2018} \times Y_{2018} + \gamma_{Ind} \times I$	-16.6 (8.9)

Table 2. Variation in the estimated mean number of reproductive-age female neighbors within a 100-m radius for males that were 3, 9, 16, 20, or 24 years of age and that had estimated individual random effect (RE) values that were 2 standard deviations below the mean value (below average RE individual), the mean (average RE individual), or 2 standard deviations above the mean value (high RE individual). Estimates are based on the quadratic model $(\text{Log}(F) = \beta_0 + \beta_1 \times \text{Age} + \beta_2 \times \text{Age}^2 + \beta_{2014} \times Y_{2014} + \beta_{2015} \times Y_{2015} + \beta_{2016} \times Y_{2016} + \beta_{2017} \times Y_{2017} + \beta_{2018} \times Y_{2018} + \gamma_{\text{Ind}} \times I$, where Y is year, and I is individual.

Age (years)	Below Average RE individual (95% CI)	Average RE individual (95% CI)	Above average RE individual (95% CI)
3	0.06 (0.03, 0.10)	0.95 (0.75, 1.17)	15.00 (9.06, 24.26)
9	0.11 (0.06, 0.18)	1.67 (1.42, 1.94)	26.58 (16.70, 41.91)
16	0.16 (0.09, 0.26)	2.40 (2.04, 2.91)	38.12 (23.88, 59.85)
20	0.17 (0.09, 0.27)	2.54 (2.17, 2.95)	40.32 (25.25, 63.26)
24	0.16 (0.09, 0.26)	2.41 (1.99, 2.86)	38.76 (23.43, 63.11)

Figure 1. Map of Erebus Bay Study Site. Labels indicate named Weddell seals breeding colonies. Offshore locations include Tent, Inaccessible, Little Razorback, and Big Razorback.

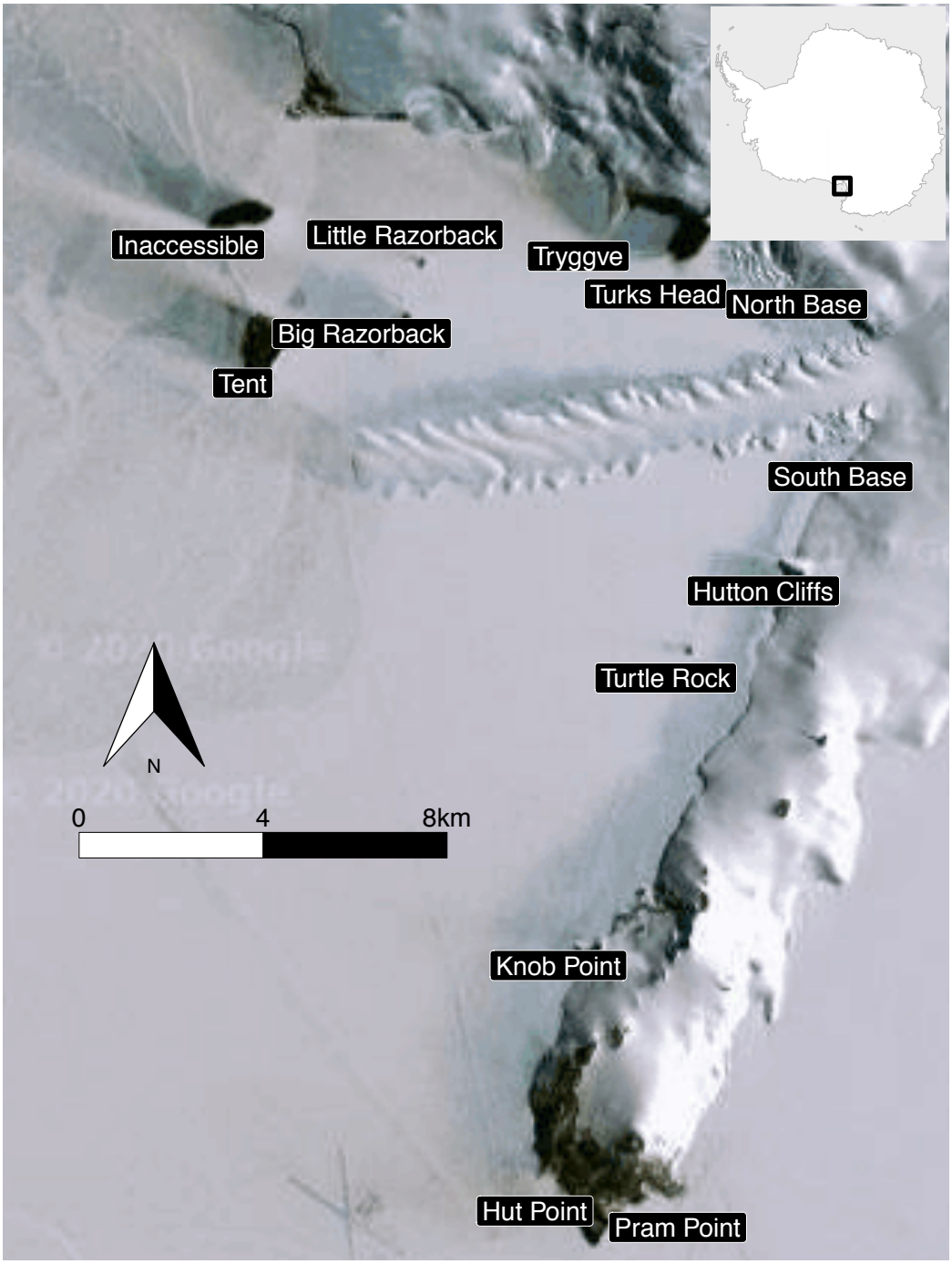


Figure 2. Number of reproductive-age female neighbors within a 100-m radius of a male for each age of observed males. Purple points show the number of reproductive-age female neighbors for each recapture, which illustrate the variation in the number of female neighbors within each age. Boxplots represent the 10% and 90% quantiles of the number of reproductive-age female neighbors for each age of males.

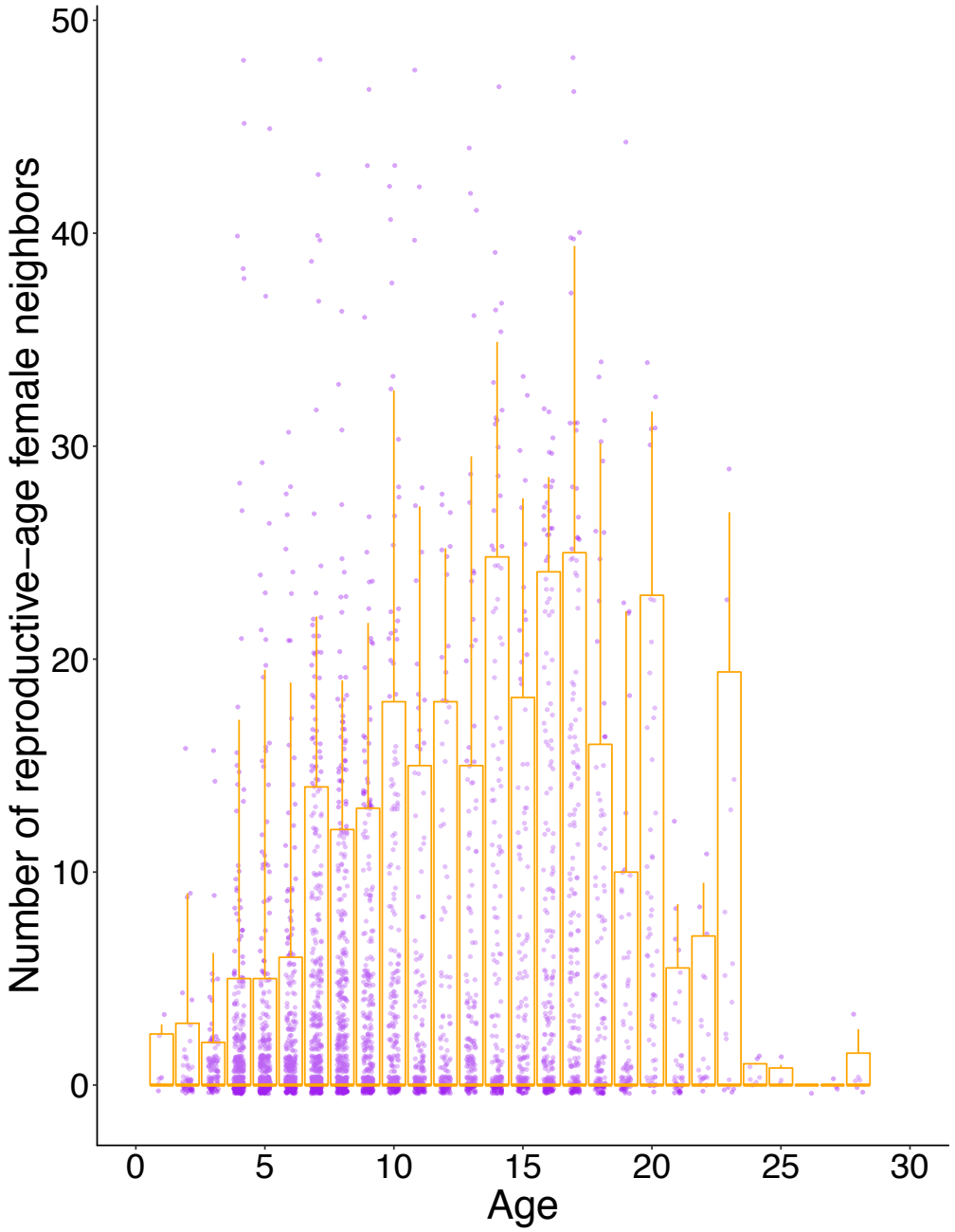


Figure 3. Female and pup kernel density estimates. Recaptures and kernel densities of prime reproductive-age female Weddell seals (A) and dependent pups (B) in Erebus Bay, Antarctica reveal that these two demographic groups are most likely to be found in the southern nearshore areas of the Erebus Bay study site. The lightest color represents a 20% isopleth, and the darkest color represents an 80% isopleth. Relative densities of dependent pups indicate areas where mothers were recaptured because dependent pups do not venture far from their mothers.

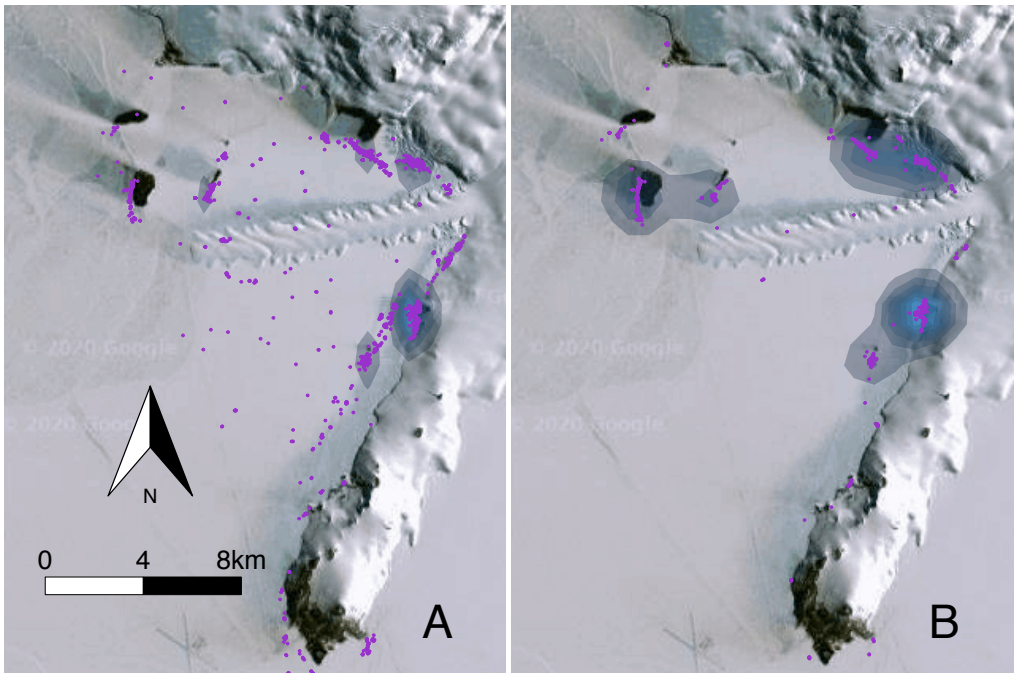


Figure 4. Male age-specific kernel density estimates. Recaptures and kernel densities of male Weddell seals (A) 2 – 4 years of age, which represents the pre-breeding through youngest known age (3 years) to engage in reproductive activity (Harcourt et al. 2007), (B) 5 – 10 years of age, which represents the earliest known age of males exhibiting territoriality (5 years) through the age at which many males are territorial (Bartsh et al. 1992) but not as likely to sire offspring (Gelatt 2001), (C) 11 – 19 years of age which represents the age by which almost all males become territorial (11 years, Bartsh et al. 1992), and (D) 20 – 28 years of age, which represents the oldest known age of siring offspring (20 years, Harcourt et al. 2007) and older. The green outline indicates the area with the greatest relative density of prime-age females. The lightest color represents a 20% isopleth, and the darkest color represents an 80% isopleth.

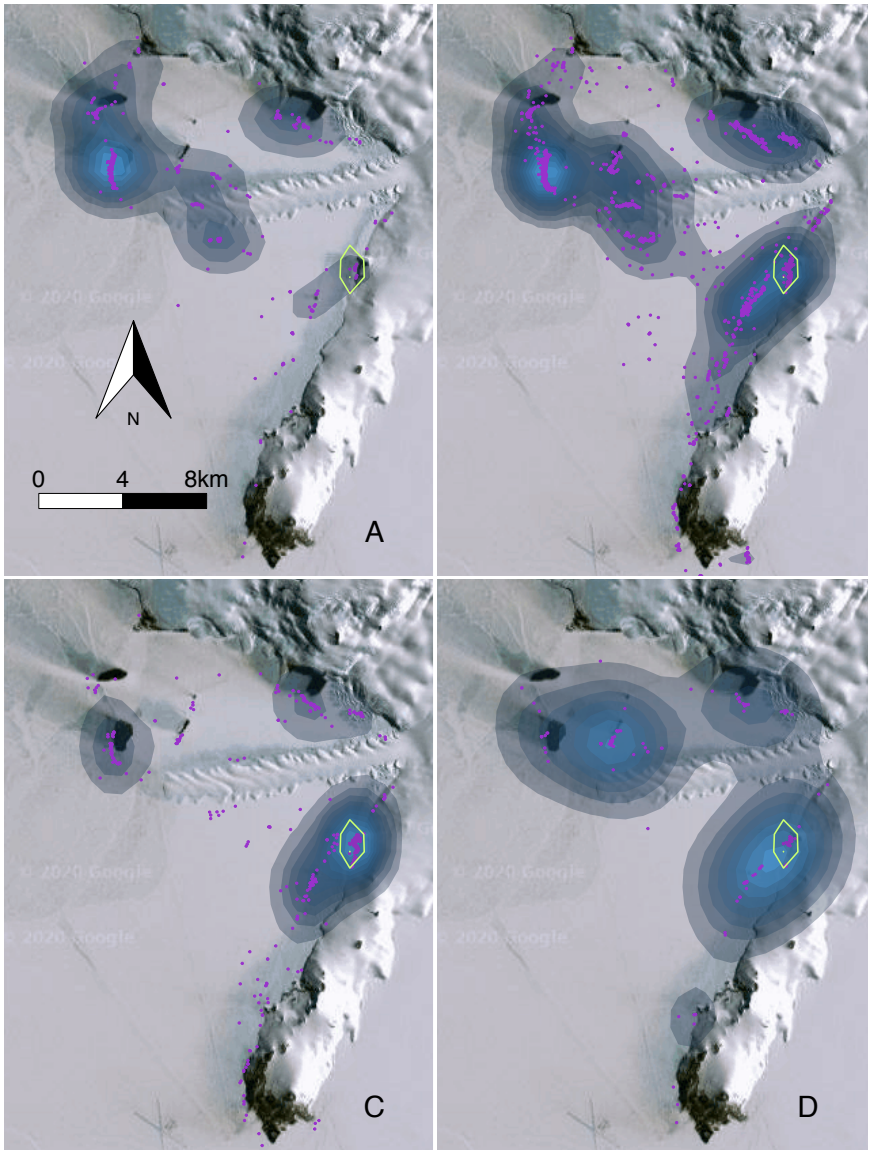
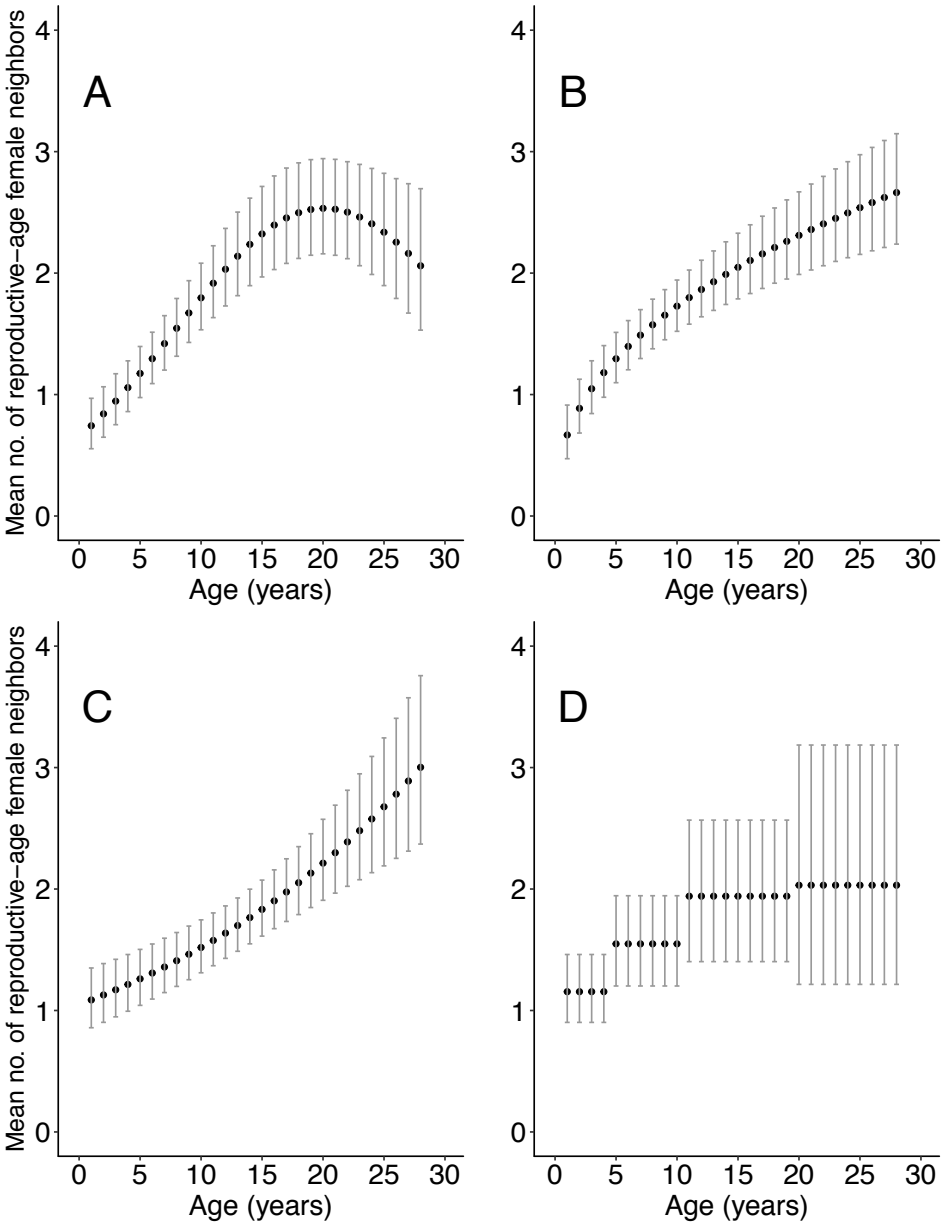


Figure 5. Age-specific mean number of reproductive-age females within a 100-m radius of a male estimated from our most supported models (A) quadratic, (B) logarithmic, (C) linear, and (D) age-as-factor; see Table 1 for full model structures. Error bars indicate 95% credible intervals.



CHAPTER FIVE

GENERAL CONCLUSIONS

This dissertation explored the patterns of life-history traits in pinnipeds related to age-specific survival and habitat use with a strong focus on Weddell seals. In alignment with the allocation principle (Cody 1966), my coauthors and I found support for a reproduction-survival tradeoff. In chapter 2, I present evidence of a reproduction-survival tradeoff in Weddell seals in that they experience actuarial senescence. In chapter 3, I present graphical support for a survival-reproduction tradeoff associated with precopulatory investment across the suborder Pinnipedia. Our results indicate that individual heterogeneity plays an important role in the survival of male Weddell seals. Individual heterogeneity has been suggested to occur in northern elephant seals, which engage in extreme polygyny and experience a large degree of sexual size dimorphism (Clinton and Le Boeuf 1993). Individual heterogeneity likely explains why northern elephant seals are one of the pinniped species with the lowest adult survival rates but are also one of the pinniped species that reach social maturity at the oldest ages, as few high-quality individuals can survive to reproductive age. We also observed that individual heterogeneity plays an important role in the number of reproductive-age females that are within a 100-m radius of a male Weddell seal.

Male Weddell seals exhibit age-specific variation in survival rates with survival rates peaking in early adulthood. My coauthors and I found evidence of senescence in male Weddell seals, which commences in early adulthood prior to

the mean age of social maturity (Bartsh et al. 1992) and immediately following the earliest known age reported for first reproduction (Harcourt et al. 2007). We also found that survival rates varied across individuals and years, but the variation across years was smaller than among individuals. Finally, we discovered that male Weddell seals appear to commence actuarial senescence at an earlier age than previously detected for females (Paterson et al. 2018). It is possible that survival consequences of investment in reproductive effort is greater for males than females in this species. Analysis of age-specific survival rates incorporating individual heterogeneity for females for ages younger than 7 years of age would provide further clarity. Additional comparisons of age at commencement of actuarial senescence between the sexes of other species would also provide additional context for our findings. Future research to include age-specific paternity data would lead to greater insight regarding the survival-reproduction tradeoffs incurred by male Weddell seals. Finally, future studies of age-specific male survival rates in other pinniped species would further elucidate survival-reproductive tradeoffs in this monophyletic group.

My coauthors and I found evidence that males of pinniped species exhibit a diversity of life-history strategies, including large variation in age- and stage-specific survival rates. From graphical analyses, the precopulatory trait of mating system appears to vary more strongly with stage-specific survival rates than the postcopulatory trait of baculum length. Mating strategies of pinniped species include seasonal monogamy, mild polygyny, moderate polygyny, and extreme polygyny. Further corroborating the results of Fitzpatrick et al. (2012), we found

that male pinnipeds either invest in precopulatory or postcopulatory male-male competition. Species engaging in extreme polygyny tended to have the greatest sexual size dimorphism but the smallest bacula. However, our inferences were made from small sample sizes and with the assumptions that the life-history trait data for each species used in our comparative analysis were representative for the species as a whole. We discovered a paucity of survival rate data for male pinnipeds, but high-quality survival rate data from a large number of species for comparative analysis are necessary for making higher-order conclusions about evolutionary life-history theory. We presented a model to incorporate uncertainty in survival rates (i.e., a response variable on the probability scale), continuous covariates (e.g., standard body length), and phylogenetic branch lengths. With a large sample size of empirical data, this modeling technique can be used for comparative analyses of life-history strategies in related taxa, including pinnipeds when additional survival rate data become available.

In territorial species, such as pinnipeds, younger males can exploit different areas of the habitat than older, more competitive males (Crawford et al. 2012). Male Weddell seals of different ages tended to use different areas of the Erebus Bay habitat during the breeding seasons of 2014 to 2018. Younger seals were more likely to be found in the more offshore areas of the habitat, which provide greater access to prey species but less protection against predators (Stirling 1969; Hastings and Testa 1998). With increasing age, the density of male Weddell seals shifted from these offshore locations to more nearshore areas, and older, but not the oldest, males clustered most-densely in the southern

nearshore areas of the habitat with the greatest density of reproductive-age females. Younger male Weddell seals also settled in areas with a lower abundance of reproductive-age females. As males endure male-male contest behavior in the form of territory defense and underwater combat, younger males likely selected less densely occupied sections of the habitat to avoid aggressive males. Although our results indicate that age related to habitat usage of the Erebus Bay study site by male Weddell seals, they also revealed that individual seals of the same age varied substantially in their habitat usage, which suggests that male Weddell seals likely also vary in their reproductive effort. This study was the first to explore fine-scale spatial patterns in Weddell seals in Erebus Bay and provides a foundation for the heterogeneous composition of male Weddell seals throughout the study site during the breeding season. Future studies to incorporate paternity analysis or other metrics of reproductive success and reproductive effort, such as GPS monitoring of underwater territory defense behavior, would provide additional context for our findings.

Remote areas with little anthropogenic activity serve as especially useful study sites for investigating natural fluctuations in survival rates that can potentially apply to a range of species. Marine species living in relatively pristine environments generally do not endure chronic stressors, such as poor water quality (Weiffen et al. 2006; Fire et al. 2015; Unsworth et al. 2015; Walsh et al. 2015), high levels of vessel traffic and tourism (Bejder et al. 1999; Sorice et al. 2003; Arcangeli and Crosti 2009; Rolland et al. 2012; Allen et al. 2014), and contaminants (Tanabe et al. 1994; de Swart et al. 1996; Ross 2002; Balmer et al.

2015). Unfortunately, many marine populations only have received research attention after they started declining (Pauly 1995). Thus, baseline information about populations living in relatively pristine ecosystems enables an understanding of natural demographic processes and a true benchmark for conservation standards.

Species living in the Anthropocene cannot fully escape anthropogenic effects but vary from highly anthropogenically influenced to very closely resembling the true wilderness of earlier geologic time periods (Cronon 1996; Ellis 2011). For example, some ecosystems in the Southern Ocean, often regarded as nearly pristine, carry the burden of low abundances of many fish and cetacean species resulting from historic exploitation of both cetaceans and fishes coupled with low recovery rates (Blight and Ainley 2008). Despite these anthropogenic influences, the Ross Sea ecosystem, a small part of the Southern Ocean, operates as the least anthropogenically affected marine ecosystem (Halpern et al. 2008). Studying the population ecology of species living in relatively pristine areas can serve as useful information for both the study species of interest and also for species with similar natural histories living in areas subject to greater human impact. Marine mammals living in the Ross Sea ecosystem are especially useful because marine mammals typically demonstrate high levels of sensitivity to environmental change because of their longevity and potential to bioaccumulate toxins (Bossart 2011). Additionally, studying Antarctic species can reveal important concepts about how populations have adapted to unstable environmental conditions. Our results indicate that male Weddell seals employ a

life-history strategy with high age-specific survival rates throughout much of life, and this investment in longevity can mitigate the challenges of living in a somewhat variable environment.

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APPENDICES

APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Figure S1. Male recaptures by age. The number of recaptures at each age is shown; note that an individual that was captured at multiple ages would be represented at each age sighted.

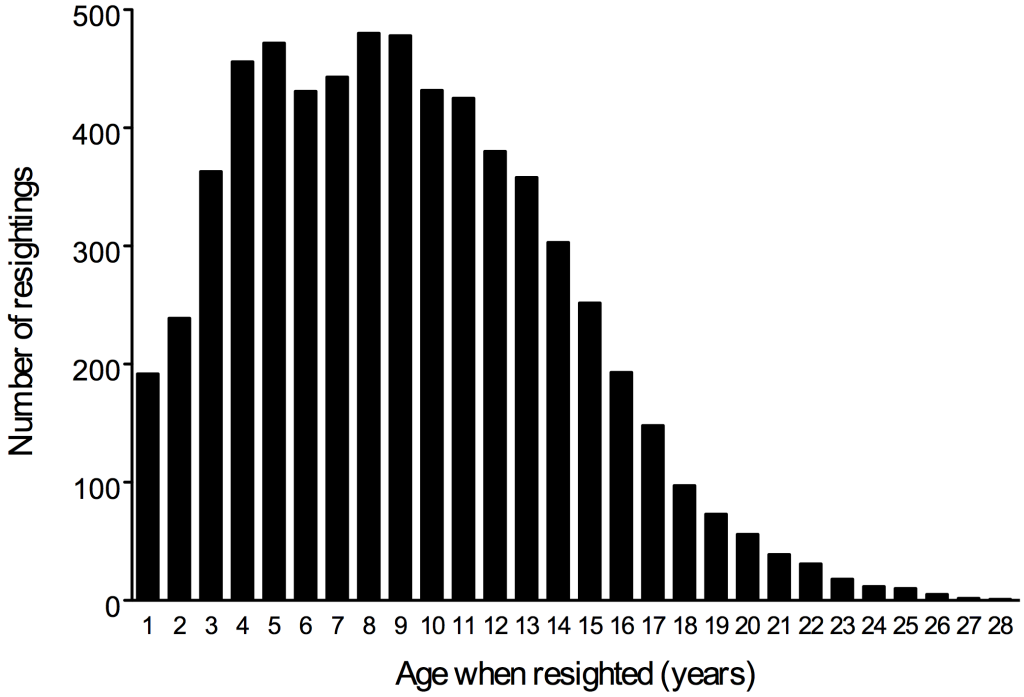


Table S1. Life expectancies of male and female Weddell seals in Erebus Bay, Antarctica. N = the number of observed individuals alive at the start of the age, NDead = the number of individuals that died from the previous age to the current age (e.g., 95 individuals died from age 7 years to 8 years), Mortality = mortality rate calculated as $1 - \varphi$, Expected years left = the expected years of life remaining after an individual has reached the current age, Life expectancy = the expected life span of an individual from birth, given the individual is guaranteed to survive to the current age (Expected years left + Age).

Male

Age	N	NDead	Mortality	Expected years left	Life expectancy
0	7516	2482	0.454	7.60	7.60
1	5034	305	0.401	10.10	11.10
2	4729	289	0.062	9.72	11.72
3	4440	277	0.063	9.32	12.32
4	4163	267	0.064	8.90	12.90
5	3896	260	0.066	8.48	13.48
6	3636	254	0.069	8.05	14.05
7	3382	250	0.072	7.62	14.62
8	3132	246	0.077	7.18	15.18
9	2886	243	0.082	6.75	15.75
10	2643	240	0.088	6.33	16.33
11	2403	237	0.100	5.91	16.91
12	2166	233	0.104	5.51	17.51

13	1932	229	0.1140	5.11	18.11
14	1703	222	0.126	4.73	18.73
15	1481	214	0.140	4.36	19.36
16	1268	203	0.156	4.02	20.02
17	1065	189	0.174	3.68	20.68
18	876	173	0.195	3.37	21.37
19	703	154	0.220	3.08	22.08
20	549	134	0.248	2.80	22.80
21	415	112	0.279	2.55	23.55
22	303	90	0.315	2.30	24.30
23	213	70	0.354	2.07	25.07
24	143	51	0.397	1.83	25.83
25	92	36	0.442	1.57	26.57
26	56	23	0.490	1.24	27.24
27	33	15	0.540	0.78	27.78
28	18	0	0.590	0	28

Female

Age	N	NDead	Mortality	Expected years left	Life expectancy
7	1274	101	0.082	8.62	15.62
8	1172	95	0.083	8.33	16.33
9	1077	89	0.085	8.02	17.02
10	987	84	0.087	7.70	17.70
11	903	79	0.089	7.38	18.38
12	823	75	0.092	7.04	19.04
13	747	71	0.096	6.70	19.70
14	676	68	0.101	6.36	20.36
15	607	64	0.107	6.02	21.02
16	542	61	0.113	5.68	21.68
17	480	58	0.121	5.35	22.35
18	422	54	0.129	5.02	23.02
19	367	51	0.139	4.69	23.69
20	316	47	0.151	4.38	24.38
21	268	44	0.164	4.07	25.07
22	224	40	0.180	3.77	25.77
23	184	35	0.197	3.48	26.48

24	148	31	0.2164	3.20	27.20
25	116	27	0.239	2.93	27.93
26	89	22	0.264	2.66	28.66
27	66	18	0.293	2.40	29.40
28	48	15	0.324	2.12	30.12
29	33	11	0.359	1.83	30.83
30	22	8	0.340	1.47	31.47
31	14	0	0.436	1.00	32

Figure S2. Apparent annual survival of male Weddell seals. The blue points and error bars represent the estimates from the model receiving the most support (lowest Watanabe-Akaike Criterion score), $\text{Logit}(\varphi) = \beta_{\text{age 0}} \times \text{age}_0 + \beta_{\text{age 1}} \times \text{age}_1 + \beta_{\text{age}} \times (\text{age 2}\ldots\text{age 28}) + \beta_{\text{age}^2} \times (\text{age 2}\ldots\text{age 28}) + \beta_{\text{year}} \times \text{year}$, $\text{Logit}(p) = \beta_{\text{age 1}} \times \text{age}_1 + \beta_{\ln(\text{age})} \times (\text{age 2}\ldots\text{age 28}) + \beta_{\text{year}} \times \text{year}$, and the red points and error bars represent the estimates from the model receiving the second-most support, $\text{Logit}(\varphi) = \beta_{\text{age 0}} \times \text{age}_0 + \beta_{\text{age 1}} \times \text{age}_1 + \beta_{\text{age 2 through 3}} \times (\text{ages 2 through 3}) + \beta_{\text{age 4 through 9}} \times (\text{age 4 through 9}) + \beta_{\text{age 10 through 16}} \times (\text{age 10 through 16}) + \beta_{\text{age 17 through 28}} \times (\text{age 17 through 28}) + \beta_{\text{year}} \times \text{year}$, $\text{Logit}(p) = \beta_{\text{age 1}} \times \text{age}_1 + \beta_{\text{age}} \times (\text{age 2}\ldots\text{age 28}) + \beta_{\text{age}^2} \times (\text{age 2}\ldots\text{age 28}) + \beta_{\text{year}} \times \text{year}$.

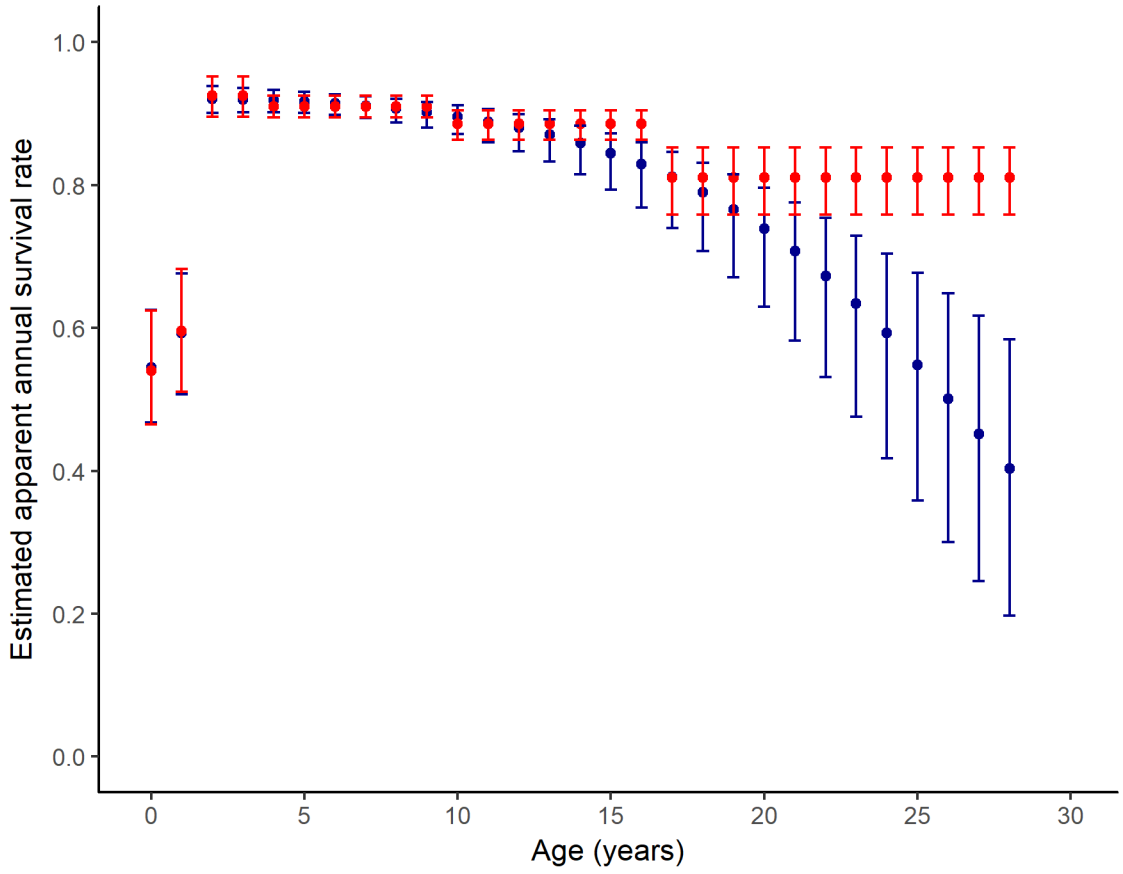
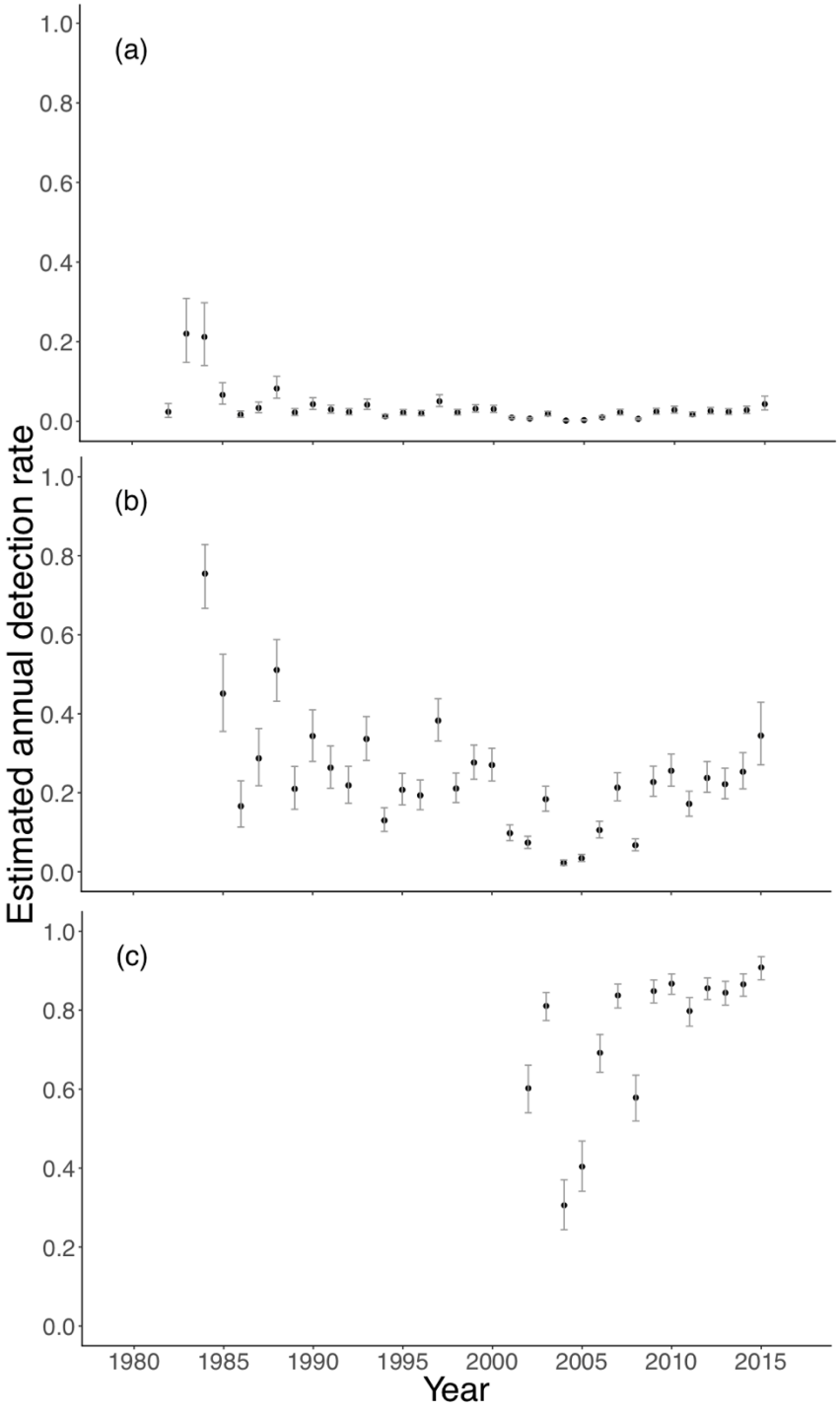


Figure S3. Detection by year of male Weddell seals. Detection rates as estimated by our best-supported model (lowest Watanabe-Akaike information criterion score), Logit(p) = $\beta_{age\ 1} \times age_1 + \beta_{ln(age)} \times (age\ 2 \ldots age\ 28) + \beta_{year} \times year$, for an individual with a random effect of 0 detected at 1 year of age (a), detected at 3 years of age (b), and detected at 20 years of age (c). Error bars show the 95% credible interval.



APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Figure S1. Relationship between mating system and the proportion of baculum length to body length for 17 pinniped species.

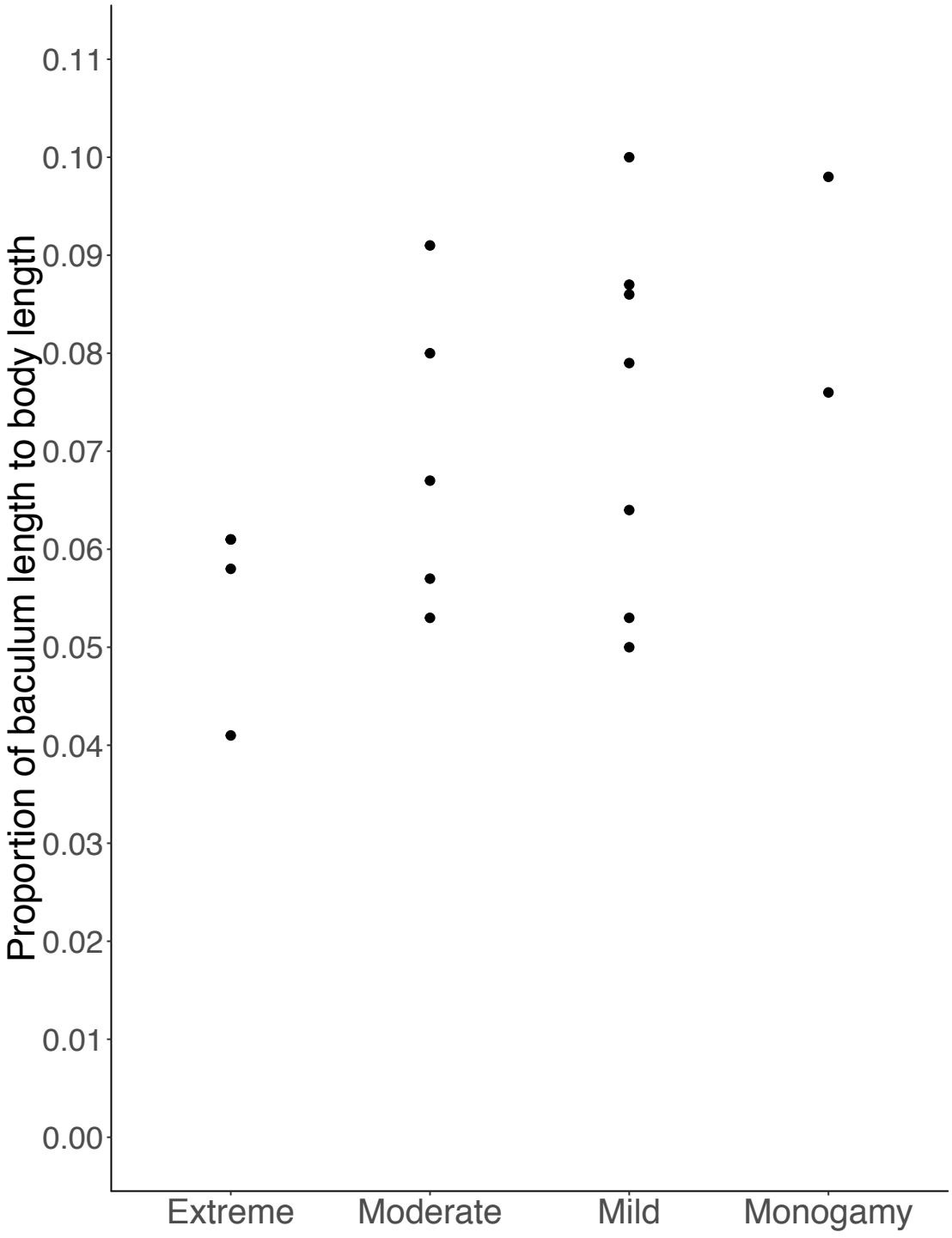


Figure S2. Relationship between baculum length and the log-odds of survival at two years of age (A), sexual maturity (B), and social maturity (C).

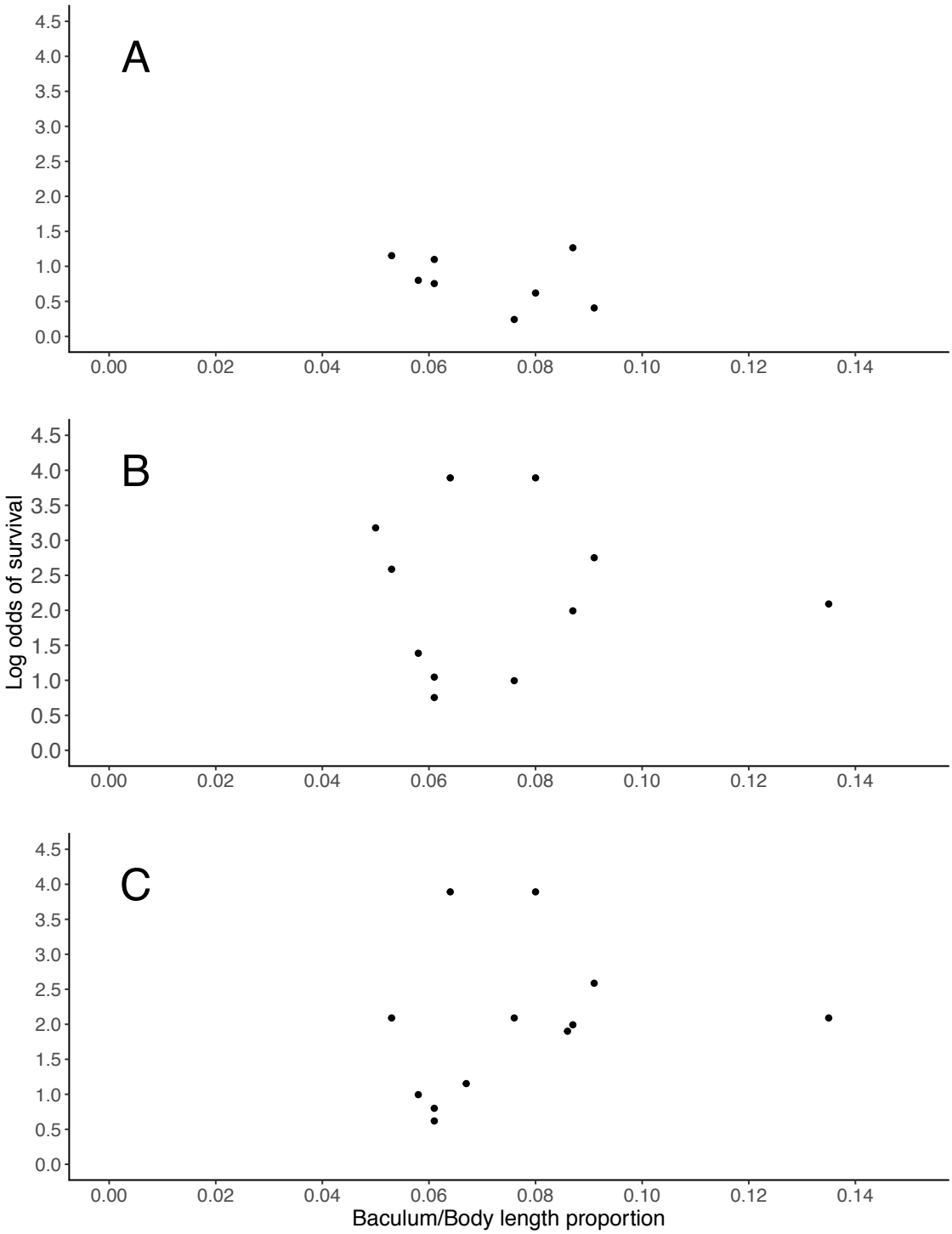


Figure S3. Residuals by species. Residuals were calculated from subtracting the predicted log-odds of survival at the age of social maturity from the observed log-odds of survival at the age of social maturity. The predicted log-odds of survival values were simulated from the posterior distribution of the Bayesian phylogenetically controlled generalized least squares model.

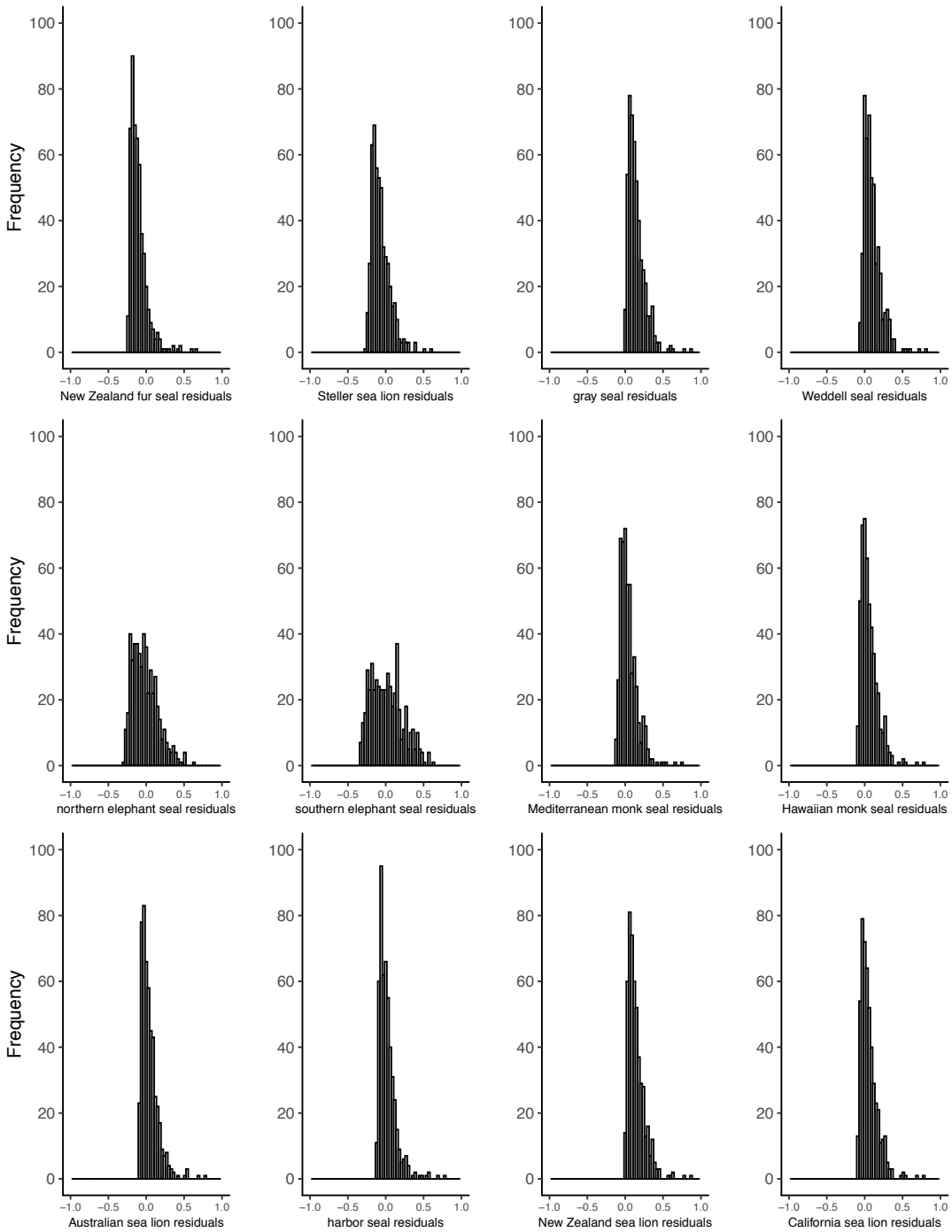


Figure S4. Posterior predictive check comparing model estimates and observed data. The relationship between standard body length and the log-odds of survival for male pinnipeds at the age of social maturity are shown for observed data (purple diamonds) and simulated data from the Bayesian phylogenetically controlled generalized least squares posterior distribution (orange regression lines). Goodness-of-fit is demonstrated by observed data points inside the distribution of regression lines.

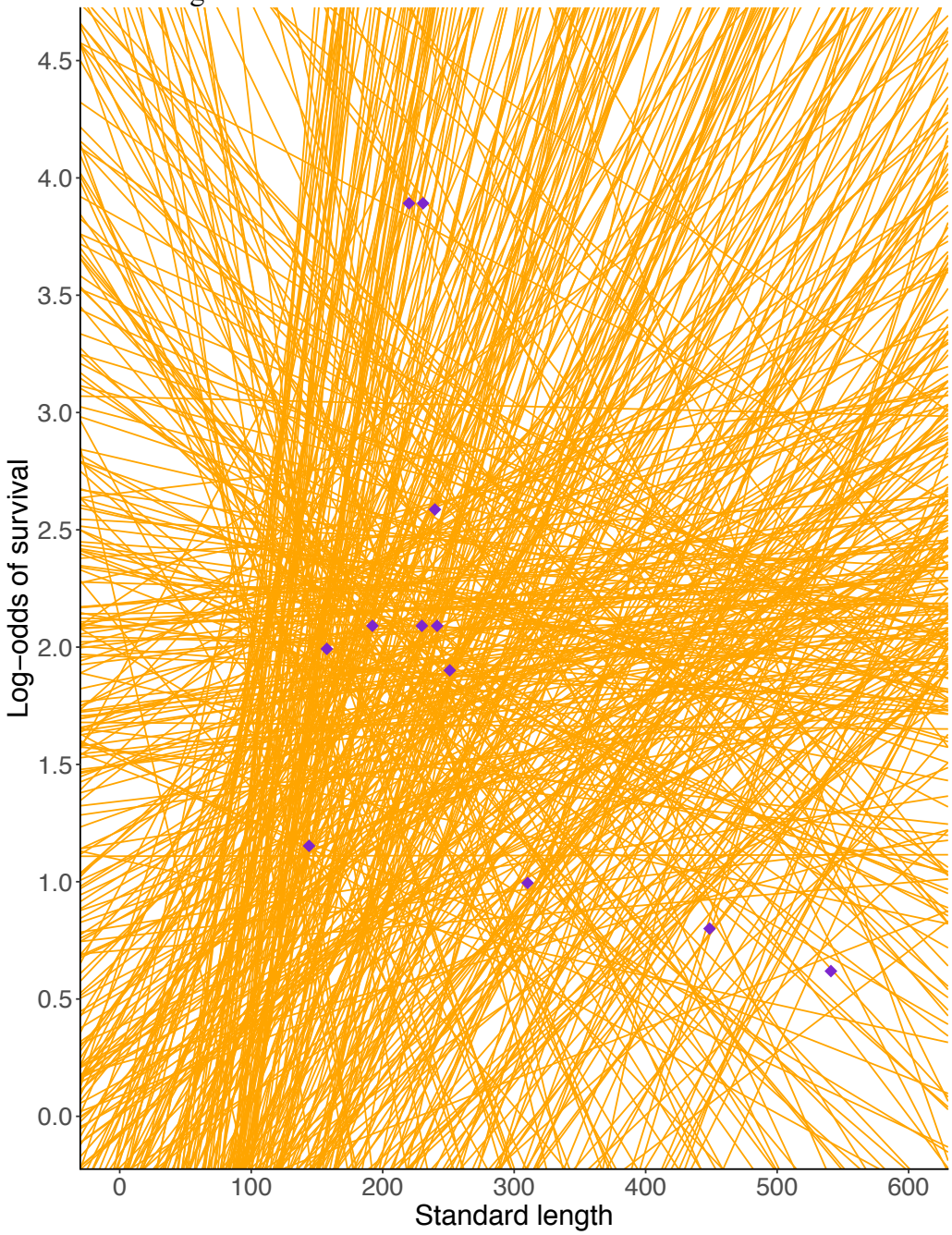


Table S1. Accessions of gene sequences used in creating phylogenetic trees of pinniped species used in the model.

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M. angustirostris	AY377352	AY377231 AY377230	AY377319	AY377301 AY377300	AY377370	AY377325 AY424646	AY377208 AY377207	AY377272	AY377162 AY377161	AY377185 AY377184	AY377139 AY377138	AY377334	AY377254 AY377253	NA	NA
M. leonina	AY377353 AM181023	AY377232 AM181023	AY377320 AM181023	AM181023	AY377371 AM181023	AY377326 AM181023 X82298	AY377209 AM181023	AY377273 AM181023	AY377163 AM181023	AM181023	AM181023	AY377335 AM181023	AY377255 AM181023	AM181023 Y08523	AM181023
M. monachus	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473	MG570472 MG570475 MG570474 MG570473 MG57047	AY377373	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	MG570472 MG570475 MG570474 MG570473 MG57047	NA	NA

M. schauinsland i	1 AY377355 AY377354 AM181022	1 AY377234 AY377233 AM181022	MG570471 AM181022	1 AY377304 AM181022	AY377372 AM181022	1 AY377327 GU174610 AM181022 X72209 AF380915 AF380914 AF380913 AF380912 AF380911 AM181020 AB510422 AB510421 AB510420 AB510419 AB510418 AB510417 AB510416 AB510415 AB510414 AB510413 AB510412 AB510411 AB510410 AB510409	1 AY377211 AY377210 AM181022	1 AY377275 AY377274 AM181022	1 AY377165 AY377164 AM181022	1 AY377188 AM181022	1 AY377142 AM181022	1 AY377337 AY377336 AM181022	1 AY377257 AY377256 AM181022	AM181022 Y08524	AM181022
N. cinerea	AM181020	AM181020	AM181020	AM181020	AM181020		AM181020	AM181020	AM181020	AM181020	AM181020	AM181020	AM181020	AM181020	AM181020	AM181020
P. vitulina	AM181032 X63726	AM181032 X63726	AM181032 X63726	AM181032 X63726	AM181032 X63726		AM181032 X63726	AY750640 AM181032 X63726	GU733705 GU733704 GU733703 GU733692 GU733691 GU733690 GU733688 GU733678 GU733677 GU733676 GU733675 GU733674 GU733673 GU733672	AM181032 X63726	JF443365 JF443364 KF281664 KF281663 JF442788 AM181032	AM181032 X63726	AM181032 X63726	AM181032 X63726	AM181032 X63726

AB510408

AM18103

2 X82306

X63726

GU733671

GU733670

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P. hookeri	KX388144 KX388143 AM181019	KX388144 KX388143 AM181019	KX388144 KX388143 AM181019	AM181019	AM181019	AF380919 KX388144 KX388143 AM181019	KX388144 KX388143 AM181019	KX388144 KX388143 AM181019	KX388144 KX388143 AM181019	AM181019	AM181019	KX388144 KX388143 AM181019	KX388144 KX388143 AM181019	AM181019	AM181019
Z. californianus	AM181017	AM181017	AM181017	AM181017	AM181017	L37020 AM422164 AM422163 AM422162	AM181017	AY750639 AM181017	AM181017	AM181017	AM181017	AM181017	AM181017	AM181017 Y08525	AM181017

AM422161

AM422160

AM422159

AM422158

AM422157

AM422156

AM422155

AM422154

AM422153

AM181017 X82310

APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Figure S1. Plot of residuals between the predicted number of reproductive-age female neighbors and the observed number of reproductive-age female neighbors within a 100-m radius of a male for 3 years of age, 9 years of age, 16 years of age, and 20 years of age. Predicted datasets were generated using the quadratic model. Note x-axes differ across plots.

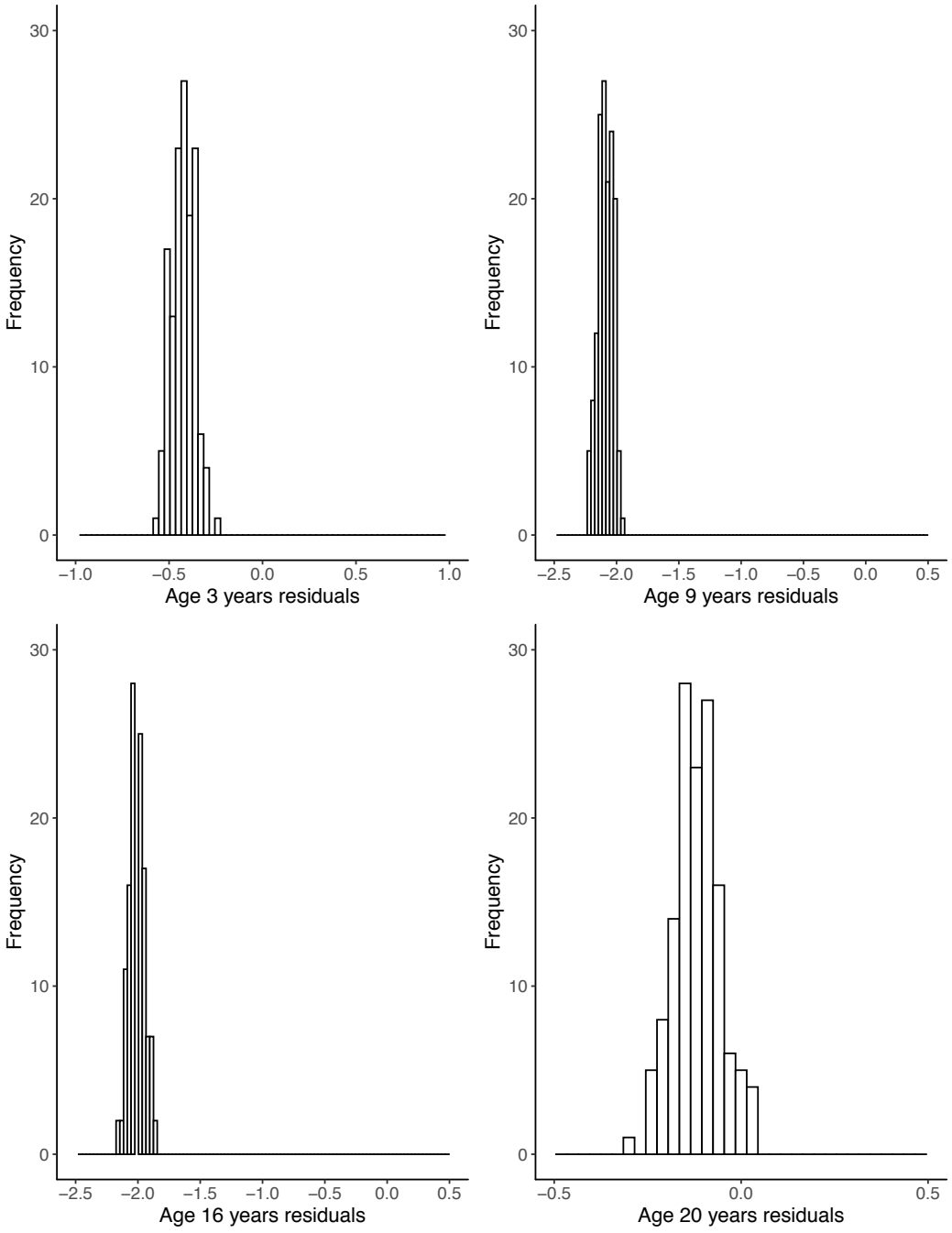

Figure S2. Comparison of the observed number of reproductive-age female neighbors and the predicted number of female neighbors within 100 m of a male. Predicted values are from the quadratic functional form model. The purple points are the observed values; the solid blue line is the predicted mean number of reproductive-age female neighbors; the dashed brown line is the predicted median number of reproductive-age female neighbors; and the gray ribbon is the 95% credible interval for the predicted mean. The predicted values are for an average male in an average year.

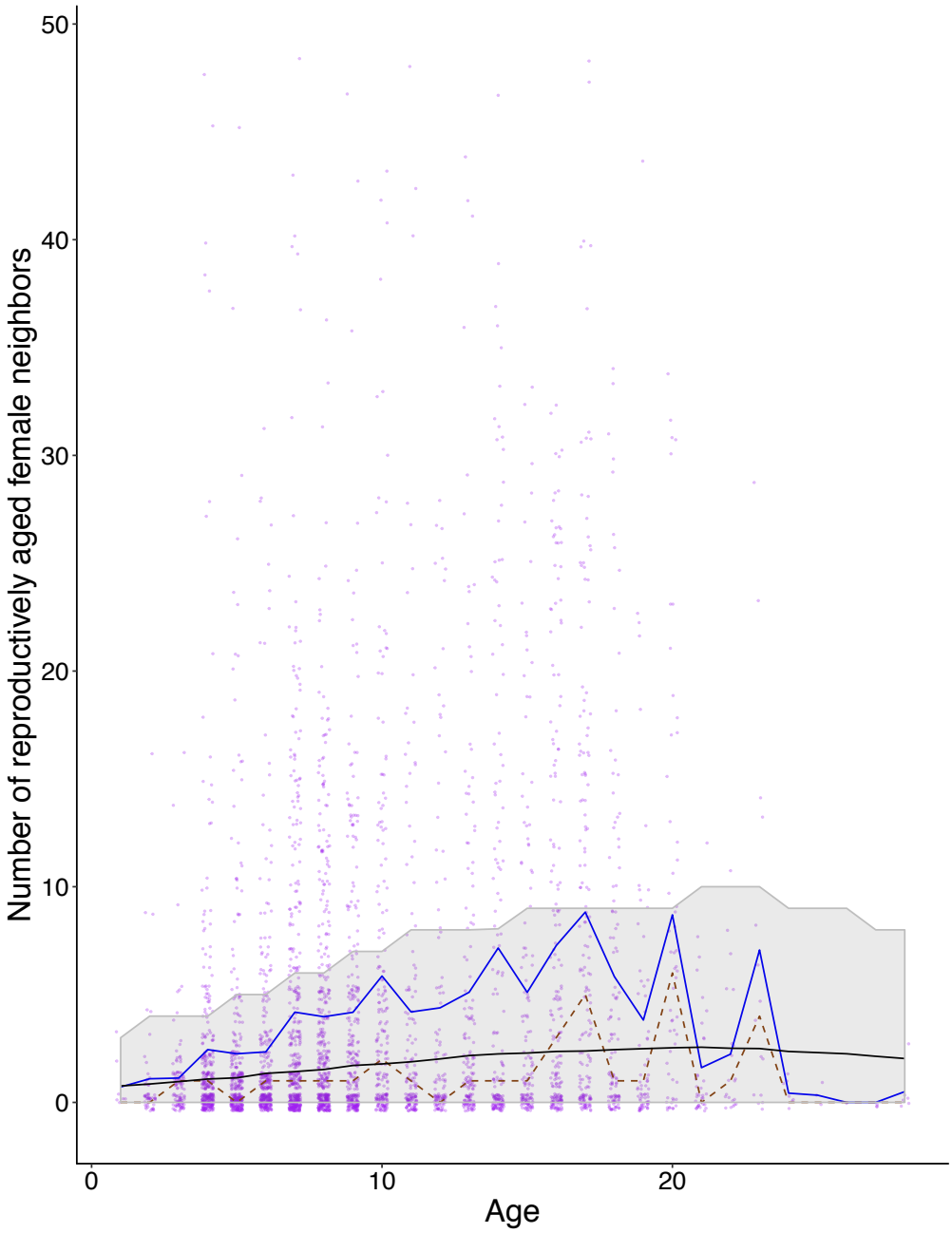

Figure S3. Comparison of the distributions of y (observed number of reproductive-age female neighbors) and y_{rep} (predicted number of reproductive-age female neighbors from 4000 simulated datasets). The plots illustrate similar distributions from the observed data and model-predicted data for all four age models, quadratic (A), logarithmic (B), linear (C), and age-as-factor (D) models. Plots were generated using the pp_check() function in the rstanarm package.