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Influence of age and individual identity in the use of breeding colony habitat by male Weddell seals in Erebus Bay, Antarctica

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Abstract

Male–male contest behavior can contribute to spatial distributions of male pinnipeds during breeding seasons. To maximize breeding opportunities, the most competitive males would be expected to be surrounded by the highest numbers of reproductive-age females. As information regarding fine-scale spatial ecology of Weddell seals is lacking, we performed an exploratory study using 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 also influenced the number of reproductive-age female neighbors. The youngest males tended to haul out in offshore areas associated with better hunting, and older males tended to settle in more nearshore areas associated with more pup production. Our findings from this preliminary investigation indicate that male Weddell seal spatial behavior during the breeding season varies with age and individual and might be related to reproductive activity.

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KEYWORDS
age, habitat usage, individual heterogeneity, *Leptonychotes weddellii*, spatial distribution, Weddell seal

1 | INTRODUCTION

Variation in habitat usage is often interpreted through the lens of natural selection, which posits that individuals should settle in the highest-quality habitat to maximize fitness (Clark & Shutler, 1999; Fretwell, 1969). However, diverse habitat features can dictate spatial patterns of animals, such as thermoregulatory resources (Wolf et al., 2005), exposure to predators and harsh weather (Krafft et al., 2007), the quality of individuals (Carrete et al., 2006) and potential mates (Trivers, 1972). Sexual selection can also influence how animals spatially distribute themselves in a habitat. Variation in spatial distribution can stem from competition of males seeking optimal sites for displaying to females (Winemiller, 1992). During the breeding season, access to reproductive females and male–male contest behavior can most strongly affect the spatial distribution of males of several taxa (Le Boeuf, 1974; Magaña et al., 2011; Post & Jeanne, 1983; Sacks et al., 1999; Sherry & Holmes, 1989; Wahlström, 1994). Observations of some species have found that older males have a tendency to obtain high-quality breeding sites (Coulson, 1968; Pärt, 2001). Although many studies have demonstrated that animals can differentially partition their habitat usage based on sex and age, determining the sex and age of marine mammals as well as obtaining a sample of diverse ages, often poses challenges. These challenges tend to limit the number of marine mammal studies investigating fine-scale habitat use by different demographic groups (Baker & Thompson, 2007; Sprogis et al., 2018).

For pinniped species, locations of where females haul out can influence where males settle and form territories during the breeding season (Krafft et al., 2007). The dominance status of males can also 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 males. Engaging in reproductive behavior can also influence spatial use of the habitat. In some species, older males can exhibit aggressive behavior towards and can deter younger males (Connor & Krützen, 2015; Wahlström, 1994), or younger, nonterritorial males might elect to avoid areas where territorial animals settle (Sacks et al., 1999). Therefore, in colonially breeding species with male–male contests, such as pinniped species, the age and quality of the individuals (e.g., physiological condition) at each colony can be a factor in where males position themselves in the habitat (Wolf et al., 2005).

Weddell seals (*Leptonychotes weddellii*, Lesson 1826) 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 2 weeks constantly on the ice in these breeding colonies before taking intermittent swims throughout the rest of the 6- to 7-week nursing period (Siniff et al., 2008; Stirling, 1969). During this time and through December, males engage in underwater male–male contests along tidal cracks associated with breeding colonies and use visual and acoustic displays to attract females, but they take breaks to haul-out on the ice in the breeding colonies among other males and females (Bartsh et al., 1992; Siniff et al., 1977). Mating occurs in December after females 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. As sexual selection favors traits that lead to breeding success (Emlen & Oring, 1977), male Weddell seals would likely compete for access to either females of the highest quality or the greatest number of females. Therefore, it is possible that better male competitors are more likely to be observed in the nearshore areas of the habitat. However, Hadley et al. (2008) found no variation in age-specific survival rates and a higher probability of age-specific first reproduction from pups that were born at offshore locations compared to nearshore locations. Because females born at offshore locations have higher probabilities of breeding than females born at nearshore sites (Hadley et al., 2008), better male competitors might, instead, make greater long-term reproductive investments by mating with females at offshore locations. Finally, the age of male Weddell seals might relate to their observed haul-out location in Erebus Bay, and age might be linked with male–male competitive ability, as has been reported for other pinniped species (Clinton & Le Boeuf, 1993; Coltman et al., 1999; Godsell, 1991; Lidgard et al., 2012, but see Lidgard et al., 2005). The oldest Weddell seal males might establish themselves in the areas most densely occupied by reproductive-age females, as they would have the most experience defending territories and might have reached a higher social rank than their younger conspecifics. Alternatively, male Weddell seals of intermediate reproductive ages (10–16 years of age; Gelatt, 2001) might have better physical prowess for male–male contests and be most likely to settle near the greatest densities of females.

The objective of this study was to describe the spatial arrangement of male Weddell seals in Erebus Bay, Antarctica, from 2014 through 2018. We specifically sought to address the following research questions: (1) Do older male Weddell seals tend to haul out in areas of the habitat that have higher densities of reproductive-age females? (2) Is there a relationship between male age and the number of reproductive-age female neighbors while hauled out on the ice?

2 | METHODS

2.1 | Study site

Data were collected in Erebus Bay, Antarctica (77.7°S, 166.5°E) from 2014 to 2018 from late September through early December, when male Weddell seals engage in underwater aggressive male–male contest behavior (Bartsh et al., 1992; Siniff et al., 1977). This behavior can include defense of an area by excluding other males from the area, but observations of this kind of territorial behavior are limited (Harcourt et al., 2000). Female Weddell seals haul out across about 13 breeding colonies 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).

2.2 | Marking and re-observation of individual males

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. Each year from early November to early December, approximately six 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 four and six 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.

2.3 | Statistical analyses

To investigate if the distribution of male Weddell seals in the Erebus Bay study site varied with age during the breeding season, we performed fixed-bandwidth kernel density analysis. To compare where males of different age groups settled in the Erebus Bay study site in relation to where prime-aged females settled (see below), we also performed kernel density analysis for females in this age range. Females reach a peak in the probability of reproducing during intermediate reproductive ages centering around 16 years of age, with a range of 12–20 years of age (Paterson et al., 2018), defined here as prime-aged females. 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 using ggmap (Kahle et al., 2019) and the R software environment (R Core Team, 2019).

Kernel density methods result in probability density functions that estimate the spatial distribution of animals, using nonparametric smoothing parameters to display the relative concentration of spatial points (Worton, 1989). 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 prebreeding through the youngest known age males (3 years) to engage in reproductive activity (Harcourt et al., 2007); 5–10 years of age, which represents the earliest known age (5 years) of males exhibiting male–male contest behavior through the age at which many males exhibit reproductive behaviors (Bartsh et al., 1992) but are not as likely to sire offspring (Gelatt, 2001); 11–19 years of age, which represents the age by which almost all males engage in male–male contest behavior (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. Reproductively active males often spend more time in the water during peak breeding, but they tend to haul out for as long as nonreproductive males early and late in the breeding season (Bartsh et al., 1992). Data were pooled across surveys and years. For kernel density estimates and plots, we used the *sp* (Pebesma et al., 2019), *MASS* (Ripley et al., 2019), *spatialEco* (Evans & Ram, 2019), and *ggspatial* (Dunnington & Thorne, 2018) packages in the R programming language (R 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 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 for females (Paterson et al., 2018) to define our lower boundary of female reproductive age. As females are known 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 reproductively active (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 the median distance between multiple observations of a hauled out male Weddell seal within a single season was 80 m. Using a radius of 50 m, only 57% of the observations had at least one female neighbor, but using a radius of 100 m, 69% of the observations had a least one female neighbor. 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. We discuss our results taking into account our selected radius.

To assess 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 with three different functional forms for age: linear, quadratic, and logarithmic (see notation below). 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. 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, i.e., approach but never reach an asymptote (Franklin et al., 2000). We rescaled 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 $\sigma^2_{\text{individual}}$, $\sim N(0, \sigma^2_{\text{individual}})$ and structured such that they allow different individuals to have different means.

We used the package *rstanarm* (Gabry et al., 2020) for R for all regression analyses. As our response data were overdispersed count data, we used a negative binomial model structure (Allison & Waterman, 2002; Berk & 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 m_i and dispersion *k*.

The mean and variance of Y_i can be defined as:

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

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:

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

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:

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

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 (Casella & George, 1992; Gelfand & Smith, 1990; Geman & Geman, 1993) using four chains. 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. We used an independent, vague normal prior with the mean set to 0 and variance as $\sigma^2_{\text{individual}}$. 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 random effects) and mean + 2 σ^2_{ind} (above-average random effects) 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 <1.1 (Gelman & Rubin, 1992), for each monitored parameter. Once convergence was achieved, we calculated k-fold information criteria (kfoldic) values by partitioning the data set 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).

3 | RESULTS

From 2014 to 2018, 31 surveys were completed to record the fine-scale spatial location data of known-age Weddell seals during the breeding season, resulting in 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 5-year study period and approximately four times per year (*SD* = 1.59, range = 1–6). The average male was 9.76 years of age (*SD* = 4.98, range = 1–28) and had a mean of 4.25 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 1). The youngest males in our study (ages 2–4 years) had a mean of 2.02 (*SD* = 5.23) reproductive-age female neighbors. Males aged 5–10 years had a mean of 3.67 (*SD* = 6.51) reproductive-age female neighbors. Males aged 11–19 years had a mean of 6.00 (*SD* = 9.14) reproductive-age female neighbors. The oldest males (ages 20–28 years) had a mean of 4.76 (*SD* = 7.64) reproductive-age female neighbors.

We found evidence that the prime-aged females settled in the southern nearshore area, where the greatest number of pups tend to be born each year (Figure 2). The plots of relative densities of males in different age groups supported our prediction that males of different ages used the Erebus Bay study site heterogeneously. As males reached 20 years of age, a greater proportion of high usage areas were found in the more southern and nearshore locations of the habitat associated with the breeding colony with the highest density of pups and reproductive-age females. 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 3). The relative densities of prime-age females and of males in different age groups provide evidence that males in the age class 11–19 years of age had the most spatial overlap with prime-age females (Figures 2 and 3). The proportion of overlap in 80% isopleth utilization distribution between prime-age females and males aged 2–4 years was only 12.6%, for males aged 5–10 years was 36.9%, for males aged 11–19 years was 65.5%, and for males 20 years of age and older was 23.4%.

Models that included age as a covariate outperformed the intercept-only model, but the three models that evaluated different functional forms of age performed similarly (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. The models differed the most 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). Further, it is important to recognize that our results only focus on a radius of 100 m, and it is possible that a different pattern might emerge with a different radius.

Model diagnostics indicated that models achieved convergence (Table S1, Figure S1). Posterior-predictive checks for the best-supported model (quadratic) 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 S2, S3, S4). Further, the coefficients for age (1.12) and age-squared (−0.83) were estimated precisely such that the 95% CIs 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.

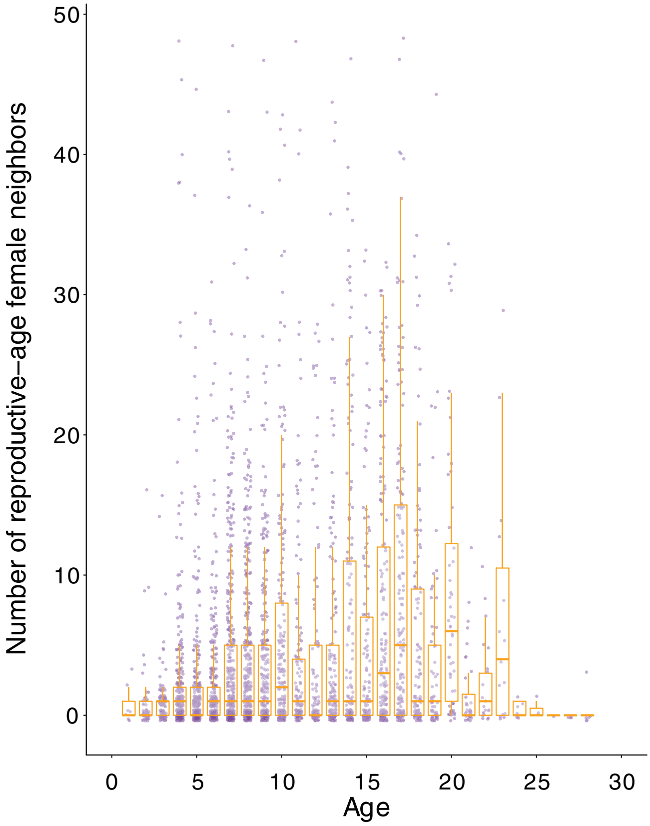

FIGURE 1 Number of reproductive-age female neighbors within a 100 m radius of a male for each age of observed males. Purple points show the number of reproductive-age female neighbors for each recapture, and boxplots represent the median and 25th and 75th quartiles of the number of reproductive-age female neighbors for each age of males.

The number of reproductive-age females within a 100 m radius of a male peaked at ages in the upper teens and early 20s (Figure 4). However, the number of reproductive-age female neighbors varied little with age, and many individuals across all ages did not have any reproductive-age female neighbors. As noted earlier, the youngest reported age for a reproductively active male Weddell seal is 3 years, and our quadratic model predicts that an average 3-year-old male would have 0.95, 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 (Bartsh et al., 1992), and the average 9-year-old male is predicted to have 1.67, 95% CI[1.42, 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 2.40, 95% CI[2.04, 2.81] 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 2.54, 95% CI[2.17, 2.95] reproductive-age females within 100 m.

For males >20 years old, the quadratic model predicts a drop-off in the number of females within 100 m. 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, 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.

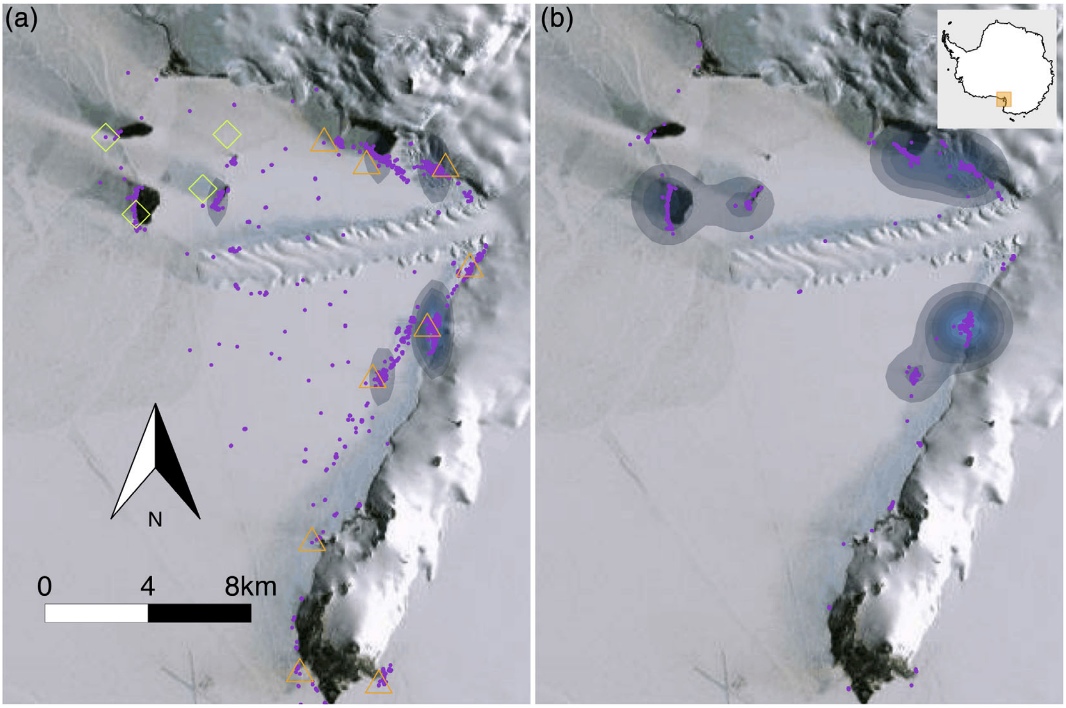

FIGURE 2 Female and pup kernel density estimates. Recaptures and kernel densities of prime reproductive-age female Weddell seals (a) and pups (b) in Erebus Bay, Antarctica reveal that these two demographic groups are most likely to be found in the southern nearshore areas of the habitat. The lightest blue color represents a 20% isopleth, and the darkest blue color represents an 80% isopleth. Relative densities of dependent pups indicate areas where mothers were captured because mothers and pups are routinely in close proximity. Green diamonds indicate offshore breeding colonies, and orange triangles indicate nearshore breeding colonies.

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 one (M = 0.17, 95% CI[0.09, 0.27]) reproductive-age female within 100 m, which is well below the mean for that age (2.54, 95% CI[2.17, 2.95]). 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.

4 | DISCUSSION

Our results provide the first fine-scale analysis of age-specific spatial patterns of male Weddell seals. Younger male Weddell seals tended to occupy the more offshore locations with lower abundances of reproductive-age females. In the more southern and nearshore areas of habitat, both densities and ages of males tended to be higher than they

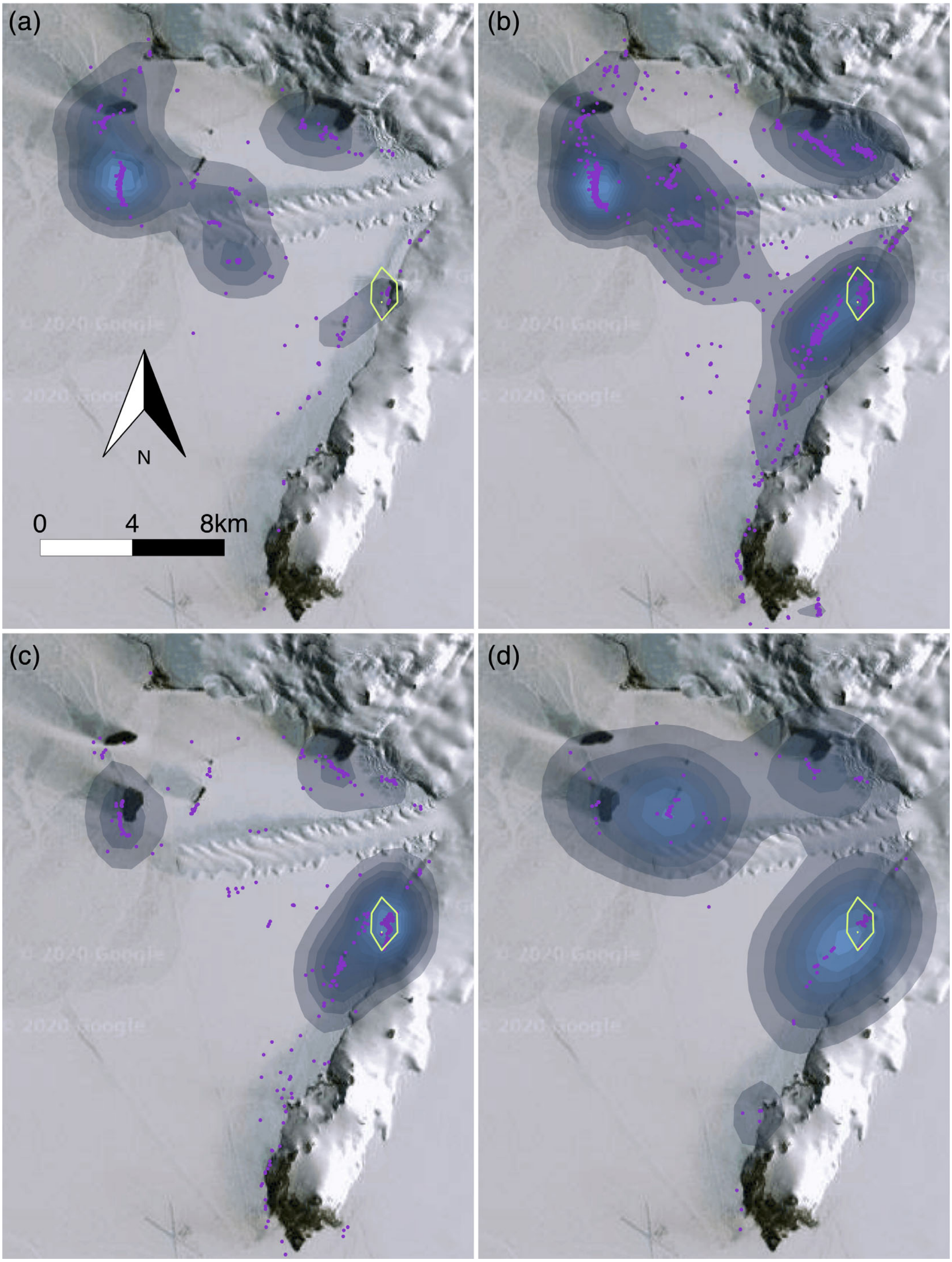

FIGURE 3 Male age-specific kernel density estimates. Recaptures and kernel densities of male Weddell seals (a) 2–4 years of age, which represents the prebreeding through youngest known age (3 years) to engage in reproductive activity (Harcourt et al., 2007), (b) 5–10 years of age, which represents the earliest known age of males exhibiting male–male contest behavior (5 years) through the age at which many males engage in male–male contest behavior (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 engage male–male contest behavior (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 blue color represents a 20% isopleth, and the darkest blue color represents an 80% isopleth.

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 data set 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 the fixed effect of year as a factor variable, and I represents the random effect of individual.

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

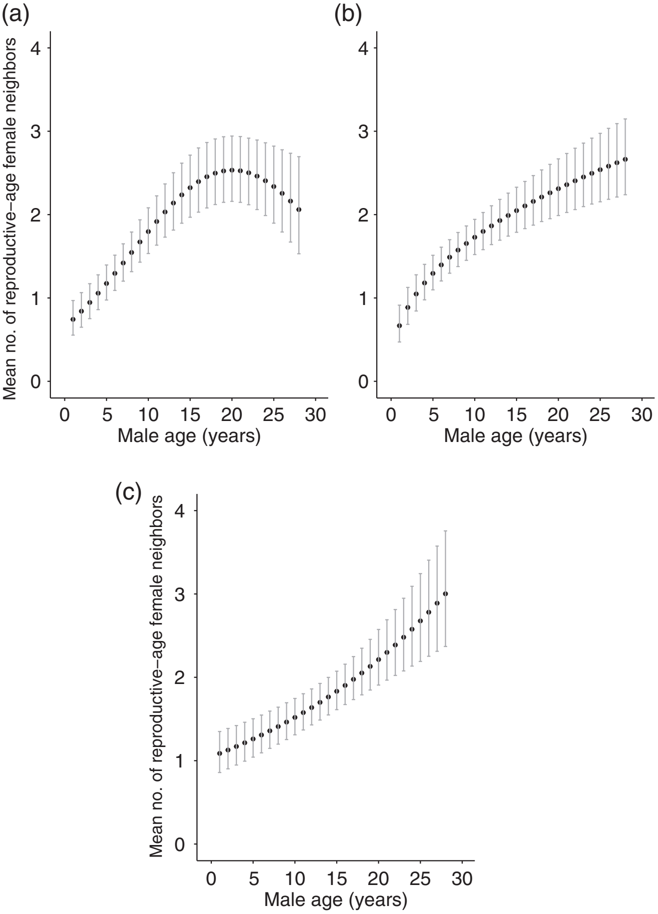

FIGURE 4 Age-specific mean number of reproductive-age females within a 100 m radius of a male estimated from our most supported models (a) quadratic, (b) logarithmic, and (c) linear; see Table 1 for full model structures. Point estimates are for an average individual for an average year. Error bars indicate 95% credible intervals.

were in other locations. Similarly, males with the greatest number of reproductive-age female neighbors within a 100 m radius tended to be older (≥10 years of age). Proximity to females had a significant relationship with the number of paternities in Galapagos sea lions, another pinniped species that does not exhibit an extreme form of polygyny

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 two standard deviations below the mean value (below average RE individual), the mean (average RE individual), or two 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, 2.81)	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)

and engages in at least some reproductive activity in the water (Pörschmann et al., 2010). The uncertainty associated with our model selection results provides unclear information regarding the spatial behavior of the males >20 years of age. Additional spatial data for these older males are necessary to better explain spatial patterns of this age group, but few males survive to reach 20 years of age or older (Brusa et al., 2020). 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. However, without movement data, we do not know the biological significance of a 100 m radius. 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 engage in reproductive activity.

Younger male Weddell seals (ages 3–8 years old) tended to occupy areas of Erebus Bay that Testa et al. (1985) reported to be abundant in food resources (northern, offshore areas), and older males, which are the most likely to be reproductively active (Bartsh et al., 1992), were most likely to be found in areas with the highest abundances of reproductive-age females (southern, nearshore areas). We speculate that many younger males are more likely to attend northern offshore colonies to decrease the number of negative interactions with older, more competitive males. 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.

Similar to other pinniped species, participation in male–male contest behavior in Weddell seals likely increases with age (Clinton & Le Boeuf, 1993; Pitcher & Calkins, 1981). 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, because male–male contest behavior and copulation of Weddell seals occur in the water, we do not know if there is a positive relationship between reproductive behavior and the spatial behavior of Weddell seals hauled out on the ice during the breeding season. Alternatively, males that reach these older ages might do so because they are not competitive, tend to spend most of the breeding season avoiding male–male contests, and, therefore, have additional energy to allocate to somatic maintenance. The number of reproductive-age female neighbors of males on the ice might not be related to the number of copulations the males gain or their male–male contest performance.

Male Weddell seals exhibited notable levels of individual variation in their number of reproductive-age female neighbors. 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. For example, some of the oldest males had many females nearby, whereas others had zero, which was accommodated by the random effect of individual included in our models. 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 & Côté, 2008). Individual quality might also have a greater influence on social rank than age in male Weddell seals. However, because our data only include, at most, 5 years for each individual, it is difficult to distinguish between an age effect rather than an individual effect.

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. The age-specific distribution of male Weddell seals in Erebus Bay, Antarctica, suggests that younger males generally do not settle in areas of the habitat associated with the highest densities of reproductive-age females and pups. 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 and if their in-water spatial behavior is similar to that on the ice. We anticipate that further age-specific behavioral and reproductive research focused on male Weddell seals will reveal the mechanisms behind the variation in relative densities of males with age in Erebus Bay. Further details regarding age-specific male spatial and reproductive behaviors will provide additional insight of how natural and sexual selection can shape male life histories of marine mammals. Our results suggest that age and, especially, individual heterogeneity are related to fine-scale spatial behavior regarding the proximity of reproductive-age female neighbors.

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AUTHOR CONTRIBUTIONS

Jamie Brusa: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing-original draft; writing-review & editing. **Jay Rotella:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing-review & editing. **Robert Garrott:** Conceptualization; funding acquisition; investigation; methodology; project administration; visualization; writing-review & editing.

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SUPPORTING INFORMATION

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