The effect of age, sex, and resource abundance on patterns of rake markings in resident killer whales (*Orcinus orca*)

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Abstract

Fluctuations in aggressive behavior of group-living species can reflect social conflict and competition for resources faced by individuals throughout their lifespan and can negatively impact survival and reproduction. In marine mammals, where social interactions are difficult to observe, tooth rake marks can be used as an indicator of received aggression. Using 38 years of photographic data, we quantified the occurrence of tooth rake marks on wild resident killer whales (*Orcinus orca*), examining the effects of age, sex, and prey abundance on rake density. Our analysis revealed sex and age effects, with males exhibiting higher rake density than females and rake density declining significantly with age. Contrary to predictions, we observed an increase in rake density across the population as the abundance of their primary food resource, Chinook salmon (*Oncorhynchus tshawytscha*), increased. These results provide indirect evidence of fluctuations in received aggression from conspecifics across the lifespan of an individual, possibly reflecting changes in patterns of social conflict which may be mediated by resource abundance. Our findings highlight the need for further research to examine the fitness consequences of aggression in killer whales and to understand

the proximate mechanisms by which resource abundance influences rates of aggression in the population.

KEYWORDS

cetacean, conflict, group-living, intraspecific aggression, killer whale, *Oncorhynchus tshawytscha*, *Orcinus orca*, photo-id, salmon, tooth rake marks

1 | INTRODUCTION

In group-living species, the benefits of living with others are countered by increased competition for resources that are vital for survival and reproduction (Andersson, 1994). To gain access to resources such as food and mates, individuals must compete against each other, often resulting in aggressive interactions between conspecifics (Hardy & Briffa, 2013). Interindividual differences in competitive ability and variation in resource availability can shape aggressive behavior (Alexander, 1974) and have a profound effect on the fitness of an individual (Holekamp et al., 1996; Kahlenberg et al., 2008; Rémy et al., 2013; Thompson et al., 2007) and the organization of animal societies. Due to the nature of group living, competition-induced aggression is therefore expected, particularly when resources are limited (Barton, 1993; Barton & Whiten, 1993; Boccia et al., 1988; Fattorini et al., 2018; Wright et al., 2014) and often arises between potential mates (Huchard & Cowlishaw, 2011; Smuts & Smuts, 1993), between competitors for mates (Clutton-Brock & Vincent, 1991), or between parents and offspring (Trivers, 1974).

While intraspecific aggression can have fitness benefits for the instigator, it can have considerable negative consequences, especially for the receivers of aggression. Not only is it energetically, physically, and physiologically costly (Georgiev et al., 2013), it can also disrupt social relationships between group-members (Aureli et al., 2002), which provide fitness benefits in several taxa (Snyder-Mackler et al., 2020). Examining the timing of such conflict and the drivers behind it is therefore key to understanding challenges faced by individuals across their lifespan.

Life history events, such as maturation and reproduction, can perpetuate aggression in animal societies as a result of competition for different resources by males and females (Clutton-Brock & Huchard, 2013). High levels of physical aggression as a result of intense competition for females (Andersson, 1994) are commonly observed among adult males in many polygynous mammal species, including primates, (King et al., 2008; Muller & Wrangham, 2009), Asian elephants (*Elephas maximus*; Seltmann et al., 2019), ungulates (Panebianco et al., 2020), and bottlenose dolphins (Smuts & Smuts, 1993). Conversely, the frequency of aggressive interactions by females is assumed to be lower than in males (Darwin, 1871) as a result of female competition being more intense over access to resources vital for reproduction, rather than access to mates (Gadgil and Bossert, 1970; Stockley & Bro-Jorgensen, 2011). Variation between males and females in the rates of received aggression may also be observed at key developmental stages, such as weaning and adolescence, when individuals begin to compete with older and more experienced group members (Hirsch, 2007; Hodge et al., 2009) for resources which are critical for survival and reproductive success (Alexander, 1974; Van Schaik, 1983; Wrangham, 1980). Similarly, in species that live in established groups, aggression is often used to establish dominance hierarchies (Pusey & Packer, 1997), often resulting in younger, subordinate individuals being subject to aggression from older, more dominant individuals.

For many species, quantifying patterns of aggression can be a significant challenge because aggressive interactions are infrequent, short in duration, or are difficult to observe. One solution to this challenge is to use wounds as indirect evidence of aggressive interactions (e.g., olive baboons, *Papio anubis*, MacCormick et al., 2012; salamanders, *Amphibia plethodontida*, Staub, 1993; chimpanzee, *Pan troglodytes*, Muller & Mitani, 2005). Direct observations of aggression are especially rare in free-ranging cetaceans where behavioral studies are generally limited to surface

observations. However, aggressive interactions in toothed whales result in scars and wounds that can be used as a proxy for the rate of aggression received (MacLeod, 1998; McCann, 1974; Samuels & Gifford, 1997; Scott et al., 2005). Tooth rake markings are long, thin parallel lines, found on cetaceans as the result of another animal running its teeth along the skins surface. They have been reported in a wide range of odontocete families, including Delphinidae, Ziphiidae, Physeteridae, and Mesoplodon (McCann, 1974), and are well-established indicators of interactions with predators or conspecifics (Heithaus, 2001; Luksenburg, 2014; MacLeod, 1998; McCann, 1974; Puig-Lozano et al., 2020; Scott et al., 2005; Visser, 1998). Although rake marks only provide an indirect measure of aggression, biting has been found to be closely associated with aggressive behavior in several species of toothed whales (Connor et al., 2000; Samuels & Gifford, 1997) and in some instances, play behavior (which may also lead to rake marks) can develop into aggression (Scott et al., 2005). As such, rake marks on toothed whales likely reflect the level and context of aggression received (Ham et al., 2021; Scott et al., 2005), which varies widely across species according to their evolutionary history. For example, in some species, including narwhals, (*Monodon monoceros*, Gerson & Hickie, 1984), Risso's dolphins, (*Grampus grisues*, MacLeod, 1998), and sperm whales, (*Physeter microcephalus*, Kato, 1984), diet specialization is believed to have driven a reduction in the repigmentation of tooth scars during wound-healing (MacLeod, 1998). In these species, scars accumulate with age and a high incidence of rake marks observed on adult males are thought to be an indicator of male quality, with more scars signaling a greater ability to fight and survive (MacLeod, 1998). Conversely, in other species, including bottlenose dolphins (Lee et al., 2019; Lockyer & Morris, 1985) and killer whales (Bigg, 1982), rakes tend to heal over time, and as such, examining patterns of these temporary rake markings can provide information about the timing and intensity of received aggression.

Killer whales, like other cetaceans, exhibit rake marks across all age and sex classes (Jourdain & Karoluissen, 2018; Mrusczok, 2017; Olson & Gerrodette, 2008; Tixier et al., 2010; Towers et al., 2015, 2019; Wellard & Erbe, 2017) but to date, very few studies have used these marks to quantify agonistic interactions within these mammals. Previous research reported "prolific" scarring on male killer whales in New Zealand (Visser, 1998) and more recently, Robeck et al. (2019) assessed sex and age differences in two killer whale ecotypes that also inhabit the Pacific Northwest; northern resident and Bigg's killer whales and found the prevalence of tooth rakes to vary demographically.

While these studies have provided important insights into patterns of rake marking in free-ranging killer whales, the cross-sectional nature of such research makes it difficult to make causal inferences, further emphasizing the necessity of longitudinal data to accurately examine behavioral responses to ecological factors over time (Lindenmayer et al., 2011; Maron et al., 2005). For some populations, long-term individual-based photo-identification data opens up the possibility to look at longitudinal patterns of aggression across an individual's lifespan and in the face of variable resource abundance. Here, we capitalize on over 40 years of individual-based photo-identification census data, together with salmon abundance measures to quantify patterns of aggression in a population of resident killer whales (*Orcinus orca*) and examine behavioral responses to fluctuations in food availability over time.

Southern resident killer whales are a genetically distinct population of whales that inhabit the coastal waters of Washington State and British Columbia (Figure 1) in the summer months. Their core social system is comprised of stable matrilines embedded within a dynamic, multitiered social system (Parsons et al., 2009). Unlike the vast majority of social mammals, neither sex disperses from the natal group, and all offspring remain in close association with their mothers for their entire lives (Bigg et al., 1990). Southern resident killer whales feed exclusively on fish, with the majority of their diet during the summer months consisting of Chinook salmon (*Oncorhynchus tshawytscha*) (Ford, 2009; Ford & Ellis 2006; Ford et al. 2000; Krahn et al., 2004).

Many marine mammals may acquire tooth rake scars from conspecifics, predators, or from interaction with their prey. However, because southern resident killer whales feed exclusively on salmon, have no natural predators, and actively avoid interactions with other killer whale ecotypes that inhabit the same area, the only interactions they have that can result in tooth rake marks are with conspecifics of their own ecotype. At the start of the census in 1976, the population numbered 71 individuals, which increased to 98 in 1995 and then rapidly declined in just

5 years to 78 whales in 2001, and the animals are now listed as "endangered" under the Species at Risk Act in Canada and the Endangered Species Act in the United States (see fig. 2 in Wiles, 2016). Observed differences in survival rates among age and sex classes have been linked to altered prey availability (Krahn et al., 2002) and now, at just 73 individuals (as of October 2021), they are vulnerable to intensifying ecological pressures (particularly a decline in salmon abundance). However, relatively little is known about the behavioral consequences of ecological factors on the population.

Here, we use rake marks to examine the effects of age and sex on received aggression within resident killer whales. We predict that males will show higher rates of tooth rakes than females, and that rake density will be higher in younger animals, as a result of receiving more aggression from older, more dominant individuals and/or engagement in more frequent bouts of play. Secondly, we quantify the influence of food abundance on aggressive behavior across the study period, predicting that higher rates of tooth rakes will be observed in times of low salmon abundance, when individuals are assumed to be competing most intensely for food.
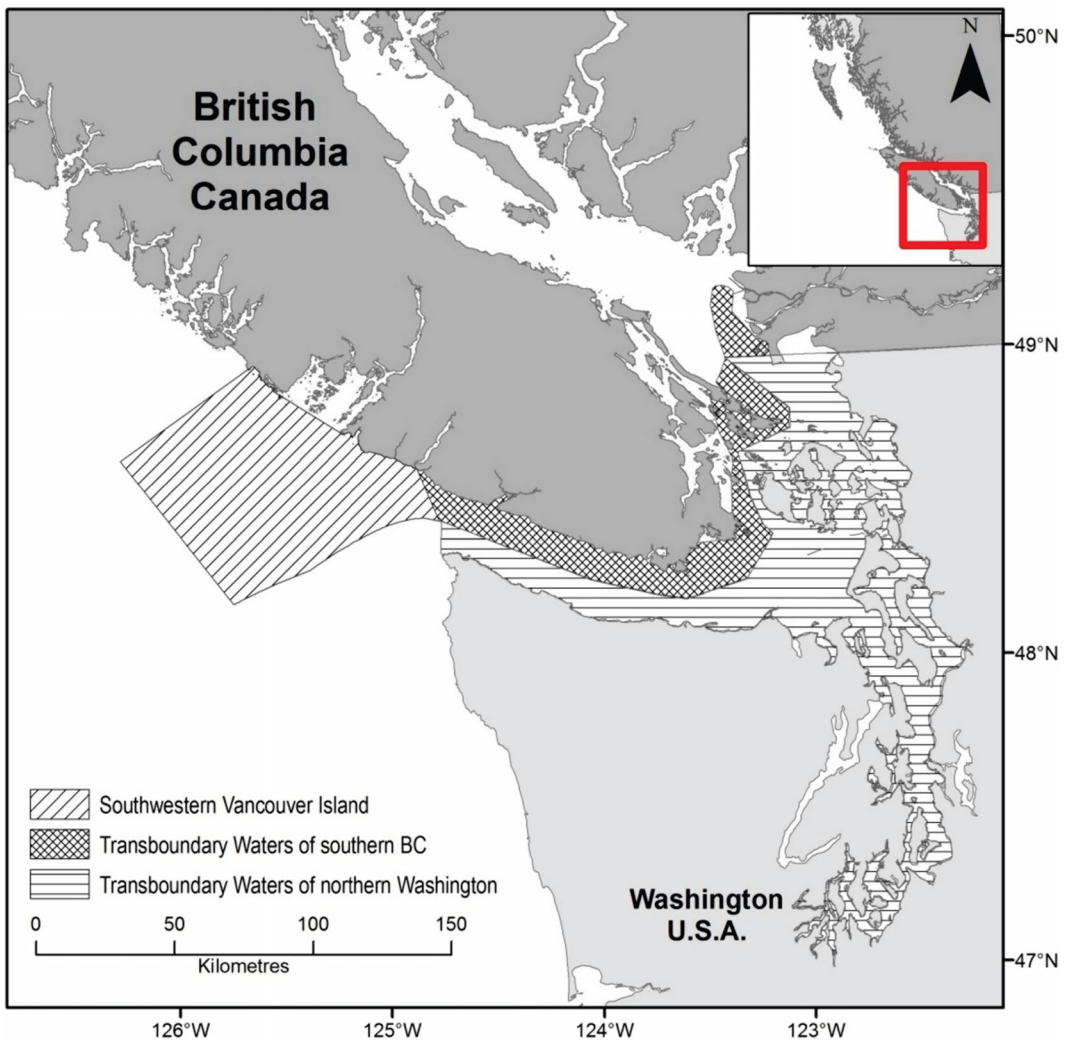
FIGURE 1 Study site and core habitat for Southern Resident killer whales. Hatched areas indicate critical habitat in Canadian and US waters as designated under SARA and U.S. ESA, respectively (Fisheries and Oceans Canada, 2018).

2 | METHODS

2.1 | Study population

Since 1976, the Center for Whale Research has been monitoring the southern residents via a photographic census using photo-ID techniques (Balcomb et al., 1982; Bigg et al., 1990; Ford et al., 1998). All individuals in the population can be identified because of the natural variability in the size and shape of the dorsal fin and area of pigmentation immediately posterior to the dorsal fin (saddle patch).

Photographs for this study were provided by the Center for Whale Research's annual census of whales from 1976 to 2013. Observations were carried out from boats (9 m trimaran and 5.5 m Boston Whaler) when conditions were suitable for photo identification, i.e., sea state of less than Beaufort 4. Photographs of all individuals present were taken during opportunistic encounters by trained staff. Both sides of the whales were captured, where possible, at a position perpendicular to the whale's direction of travel when the whales came to the surface to breathe.

2.2 | Scoring of rake marks

All slide film and digital images were first analyzed to assess quality. Those that were not of high enough quality to identify and score rake marks with certainty were omitted from the study. From 1976 to 2005, photographs were taken on black and white slide film and only one image, or one pair of images (one from each side of the whale) were available for each individual in each year. Digital color images were produced from 2006 onwards. The number and ease with which multiple digital pictures can be taken allows each side of the whale to be photographed consecutively. Where there were multiple photos of each whale taken in one encounter, the highest quality images of both sides of the whale were selected from each month and used in our analysis. Like bottlenose dolphins, superficial wounds on killer whales have generally been observed to heal within 2–20 months (Bigg, 1982; Lee et al., 2019; Lockyer & Morris, 1985) and so analyzing photographs every month, where possible, accounted for any new rakes that would have been acquired within a monthly time frame to be scored, before they faded. In killer whales, rake marks appear as long, thin lines of depigmentation and in this study, one group of parallel lines was considered as one rake mark (Figure 2) and only new (previously unobserved) rakes were recorded when they first occurred in the data set so as to not record the same event twice. The first image of each whale in the data set was not scored for rakes as there was

FIGURE 2 New tooth rakes indicated by white, parallel lines on the anterior peduncle of a male killer whale.

no way of linking the appearance of these rakes to a point in time. Instead, these images were used as primary reference images only, to indicate whether rakes that appeared in subsequent images were new (no rake of that shape/size previously seen at that location, often white). Where there was more than one year of previous data, we were able to use reference images from the previous 2 years to distinguish between new rakes from old rakes.

All image scoring was conducted through GNU Image Manipulation Program (GIMP) version 2.8. The visible surface of whale in each image was drawn around using the Free Select tool and the number of pixels occupying the selected area, shown in the Histogram dock, were recorded (Figure 3a). Each new rake in the image was selected using the Fuzzy Select tool and total number of pixels occupying the area was recorded (Figure 3b). As with many odontocete species, it is possible that tooth rake marks are distributed on all areas of killer whales. Due to the surfacing behaviors of these animals and the opportunistic way in which the photographs used in our study were taken, it was only the anterior, dorsal, mid flanks, and peduncle regions that were consistently visible in the images and thus available for tooth rake scoring. While this made it impossible to assess the whole body, in other dolphin species where all body sections were examined for the presence of tooth rakes, the highest prevalence occurred on the anterior, dorsal, mid flanks, and anterior peduncle regions (Scott et al., 2005). Based on this, it is likely that we can detect a large enough proportion of rakes in this area to be representative of the rake marks received by a given individual.

We took two measures for each whale. First, we recorded the number of new rake marks present in each photograph, likely reflecting the frequency of aggressive interactions. Second, we recorded rake density as a measure of the intensity of aggressive interactions, which was calculated as the total rake mark pixels and total visible surface area pixels each year, and then subtracting the number of rake pixels from total visible pixels to obtain raked and nonraked pixel counts. Since the amount of total exposed area differed for each individual, (e.g., depending on the angle from which the photograph was taken, and the amount of the whale that surfaced) pixels were considered in relation to the number of pixels occupied by the entire visible surface of the whale in each image. This approach also standardized for the divergent resolution of film photographs from earlier years compared to digital photographs from later years. Measurements of rake frequency and density were totaled for each whale, each year, for our analysis.

2.3 | Sex and age classes

Demographic data were provided by the Center for Whale Research for all individuals, including sex, year of birth, and year of death (where applicable). The sex of all but 17 individuals had been identified prior to this study based on observation of the genital slits (Ford et al., 2000). When not available, sex was determined using the presence of a calf with a female or male's dorsal fin growth during adolescence (Olesiuk et al., 1990).

All individuals born after 1972 were of known age. Prior to this, the age of adult females was estimated in reference to the year they gave birth to their first calf, which is around 14 years old (Olesiuk et al., 1990). Due to the large sexual dimorphism and differences in age of maturation, males and females were assigned to different age categories based on previous work by Jacobsen (1986) and Olesiuk et al. (1990). Since males reach sexual maturity at around 12 years but do not stop growing until they are about 20 years old (Noren, 2011), we assigned male categories as follows: calves (0–3), juveniles (4–12), subadults (13–20), and adults (>20). For females, which are sexually active between the ages of approximately 12 and 40 (approximately the age at which they undergo reproductive senescence; Ellis et al., 2018; Olesiuk et al., 1990), we assigned female categories as follows: calves (0–3), juveniles (4–12), adults (13–40) and postreproductive (>40), with postreproductive females assumed to have undergone reproductive senescence.

2.4 | Salmon Abundance Index

Annual chinook salmon abundance was extracted from the yearly technical reports published by the Pacific Salmon Commission test fisheries (https://www.psc.org/publications/technical-reports/). Abundance indices were provided
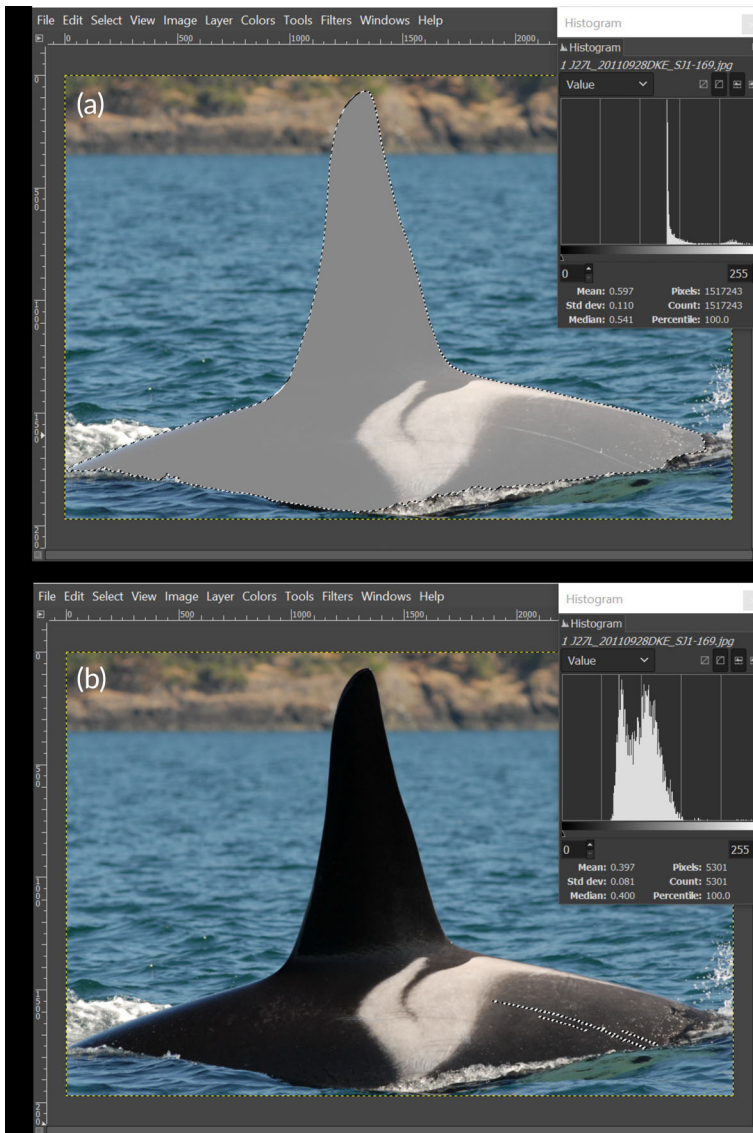
FIGURE 3 Example of the process used to capture (a) entire whale pixels in each photograph. The visible surface of the whale was selected and the number of pixels that occupied the selected area was obtained from the Histogram dock and (b) rake marks that were selected using the Fuzzy Select tool and the number of pixels occupying the area recorded from Histogram dock. This image serves to provide a visualization of a tooth rake and how each new rake was selected, but is not representative of the complete coding process. Each new image was assessed in relation to previous images of the same side of the same individual to assess whether rake marks were new and therefore needed to be coded, or whether they were present in previous images and had already been accounted for.

from West Coast Vancouver Island and Northern British Columbia (two areas that the southern residents frequent) based on test fishing results before and after commercial fishing seasons. The mean value of West Coast Vancouver Island and Northern British Columbia salmon abundance indices were calculated for each year and used in our analysis. Salmon measures prior to 1979 were not available so rake mark images from years prior to this were omitted from the data set for this analysis.

2.5 | Ethical considerations

All images used in this study were collected under whale watch guidelines or under Marine Mammal Protection Act research permit #532–1822 and/or Department of Fisheries and Oceans license #2006-08/SARA-34 awarded to the Center for Whale Research. This study was also approved by the University of Exeter Psychology Ethics Committee.

2.6 | Data analysis

We ran two generalized additive models (GAM; Hastie & Tibshirani, 1986) in R with quasi-binomial error distributions and log link functions to investigate effects of age, sex, and salmon abundance on tooth rake density, which we defined as the proportion of visible pixels of the whale that were raked at a given time. We used the quasi-binomial error distribution to account for over dispersion relative to the binomial distribution due to the dependence between adjacent pixels. Rake density was included as the response variable in our analysis; a two-column success/failures integer matrix with the first column giving the total number of raked visible pixels per whale, per year, and the second column giving the total unraked visible pixels per whale, per year. We performed an additional analysis using rake frequency (the number of new rake marks per photograph) as the response variable (Supplementary Information). This analysis comes with limitations, however, as rake mark frequency does not account for the total amount of visible surface area of each individual in each photograph. Two whales may be the same size, but if there is more surface area visible for one whale, then the detection and therefore frequency of rakes is likely to be greater than that of a whale who had a smaller amount of surface area showing. Our measure of rake density accounts for this variation in visible surface area between individuals, and therefore is a more reliable measure of received social interactions in this population. It is also possible that at a given rake frequency, rake density could differ among individuals of different body sizes due to the differences in the angle of attack and surface area of younger, smaller whales and older, bigger whales. Accordingly, prior to our main analysis we examined the relationship between rake frequency and rake density and found no evidence that body size modulated the observed density of rakes (Tables S1 and S2).

To investigate patterns of rake density (r), we included sex and age in our first model (SA) as an 8-level categorical factor: male and female calves, male and female juveniles, subadult males, male and female adults and post reproductive females. Number of photographs per year (P) was included as a continuous, linear term, to account for sampling effort and whale ID (ID) and year (year) were included as smooth random effects (s: ridge penalized "random effect" smooth implemented in mcgv (Wood, 2012), to account for the repeated measures structure of the data:

$$r \sim SA + P + s(year) + s(ID).$$

We used Tukey's method to carry out post hoc comparisons to further examine differences in rake density between male and female calves, juveniles, and adults. For this analysis, the adult class combines subadult and adult males and for females, the adult class combines adult females and postreproductive females.

A second model was run to examine the effect of resource abundance on received rake density across the population. We included salmon abundance (Sa) as a continuous linear term based on the best model fit from quasi-AIC comparisons (Table S3) and year as a continuous, smooth fixed effect to account for the nonindependent relationship between salmon and year. As before, the model was fit using the quasi-binomial error distribution, with number of photographs (P) fitted as a linear term and whale ID (ID) and year as smooth, random effects:

$$r \sim Sa + P + s(year) + s(ID).$$

All models were fit applying the restricted maximum likelihood approach (REML), using the multiple generalized cross validation package (*mgcv*; Wood, 2012) in the R version 1.2.5033 environment.

Over the course of the study period, 188 individuals were encountered. Individuals of unknown sex ($n = 17$) and those that did not have more than 1 year of photographs to score ($n = 4$) were omitted from the study resulting in a total of 167 individual whales being included in the analysis (77 males and 90 females and see Figure S2 for demographic breakdown of the population over the study period). A total of 8,744 images were analyzed, of which 4,023 (46%) displayed at least one new rake mark.

3 | RESULTS

Most of the males exhibited at least one new rake mark over the course of the study (76 out of 77, 98%) as did females (87 of 90, 96%). When all age classes were combined, males were observed to have significantly greater rake density than females ($ß = 0.36 \pm 0.31$, $t = 28.10$, $p = .001$; Table 1), and age effects on rake density were also observed across the sexes. For females, rake density was highest in young whales and lowest in older females. Female calves experienced significantly higher rake density than all other age categories, over double that of juveniles ($ß = 0.57 \pm 0.04$, $t = -14.04$, $p = .004$), four times higher rake density than adult females ($ß = 1.46 \pm 0.045$, $t = -32.16$, $p < .001$; Figure 4), and six times higher than postreproductive females ($ß = 1.9 \pm 0.06$, $t = -30.05$, $p < .001$; Figure 4). Juvenile females also exhibited a rake density that was twice as high as adult females ($ß = 0.88 \pm 0.03$, $t = -27.10$, $p < .001$) and four times higher than postreproductive females ($ß = 1.33 \pm 0.05$, $t = -23.86$, $p < .001$) and adult females exhibited double the rake density of postreproductive females ($ß = 0.44 \pm 0.04$, $t = -8.98$, $p < .001$). Similar results were obtained when examining rake frequency, with female calves and juveniles exhibiting higher rake frequency than adult and postreproductive females (Table S1.1 and Figure S1.1).

Age effects on rake density were also observed in males, with older individuals exhibiting a lower rake density than younger whales. No significant difference in rake density was found between male calves and male juveniles ($ß = 0.05 \pm 0.03$, $t = -1.795$, $p = .07$), and both age classes exhibited over double the rake density of subadults (calves, $ß = 0.81 \pm 0.03$, $t = -21.32$, $p < .001$; juveniles, $ß = 0.76 \pm 0.029$, $t = -25.99$, $p < .001$) and three times that of adult males (calves, $ß = 1.15 \pm 0.04$, $t = -23.834$, $p < .001$; juveniles, $ß = 1.09 \pm 0.04$, $t = -26.79$, $p < .001$; Figure 4). Subadult males also had significantly greater rake density than adults ($ß = 0.33 \pm 0.04$, $t = -8.236$, $p = .001$). Similar patterns of rake frequency were also observed, with calves and juvenile males being significantly

TABLE 1 Summary statistics showing the proportion of visible pixels of a whale that were occupied by rake mark pixels, for each age-sex class.

	Age category	Mean ± SD	Minimum	Median	Maximum
Male	Calf	0.43 ± 0.65	0	0.18	4.6
	Juvenile	0.45 ± 0.70	0	0.207	4.69
	Subadult	0.19 ± 0.39	0	0.047	4.14
	Adult	0.11 ± 0.29	0	0.00	3.25
	All males	0.27 ± 0.53	0	0.06	4.69
Female	Calf	0.32 ± 0.58	0	0.07	4.41
	Juvenile	0.28 ± 0.48	0	0.82	4.01
	Adult	0.087 ± 0.24	0	0	4.01
	Postreproductive	0.62 ± 0.21	0	0	3.31
	All females	0.12 ± 0.32	0	0	4.41
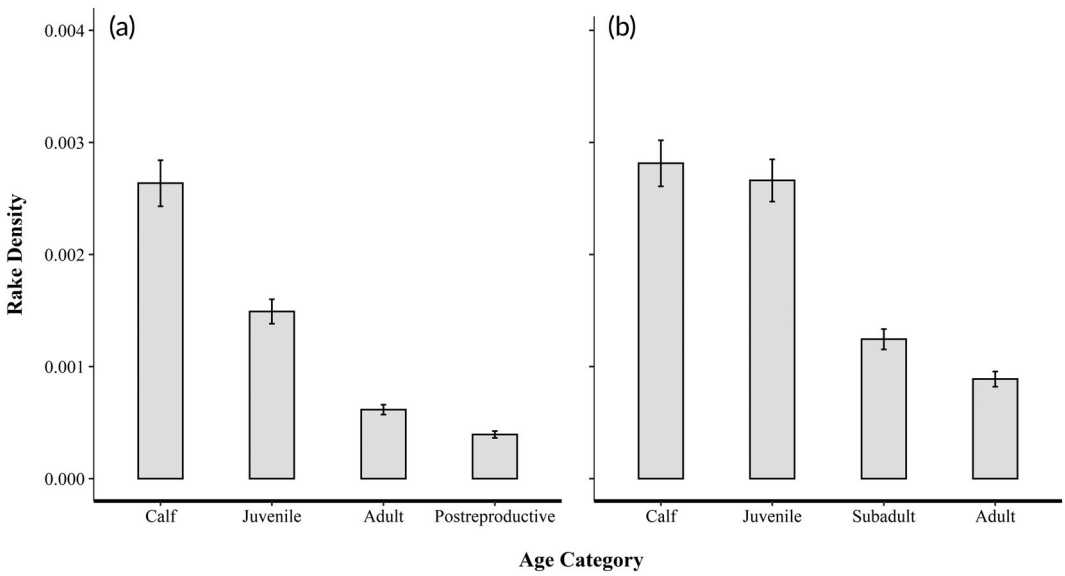
FIGURE 4 Modeled rake density for (a) female age categories (calf:0–3 years, juvenile: 4–12 years, adult: 13–40 years and postreproductive: >40 years) and (b) male age categories (calf: 0–3 years, juvenile: 4–12 years, subadult: 13–20 years, and adults: >20 years). Predicted mean ± *SE* for each class are shown.
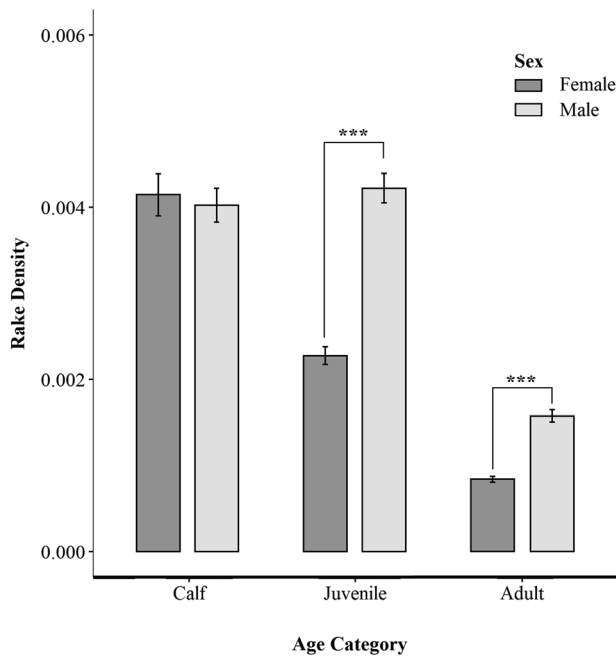
FIGURE 5 Modeled rake density (mean ± *SE*) for male and female calves and juvenile age categories (calves: 0–3 years; juveniles: 4–12 years; adults: 13+ years). Significant differences were observed between juvenile and adult males and females (*** = $p < .001$).
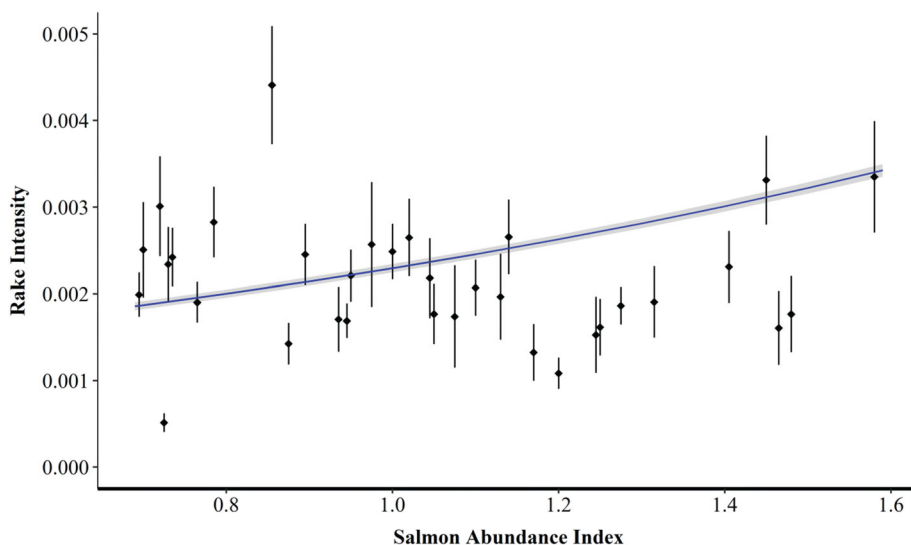
FIGURE 6 Visualization of the raw data, presenting the relationship between salmon abundance and rake density (mean ± SD) across the study population. Data points represent a summary of rake density for every unique value of salmon abundance and the fitted line represents predicted values from the GAM output with 95% confidence bounds (controlling for year and number of photos of each whale per year with whale ID and year (as a factor) included as random effects). Please refer to the Supplementary Information for further information on number of photographs analyzed (Figure S3) and salmon abundance index across the study period (Figure S4). An additional model was run in which outliers were excluded, to confirm that the final GAM model output was not driven by any outlying values.

more raked than adult males, and juvenile males exhibiting the highest rake frequency of all male age classes (Table S1.1 and Figure S1.1).

When comparing age classes between the sexes (i.e., calves, juveniles, and adults) no significant difference was found between male and female calves (ß = 0.03 ± 0.07, $t = -0.39$, $p = .96$; Figure 5) but both juvenile and adult males had significantly higher rake density than their female counterparts (juvenile male–juvenile female, ß = 0.61 ± 0.06, $t = 10.03$, $p < .001$; adult male–adult female, (ß = 7.51 ± 0.05, $t = 10.52$, $p < .001$, Figure 5). Similar results were reported for rake frequency; however, the effect was greater, with all males exhibiting significantly higher rake frequency than females in all three age categories (Figures S1.1 and S1.2).

Interestingly, we found salmon abundance to be significantly related to rake density across the population (ß = 0.28 ± 0.03, $t = -1.789$, $p = .003$), with highest rake densities observed in times of highest salmon abundance (Figure 6).

4 | DISCUSSION

To the best of our knowledge, this is the first study to use tooth rake marks to examine patterns of aggression across the lifespan of killer whales, the findings of which will help to identify challenges faced by individuals at each life stage. We found age effects on rake frequency and density in both males and females, suggesting that individuals experience more frequent and intense social interactions in the early stages of life and that these interactions decline with age for both sexes. We also observed that resource abundance has an impact on patterns of rake marks but, contrary to our prediction, we found higher density of rake marks in years of high salmon abundance.

Both males and females in our study experienced most rakes in early life, and their occurrence diminished around the age each sex reaches maturation, continuing to decline thereafter. These whales exist in highly stable,

hierarchically structured matrilineal units (Bigg et al., 1987, 1990; Ford et al., 2000; Parsons et al., 2009). In other social species that are organized into hierarchal, matrilineal units, such as spotted hyenas (East et al., 2009; Engh et al., 2000) and many cercopithecine primates (Bernstein, 1969; Cheney, 1977; Holekamp & Smale, 1991; Kawai, 1965; Silk et al., 1981), female rank is determined by familial rank, which begins in infancy and once established, remains stable over time (Goyman et al., 2001), whereas males compete for rank across the lifespan. In some species, wounds are observed at key developmental stages when individuals compete most aggressively for rank (MacCormick et al., 2012). While little is known about the establishment of rank in the southern resident killer whales, or even if there is linear or other dominance rank system, we have clearly shown a high density of rakes in young individuals and lowest rates in old age classes, similar to patterns of aggression seen in other social species where dominance hierarchies exist.

Our finding that rake density is higher in adult males than in females is similar to patterns of tooth rakes previously reported in multiple dolphin species, including killer whales (Lee et al., 2019; Leone et al., 2019; Marley et al., 2013; Robeck et al., 2019; Scott et al., 2005), where rakes at this stage have largely been attributed to inter-male competition for females. The sex differences observed between adults in our study suggests that there may be competition between males over access to females, which may fluctuate in response to the availability of reproductively aged females in the population. Furthermore, since rake density is a measure of received interactions from others, these sex differences indicate that males might also be subject to aggressive contacts from females. The lower rake density and frequency of rakes observed in adult females suggests that while they themselves may not be the targets of high numbers of aggressive interactions, particularly as they age, this does not preclude them from being the instigators of such contact events. Further work that includes additional data, such as the availability and cycling status of mating age females, in conjunction with behavioral observations of social interactions, would give important insights into the role of sexual competition in aggressive interactions in this system.

Social organization may also play a role in mediating adult aggression in resident killer whales. Robeck et al. (2019) reported similar patterns of rake prevalence in northern resident killer whales which also exhibit natal philopatry (Bigg et al., 1990), with adult males having a higher incidence of rakes than their female counterparts. Interestingly though, in sympatric Bigg's killer whale populations, where individuals of both sexes may disperse as adults (Baird & Whitehead, 2000), rake prevalence was high in both male and female adults. The difference in rake patterns observed in the two ecotypes may in part then be due to the differences in social behavior between the populations and suggests that behavioral mechanisms, such as habituation, may facilitate conflict avoidance in resident killer whales, as is observed in other mammal species (Rychlik & Zwolak, 2005).

In species where offspring are reared together there is typically competition between siblings for resources, which can result in physical aggression (Hodge et al., 2009; Mock & Parker, 1997) and which may explain the high rake density observed in calves and juvenile males in our study. Food sharing between kin is common in killer whales (Wright et al., 2016), but there is still likely to be competition between young siblings as to who gains priority access to food until they are of an age where they can forage successfully alone. During weaning, calves may start competing with similar aged conspecifics for food and their elevated rake density may reflect this new competition. Similarly, juvenile males undergo major growth during this period and have high energetic needs (Noren, 2011), making competition for food likely to be particularly intense. This might also lead to an increase in social conflict and subsequent increased rake density in young males.

The patterns of rake density reported here correspond to age effects on sociality observed in southern resident killer whales, providing further support that younger whales engage in more frequent social interactions than their older counterparts (Weiss et al., 2021) and suggests that some of the rake marks recorded in this study may be the result of play behavior. Juvenile males also exhibited significantly higher rake density than females, a pattern which is consistent with those observed in bottlenose dolphins (*Tursiops* spp.), where a higher prevalence of rakes in males at this age has been attributed largely to rough-and-tumble play prior to maturation and the formation of stable bonds (Lee et al., 2019; Mann, 2006; Scott et al., 2005). In many mammalian species, high levels of play and mock fighting have been observed in younger individuals compared to older ones (Burghardt, 2005; Connor et al., 2000;

Fagen, 1981; Paolos et al., 2010), and the same is true of killer whales, particularly amongst juvenile and subadult males (Rose, 1992). Due to the similarity in which cetaceans behave when engaging in social play and aggression, it can be difficult to differentiate between the two behaviors. For example, in bottlenose dolphins, interactions that started in a playful nature frequently turn aggressive (Scott et al., 2005). Further work is needed to quantify patterns of social interactions and their context during these socializing events and establish how and when rake marks occur. Video collection using unmanned aerial vehicles coupled with acoustic monitoring provides an exciting opportunity to address this research question. For example, acoustic monitoring techniques have reported clear acoustic repertoires to reflect different behavioral states in killer whales (Ford 1989; Simon et al., 2007; Thomsen et al., 2002) including those that appear aggressive (Graham & Noonan, 2010), and may provide important insights into the nature of killer whale behavior when direct observations are limited.

Contrary to our expectations, rake density increased linearly for both sexes in response to increasing salmon abundance. Classic game theory predicts that aggression will increase at times of low resource availability as group-members compete for limited resources (Schoener, 1973; Titman, 1976). However, given that aggression is energetically costly, it is possible that aggression may be reduced when resources are limited. Evidence of this has been observed in chimpanzees (Georgiev et al., 2013) and macaques, where aggression levels rise in response to an increase in the quality and abundance of food (Loy, 1970). Other energetically social behaviors, including play, also appear to be influenced by food availability. In vervet monkeys (*Chlorocebus pygerythrus*, Lee, 1984), gray langurs (*Presbytis entellus*, Renouf, 1993; Sommer & Mendoza-Granados, 1995), geladas (*Theropithecus gelada*, Barrett et al., 1992), and harbor seals (*Phoca vitulina*, Renouf, 1993) an increase in energetic play behaviors have been documented during periods of high quality and abundant resources. Similarly, in meerkats (*Suricata suricatta*, Sharpe et al., 2002), play is more frequent between younger individuals when food provisioning towards them is increased. With rakes providing indirect evidence of tactile body events, the high density observed when salmon is abundant may be a product of more frequent social interactions between conspecifics, facilitated by elevated energy levels at this time. Conversely, when food is in short supply, resident killer whales fragment into smaller social groups, become more dispersed (Lusseau et al., 2004), and have less interconnected social networks (Foster et al., 2012; Parsons et al., 2009), reducing opportunities to receive rakes. While it is difficult to delineate play from aggression in cetaceans, direct observations of behavior prior to rake markings may help to understand the context in which these marks are obtained.

Overall, this study provides evidence of sex and age differences in received rake marks in southern resident killer whales, indicating that males and younger individuals experience more frequent and intense physical interactions with other group members. By using historical data collected for photo ID research, we were able to examine the longitudinal patterns of aggression in a wild killer whale population. Our approach, however, limited us to only analyzing areas of the body that were visible during the whale surfacing. Future work using aerial photography or underwater video to capture and assess more of the body's surface area, as well as the direction and location of rake marks, would be particularly valuable. Furthermore, since tooth rake marks only provide indirect evidence of interactions, we are limited in our inference of when and by whom these events are initiated and whether they are intended to be aggressive or affiliative. Higher incidences of rake density and frequency in times of high food abundance contradicts results from other group-living species and suggests that, in addition to aggression, food availability may be driving other social behaviors such as play. Other factors, such as social network structure, may also be regulating behavior in southern resident killer whales. Expansion of this study using drones to conduct direct observations of behavior will allow us to draw more substantial conclusions around the factors driving patterns of rake marking within this population. Further exploration of the impact of social structure on aggressive interactions within the population would also be prudent to further our understanding of the evolution and moderation of aggression within this highly complex society.

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AUTHOR CONTRIBUTIONS

Charli Grimes: Conceptualization; data curation; formal analysis; visualization; writing – original draft. **Lauren Brent:** Conceptualization; data curation; methodology; supervision; writing – review and editing. **Michael Nash Weiss:** Conceptualization; data curation; formal analysis; writing – review and editing. **Daniel Franks:** Conceptualization; funding acquisition; writing – review and editing. **Kenneth C Balcomb:** Data curation; funding acquisition; investigation; methodology; writing – review and editing. **David K Ellifrit:** Conceptualization; data curation; investigation; methodology; writing – review and editing. **Samuel Ellis:** Conceptualization; data curation; formal analysis; funding acquisition; writing – review and editing. **Darren Croft:** Conceptualization; funding acquisition; methodology; supervision; writing – original draft.

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