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FEATURED STUDENT RESEARCH PAPER

Divergent killer whale populations exhibit similar acquisition but different healing rates of conspecific scars

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Abstract

Scars obtained from interactions with conspecifics may be caused by both playful and aggressive activities, making them useful when studying cetacean behaviour. This study investigates the effects of age and sex on conspecific scar acquisition and healing in three genetically distinct populations of killer whales (*Orcinus orca*) each with unique diets and social structures. The sample consisted of 50 of the most commonly photo-identified individuals from all sex and age classes in each of the Bigg's, Northern Resident, and Crozet killer whale populations. The number of new scars annually acquired by an individual as well as how long it took them to disappear were extracted from annual photo-identification images of these individuals taken between the years of 2008 and 2021. Scar acquisition was analysed using a generalized additive model while scar healing was assessed using Kaplan-Meier survival curves. Results showed an inverse relationship between scar acquisition and age, as well as an effect of sex with males being more scarred than females amongst all age classes. No significant differences in scar acquisition between populations was found. Scar re-pigmentation was faster in Northern Residents compared to Crozet and Bigg's individuals and varied amongst age classes, with scars on calves and juveniles disappearing more quickly than those on adults. These population- and age-based differences in healing may be due to scar severity, while results around scar acquisition suggest that the nature of physical interactions between sex and age classes in this species are homogenous despite cultural and genetic differences that have evolved between populations.

Significance Statement

In several species of odontocetes, including killer whales, scars caused by the teeth of conspecifics are typically attributed to social behaviours associated with reproductive competition. Previous research has suggested that divergent but sympatric populations of killer whales each with unique diets, social structures, and behaviours have frequencies of scarring which differ amongst sex and age classes in each population. Using more robust data we conclude that rates of scar acquisition between these same populations and another non-sympatric population are remarkably similar when compared between sex and age classes, but that one population exhibited significantly different rates of healing. These results suggest that sexually selected behaviours have not diverged as strongly as ecological adaptations have in this species, but that scars are likely caused by mild to intense play and aggression which are specific to population, sex, and age class.

Keywords *Orcinus orca* · Sexual selection · Social behaviour · Demographic factors · Population health

Introduction

Body marks can be used to make inferences about trends in unobserved interactions within and between many species. They can provide information about interspecific interactions between predator and prey (Reimchen 1988; Fryer 1998; Heithaus 2001; Voight and Sigwart 2007; Jayewardene et al. 2009; McCordic et al. 2013; Tyler et al. 2019; Corsi et al. 2022) or anthropogenic sources and wildlife (Bradford et al. 2009; Neilson et al. 2009; Knowlton et al.

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2012; McGuire et al. 2020; Penketh et al. 2021; Burek-Huntington et al. 2023; Von Hagen et al. 2023), whereas marks inflicted by conspecifics can contribute important insights into a species' social behaviour (Blanchard et al. 1985; Staub 1993; Rosso et al. 2011; Crawford et al. 2015; Lanyon et al. 2021; Grimes et al. 2023). These injuries can range from surface abrasions to deep wounds caused by either rough play or more confrontational interactions which often result in scarring (McCann 1974).

Scarring from conspecifics is usually associated with sexual conflict (Reinhardt et al. 2015; Burke and Holwell 2021; Lanyon et al. 2021) or resource competition (Forman and Brain 2006; Donihue et al. 2016; Mayer et al. 2020). As such, age and sex often influence the extent of conspecific scarring on individuals. For example, wound scars tend to accumulate in many taxa as competition and conflict increase between conspecifics with age (Arlet et al. 2009; Crawford et al. 2015; Lanyon et al. 2021; Brown et al. 2022). Mating systems also play a role in the acquisition of scars inflicted by conspecifics with adult females having higher scarring rates in a variety of insect taxa due to copulatory wounds inflicted by males (Reinhardt et al. 2015; Burke and Holwell 2021), whereas mating competition between adult males results in higher scarring rates in this sex in several species of testudine (Keevil et al. 2017), primates (Cristóbal-Azkarate et al. 2004; Cords and Arguelles 2023) and cetaceans (Kato 1984; Gerson and Hickie 1985; Chu and Nieukirk 1988; MacLeod 1998; Scott et al. 2005; Martin and Da Silva 2006; Marley et al. 2013; Orbach et al. 2015). In cetaceans, severe wounds inflicted by conspecifics can be directly fatal (e.g. infanticide, Patterson et al. 1998; Dunn et al. 2002; Zheng et al. 2016; López et al. 2018; Towers et al. 2018) and in other cases they can result in serious health impacts (Parsons et al. 2003; Robinson 2014). Scarring from severe wounds can also impact individual fitness by compromising skin elasticity and therefore hydrodynamic qualities and diving abilities, which can result in reduced foraging efficiency and predator evasion (Ridgway and Carder 1990). However, several physiological adaptations are characteristic of enhanced wound healing capabilities of cetaceans. Their epidermis is significantly tighter and thicker as well as more prolific and glabrous than in most other mammals, which together serve to limit colonization by microbes (Menon et al. 2022). These features in combination with antimicrobial compounds in their adipose tissue likely expedite healing processes (Zasloff 2011; Su et al. 2022a). Their thick adipose tissue also reduces the chances of wounds reaching the muscle (Brown et al. 1983; Bruce-Allen and Geraci 1985), but some individuals can survive muscle or bone deep injuries (Bloom and Jager 1994; Bossley and Woolfall 2014; Dwyer et al. 2014; JRT unpubl. data). In such cases necrotic tissue at the wound site may help maintain homeostasis during the process of re-epithelialization (Su et al. 2022a). Remarkably, scars from wounds on some cetaceans fully re-pigment at the wound site showing no evidence of previous injury (Su et al. 2022b). The processes associated with tissue healing and skin re-pigmentation in cetaceans may be influenced by a variety of factors including ocean temperature, salinity, inherent gene loss, as well as compounds impacting vascular function such as melanocytes, contaminants, lipids, proteins, or hormones associated with environmental or demographic factors (Wilson et al. 1999; Ashcroft and Ashworth 2003; Hong et al. 2015; Lee et al. 2019; Menon et al. 2022; Su et al. 2022a, b; Chaudhary et al. 2024; Suzuki et al. 2024).

Killer whales are an appropriate model to study conspecific scarring due to their contrasting pigments, highly social nature and complex matrifocal societies (Bigg et al. 1986). As one of the most cosmopolitan cetacean species, killer whales are found in all the world's oceans (Wade and Forney 2007). While still being classified as a single species, multiple populations have been described based on physical, behavioural, and genetic differences (Ford 1991; Ford et al. 1998; Pitman and Ensor 2003; Morin et al. 2010; Pitman et al. 2011; de Bruyn et al. 2013). One of the key behavioural differences between killer whale populations is their diet. Some populations specialise in a certain taxon such as marine mammals for the Bigg's or fish for the Northern Residents, two sympatric populations in the northeastern Pacific Ocean (Ford et al. 1998). Others, like the Crozet population in the southern Indian Ocean, are generalists and feed on marine mammals, fish, and penguins (Guinet 1992; Tixier et al. 2019).

There are several reasons for which conspecific scarring may be population specific. Firstly, distinct killer whale populations are often faced with different trends in prey availability (Ford et al. 2010; Poncelet et al. 2010; Tixier et al. 2015, 2017, 2021) that, when paired with variations in population abundance and density (Towers et al. 2019a, 2020; Tixier et al. 2021), may lead to variances in interactions between conspecifics associated with competition for resources. Grimes et al. (2022) have shown that tooth rake density increased with prey abundance in one fish-eating population of killer whales, possibly since there is more time for interaction when food is not scarce. It may also be expected that conspecific scarring would differ due to divergent social organization and reproductive behaviour between populations. Robeck et al. (2019) used scars to infer that physical interactions and aggression do indeed vary from one population to another. However, their data were limited to one photo per whale and therefore produced results on cumulative scarring without considering acquisition or healing rates. To our knowledge, no research has compared conspecific scar acquisition and healing rates in individuals over time between killer whale populations. Yet such information would be essential in further understanding rates and intensity of interactions within populations and between sexes and age classes, demographic and physiological nuances in the scar healing process, and how ecological divergence may influence social behaviours in this species.

This study investigates the effects of age and sex on conspecific scar acquisition and healing (skin re-pigmentation) using long-term photo-identification data of individuals from three distinct killer whale populations with different prey preferences and social organisation: Bigg's and Northern Residents in the northeastern Pacific Ocean and killer whales around the Crozet Islands in the southern Indian Ocean. At a population level, we hypothesise that if prey can affect social structure, culture, and behaviours (Ford and Ellis 2014), which result in scarring (Grimes et al. 2022) then scarring rates would differ between populations as proposed by Robeck et al. (2019). We also anticipate that healing time may be influenced by population health, scar severity, and demographic factors such as age and sex.

Methods

Study populations

The Northern Resident (NR) and the Bigg's killer whale are sympatric populations ranging throughout coastal waters off western North America and represent two distinct killer whale ecotypes (Ford et al. 1998). The NRs consist of a population of over 300 piscivorous individuals which live in large social units (1–19 individuals) and do not associate with conspecifics outside their population (Ford et al. 1994; Towers et al. 2020). Nearly all descendants remain philopatric to their matriline, resulting in an extremely stable society (Ford et al. 1994). The coastal population of Bigg's killer whale includes nearly 400 individuals which maintain smaller social units (1–8 individuals; Towers et al. 2019a) better suited to hunting their preferred prey of marine mammals (Bigg 1982; Ford et al. 1998). Social structure is less stable than in NRs, as dispersal of both sexes is well documented in Bigg's (Baird and Whitehead 2000; Nielsen et al. 2023) and individuals are known to mingle with a larger number of conspecifics. Despite inhabiting the same area, these two populations do not interact, resulting in reproductive isolation and genetic differences (Barrett-Lennard and Ellis 2001) that have evolved over the past 350,000 years (Morin et al. 2015). Due to limited population abundance and prey availability, as well as a variety of anthropogenic threats, both populations have been listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2001 and subsequently under Canada's Species at Risk Act (SARA).

The core Crozet killer whale population (CR) includes ~ 100 animals that exist within a potentially larger population of individuals in the waters surrounding the Crozet Archipelago in the southern Indian Ocean. The core population is composed of 23 social units of between 1 and 11 individuals (Tixier et al. 2021). The population has a generalist diet which includes marine mammals, seabirds, and fish depending on the season and availability (Guinet 1991, 1992; Tixier et al. 2019). They also regularly feed on Patagonian toothfish (*Dissostichus eleginoides*) caught on longlines deployed by the local fishery, a behavior termed "depredation" (Tixier et al. 2010, 2016). This population is in severe decline and has been listed as endangered on the regional Red List of the French committee of IUCN (2015). 60% of the individuals around Ile de la Possession (the archipelago's largest island) were lost between 1988 and 2000, predominantly due to illegal fishers' use of lethal means such as firearms and explosives (Poncelet et al. 2010; Guinet et al. 2015). The trend appears to continue with a 5% decrease in population size between 2005 and 2020 making it a high priority for conservation (Tixier et al. 2021).

Sample details

Photo-identification data for this study were collected by the Centre d'Etudes Biologiques de Chizé (CEBC-CNRS, within the Program 109 of the French Polar Institute), the Muséum National d'Histoire Naturelle (MNHN) of Paris and by the Terres Australes et Antarctiques Françaises (TAAF) for the CR killer whale population for the period of 2008–2020. The Cetacean Research Program at Fisheries and Oceans Canada and Bay Cetology provided the data for the NR and Bigg's populations for the periods of 2009–2021 and 2008–2020 respectively. The sample consisted of 50 of the most frequently encountered individuals from each population (Table 1). An encounter was defined as the period starting and ending when a group of individuals were first and last photographed respectively on a given day (Tixier et al. 2021). Half of these individuals ($n = 25$ per population) were known or inferred to have been born during the study period based on their size when first observed and close proximity to an adult female (Towers et al. 2019a, 2020; Tixier et al. 2021). The remaining 25 individuals per population were born before the year 1999 making them at least 10 years of age in the first year of the study. This allowed for scarring to be tracked on individuals across life stages from birth to sexual maturity (10–15 years old, Olesiuk et al. 1990; Ford et al. 1994), through adulthood and into menopause for some females (> 40 years old, Brent et al. 2015; Nielsen et al. 2021).

Table 1 Data summary. Sample size represents sum of the number of years during the 13-year study period for which there were photo data available for a given individual of an acceptable quality. NR = Northern Resident and CR = Crozet

	Total	Bigg's	NR	CR
Individuals				
Number of individuals included in the study	150	50	50	50
Number of male individuals	53	19	23	11
Number of female individuals	73	30	24	19
Number of individuals of unknown sex	24	1	3	20
Mean age ± SE	18 ± 0.36	19 ± 0.70	16 ± 0.50	18 ± 0.68
Photos				
Total number of photos in the sample	1300	495	526	279
Number of photos of male calves	91	37	53	1
Number of photos of female calves	85	54	27	4
Number of photos of calves of unknown sex	59	2	10	47
Number of photos of male juveniles	147	47	92	8
Number of photos of female juveniles	136	80	47	9
Number of photos of juveniles of unknown sex	55	6	13	36
Number of photos of male subadults	79	24	31	24
Number of photos of female adults	400	148	176	76
Number of photos of male adults	187	64	70	53
Number of photos of post reproductive females	61	33	7	21
Mean ± SE number years with no photo for a given individual	1.14 ± 0.12	0.34 ± 0.08	2.14 ± 0.14	0.94 ± 0.25

Data extraction

Raw photo-identification data for all three populations for the 13-year study period consisted of over 595,000 photos (Bigg's ~ 329,000; NR ~ 117,000; CR ~ 149,000). Data were not extracted blind because the study involved examining high quality photos of unique individuals with distinct characteristics and sightings histories. Identification images of NR and Bigg's killer whales were chosen by searching a photo-identification database for photos with a quality rating of 3 or 4 out of 4 for each relevant individual to ensure that reference material was high resolution, in focus, and with dorsal fin and saddle patch perpendicular to the camera (Towers et al. 2012). Identification images of CR individuals were chosen by searching a photo-identification database for photos of relevant individuals with a quality rating of 2 or 3 out of 3 for both saddle patch and dorsal fin exposure (Roche et al. 2014). When there was no photo with such a rating available for a certain year, unrated and lower rated photos were searched for an image in which the majority of the scar details on the whale's body were in focus. The photo of the highest quality showing the largest section of the saddle and dorsal fin for the left side of every individual was selected for each year. Of the 1300 photos used in the study (Table 1), 842 (65%) were considered to be of excellent quality and 458 (35%) of good quality. A gap of a minimum of 6 months between photos from different years was maintained enabling the monitoring of scar acquisition and healing at standardised intervals. Years were defined as the period of January 01 – December 31 for the two populations in the northern hemisphere and July 01 to June 30 for the population in the southern hemisphere due to summers in each respective hemisphere being the times that most data from each population were collected. All photos were visually examined in chronological order using Photo Mechanic Plus by the same analyst.

A bounding box approach including the dorsal fin, surrounding dorsum and saddle patch was chosen to standardise the delimitation of area of the body analysed for scarring because although killer whales may incur scars anywhere on their body, some parts perhaps more than others, this is the only area of their body that can be easily photographed (Fig. 1). It is generally accepted that scars on this species that are obviously not from anthropogenic sources are caused by conspecifics (Robeck et al. 2019; Grimes et al. 2022, 2023; Wright et al. 2023), but for this study a scarring event was defined as a set of two or more parallel scars that were caused on the same occasion, ensuring that they were due to an interaction with the teeth of another killer whale. Single line scars were excluded from the study since there is a greater chance they may have been caused by sources other than the teeth of conspecifics. It cannot be ruled out that scars may be caused by the teeth of pinnipeds but, despite being prey for the CR and Bigg's populations, seal and sea lion species within the range of killer whale populations used in this analysis have not been observed inflicting wounds visible in identification photographs on killer whales whereas conspecifics have (JRT and PT unpubl. data; Towers et al. 2018). Each new scarring event was recorded along with its location (on dorsal fin, not on saddle patch, on saddle patch). Then photos of the same individual for following years were examined and it was recorded whether the scar was still visible or had disappeared (Fig. 1). Since right side photos were not available

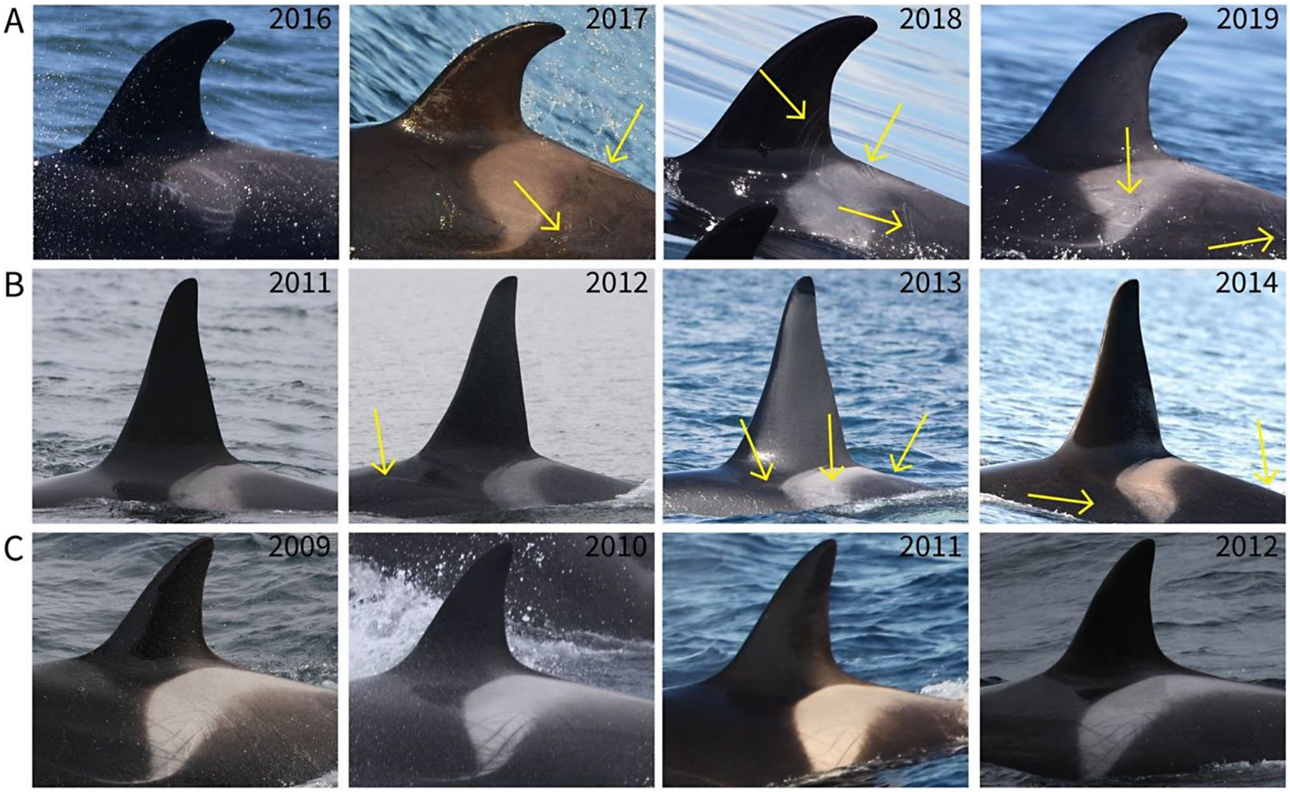

Fig. 1 The side and area of the body analyzed for scar acquisition and healing with each image in a bounding box. **A**: juvenile male T065A5 showing healing and acquisition of scars between 2016 and 2019 with two new scars in 2017, three in 2018, and two in 2019, **B**: subadult male A061 showing healing and acquisition of scars between 2011 and 2014 with one new scar in 2012, three in 2013, and two in 2014, and **C**: adult female CR019 showing no new scars acquired between 2009 and 2012 (Supplementary Tables 1 and 2)

for the NRs due to differing data collection methods for this population, only the left side of each individual was analysed for all three populations. This was unlikely to have biased the results since no evidence exists to suggest that interactions between conspecifics are laterally distributed in killer whales.

Demographic data

Demographic and social data were accessed for all individuals in the form of published catalogues (Towers et al. 2019a, 2020; Tixier et al. 2021) and more up-to-date unpublished information. These data included year of birth/year first encountered, and year of death/year last encountered (where applicable) as well as the sex and the ID. The following sex-specific age classes were assigned based on classifications made in Towers et al. (2019a); Tixier et al. (2021): male and female calves (≤3), male and female juveniles (4–12), male sub-adults (13–20), male adults (>20), female adults (13–40), and post-reproductive females (>40). Since many individuals cannot be sexed until they are more than 12 years old, two more age classes were added to incorporate the young, unsexed individuals. These were unknown calves (≤3) and unknown juveniles (4–12) resulting in a total of ten classes. These age classes were assigned to test whether individuals are more exposed to conspecific scarring during different stages of their life (Table 1).

Statistical analyses

Scar acquisition

A generalized additive mixed model (GAMM; Hastie and Tibshirani 1986) with a negative binomial error distribution and a log-link function was used to investigate effects of age, sex, and population on the rate of new scar acquisition. This response variable, “new scars”, was included as a numerical variable in which each value was the number of scars acquired by a given individual in a given year (Supplementary Table 1). For this part of the analyses, each scar was counted once. A negative binomial error distribution was chosen using the ‘family’ term to account for over dispersion and zero inflation in the response variable. Year was included as a random numeric smooth (i.e., a smooth component of the GAMMs that act as a random effect) to account for additional environmental variability (Grimes et al. 2022). Sex and age were incorporated simultaneously through use of the previously described 10 sex-specific age classes (SAc). Population was included as a factorial variable to test for differences in overall scarring rates, and separate smooth functions of 'year' were fitted for each level of the 'population' factor (this allowing the effect of environmental variability to act differently on each population). Thin-plate regression splines (Wood 2003) were used as smoothers, with optimal effective degrees of freedom chosen automatically using the restricted maximum likelihood approach (REML) in the generalized cross validation package (*mgcv*, Wood 2006, 2017). The result was the following model:

New Scars ~ SAc + population + s(year, by = population).

We compared this initial model to the following alternative model which includes an interaction between population and SAc:

New Scars ~ SAc * population + s(year, by = population).

The results of this model demonstrated that the Bigg's-SAc and NR-SAc terms were not statistically significant and the CR-SAc terms lacked sufficient data to determine the presence of an interaction. This allowed us to conclude a lack of differences in rates across age-classes between Bigg's and NR, but not for CR. Furthermore, this model showed a poorer fit (higher AIC and BIC) than the initial non-interaction model (Supplementary Material 1). We also explored including ID as a random variable but this resulted in overfitting (Supplementary Material 1). Therefore, we used the initial model to investigate all aspects besides the interaction between population and SAc. Pairwise post hoc tests were carried out for the factor variables SAc and population using the *emmeans* package (Lenth 2023) to check if differences in scarring rates between groups were statistically significant. Next, predictions for new scars based on predictors of interest (population and SAc) included in the model were plotted using the *plot_model* function. Individuals of unknown sex were excluded from these plots to facilitate interpretability. All analyses were carried out in the R version 4.4.0 (R Core Team 2023) and RStudio version 4.2.2 (RStudio Team 2023).

Table 2 Variables and groups used in Kaplan-Meier survival analyses

Variable	Group 1	Group 2	Group 3
Sex	Female	Male	unknown
Age-class	Calf (≤3 yrs)	Juvenile (4–12 yrs)	Adult (≥13 yrs)
Population	Bigg's	Crozet	Northern Resident
Location	On Dorsal Fin	Not on Saddle Patch	On Saddle Patch

Scar healing

Four Kaplan-Meier (K-M) survival curves were constructed to assess the effects of four separate variables on scar healing time (Table 2), inspired by Lee et al.'s (2019) use of similar survival analyses. These variables were: (1) sex, (2) age class of the individual at the time when the scar was acquired, (3) population, and (4) physical location of scar on body. Scars recorded as crossing the limit between two body location categories/groups were split and the part of the scar in each area was treated separately to allow for repigmentation rates between body areas to be compared (Supplementary Table 2). The scar healing time was calculated in years and covered the period beginning when the scar was first visible in a photograph and ending either when the scar was no longer visible due to successful re-pigmentation or in the year with the last available photo (either due to the end of the study period or lack of data). If scars remained visible in the last available photo of an individual, they were considered to be censored (Supplementary Table 2). Log-rank tests were used to determine statistically significant differences between groups. Plots of the K-M curves were created using the *ggsurvplot* function. Individuals of unknown sex were excluded from these plots to facilitate interpretability. All analyses were carried out in the *Survival* (Therneau 2024) and *Survminer* (Kassambara et al. 2021) packages in RStudio version 4.2.2 (RStudio Team 2023).

Results

Scar acquisition

Of the total 1,300 images analysed, 764 (58.8%) displayed at least one new rake mark. The constructed GAMM fitted to the number of new scars from conspecifics per individual per year had an adjusted R squared of 0.23. There were no significant differences in the number of scars between the three populations with individuals from all three populations predicted to acquire a mean of ~2.4 new scars each per year (pairwise comparisons: Bigg´s: CR $p=0.297$; Bigg´s: NR $p=0.236$, CR: NR $p=0.945$, Table 3). All male age classes were predicted to have more scars than their female counterparts (Fig. 2) but, these differences were only significant between male subadults and adult females ($p<0.0001$) and between adult males and post reproductive females ($p=0.0005$). Predicted scarring decreased as age increased for males with male calves having the most scars (~2.1) and adult males the least (~0.7, Fig. 2). Male calves and juveniles were predicted to have significantly more scars than male subadults and adult males (male calf: male subadult $p=0.0009$, male calf: male adult $p<0.0001$,

Table 3 Model output for the generalized additive mixed model: New scars ~ SAc + population + s(year, by = population). Estimates for the male calf of the age class predictor and the Bigg's population of the population predictor are represented by the intercept. CR = Crozet, NR = Northern Resident

Terms	Estimate	Standard Error	t	*p*
Intercept	0.868	0.111	7.825	< 0.001
Male Juvenile	-0.016	0.130	-0.121	0.904
Male Subadult	0.710	0.166	-4.290	< 0.001
Male Adult	-0.974	0.136	-7.167	< 0.001
Female Calf	-0.423	0.155	-2.573	0.006
Female Juvenile	-0.210	0.135	-1.553	0.107
Female Adult	-1.559	0.127	-12.322	< 0.001
Female Post reproductive	-1.937	0.227	-8.523	< 0.001
Unknown Calf	-0.476	0.189	-2.516	0.012
Unknown Juvenile	0.064	0.178	0.361	0.718
CR population	-0.151	0.102	-1.489	0.137
NR population	-0.119	0.074	-1.624	0.105
Smooth terms	**Effective df**	**Reference df**	**F**	**p**
Year Bigg's population	< 0.001	1	0	0.078
Year CR population	< 0.001	1	0	0.267
Year NR population	< 0.001	1	0	0.871

male juvenile: male subadult $p=0.0003$, male juvenile: male adult $p<0.0001$, Table 3). Female juveniles were predicted to acquire more scars than the other female age classes (~ 1.7), but the difference between female juveniles and female calves (~ 1.4) was not significant ($p=0.9$). Adult and post reproductive females were predicted to have the least scars out of all sex-specific age classes, being the only two age groups to have significantly different scarring rates from all other groups (p-values between these two groups and the other all $p<0.01$) except each other ($p=0.0005$). Both unknown calves and juveniles were predicted to have similar scarring rates to the same age classes of both sexes (unknown calf: male calf $p=0.265$, unknown calf: female calf $p=1$, unknown juvenile: male juvenile $p=1$, unknown juvenile: female juvenile $p=0.833$), while differing significantly from adults and post reproductive females ($p<0.0001$). Furthermore, even without a term to formally test for an interaction between sex-specific age classes and populations in the final model, predictions of scarring followed the same qualitative pattern across sex-specific classes (Fig. 2). This supports the preliminary results of the alternative model including an interaction between population and SAc that was presented in the methods. The smooth random effect, year, was not statistically significant (year: Bigg´s $p=0.077$, year: CR $p=0.267$, year: NR $p=0.871$, Table 3).

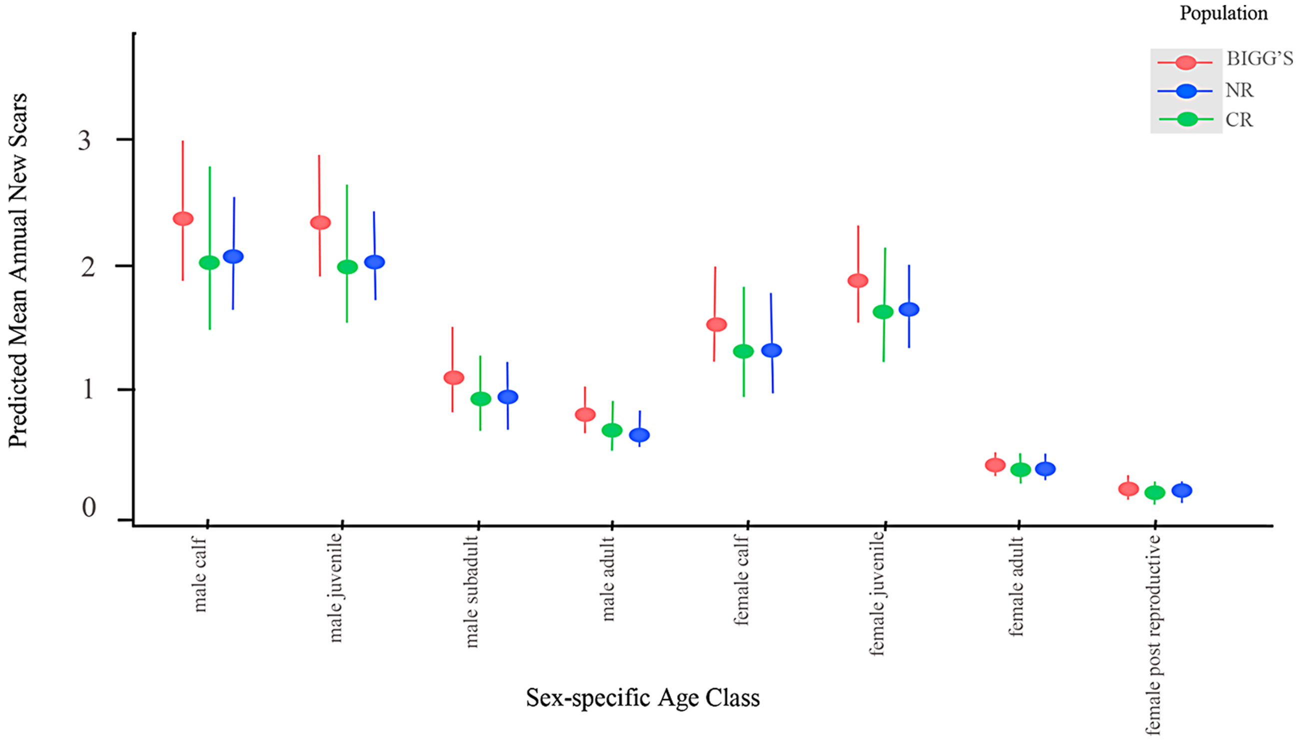

Fig. 2 Predicted mean annual new conspecific scars on killer whales per population by sex-specific age class based on the generalized additive mixed model: New Scars ~ Sac + population + s(year, by = population). Where SAc refers to the following sex-specific age classes: male calves (≤3), male juveniles (4–12), male subadults (13–20), male adults (>20), female calves (≤3), female juveniles (4–12), female adults (13–40), post-reproductive females (>40). CR = Crozet and NR = Northern Resident. Vertical bars represent the 95% confidence intervals

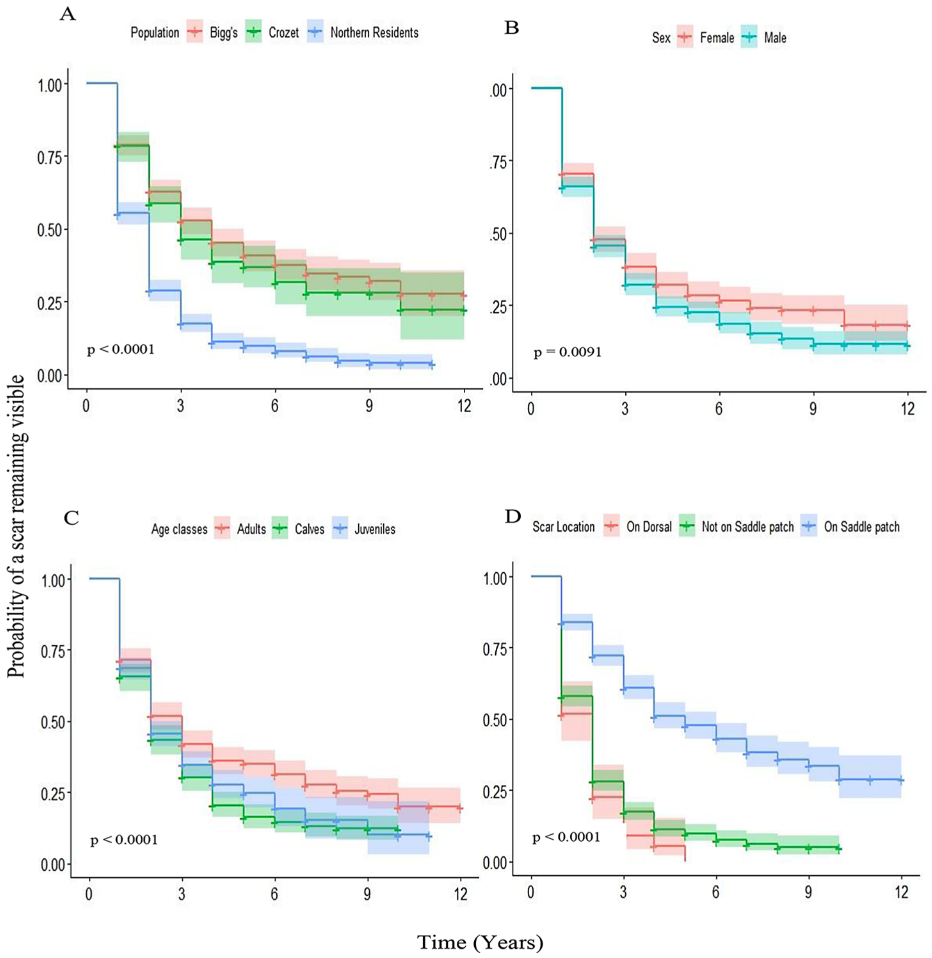

Fig. 3 Predicted conspecific scar healing time in killer whales using Kaplan-Meier Survival Curves. **A**) by population. **B**) by sex. **C**) by age class with scars first acquired as calves (≤3), juveniles (4–12), adults (≥13). **D)** by scar location on the body. Vertical notches represent censored individuals (for which no further information was available). The shaded areas around each curve represent the 95% confidence interval

Scar healing

Across all populations, sexes, and age classes, >50% of conspecific scars had disappeared after 2 years and >85% by 12 years. Scars healed significantly faster in NR with >95% of scars having disappeared after 9 years compared to >75% in CR individuals and ~70% in Bigg's individuals ($p < 0.0001$, Fig. 3A). There was a slight difference in healing between sexes with scars on males consistently disappearing before those on females ($p = 0.0091$, Fig. 3B). Healing also varied by age class. Scars acquired by calves healed faster than those in juveniles for the first nine years after they were acquired. Scars acquired by calves and juveniles healed at a similar rate once 9 years had passed since they were acquired. Scars acquired by adults healed the slowest of all age classes. After 10 years ~10% of scars acquired by calves and juveniles, and ~20% by adults remained visible ($p < 0.0001$, Fig. 3C). Finally, healing time varied depending on the location on the body where the scar was acquired with 100% of scars on the dorsal fin disappearing after 5 years compared to ~95% off the saddle patch and <75% on the saddle patch ($p < 0.0001$, Fig. 3D).

Discussion

Scar acquisition

The results of this study showed that the number of new scars from conspecifics did not differ significantly between highly divergent killer whale populations. This was unexpected as it was hypothesized that differences in prey type between these populations which are related to differing social structures, communication patterns, movements, and other behaviours (Ford and Ellis 2014), would similarly be associated with the ways in which individuals within populations interact physically with each other. Moreover, a previous comparison of conspecific scarring on NR and Bigg's killer whales found significant differences between these populations (Robeck et al. 2019). The data and analysis conducted by Robeck et al. (2019) differed from our study in several ways that may explain those differences. Most importantly, Robeck et al. (2019) only analyzed one photograph per individual, did not count individual scarring events, or select criteria to ensure scars potentially caused by sources other than conspecifics were excluded. Together, these factors could limit understanding of cumulative scarring history because healing and acquisition rates over time could not be accurately accounted for. Furthermore, overall sample sizes per population were unbalanced with NR data vastly outweighing Bigg's data. Most of the images used by Robeck et al. (2019) were also from an earlier point in time than the current study. Nevertheless, prey availability for the study populations can vary over time and the abundance of prey has been shown to have a correlation with scar acquisition in the Southern Resident (SR) killer whale population with more scars apparent during years of higher prey abundance (Grimes et al. 2022). Prey availability may affect scarring rates in the populations used in our analysis, but if differences in resource abundance were strong, we would not expect all populations to exhibit such similar scarring patterns over the same 11-year time series. The same may be true if the effects of resource competition were significantly contributing to scarring rates at the population level. Intra-population resource competition has been proposed under conditions where killer whales depredate prey from fisheries (Towers et al. 2019b) but seems unlikely to be a factor driving many interactions resulting in scarring, especially considering widespread sustained customs around reciprocity in this species which include prey-sharing with both related and unrelated conspecifics (Ford et al. 1998; Guinet et al. 2000; Wright et al. 2016). The similarity in scarring rates between populations therefore suggest that resource type, abundance, and associated lifestyles do not play a significant role in determining the kinds of physical interactions between all sex and age classes that result in scars.

In all three populations conspecific scar acquisition was influenced by sex and age. Scarring was shown to be overall higher in males than females and age was generally negatively correlated with new scar acquisition in both sexes. However, juveniles were scarred at near equal rates to calves. Grimes et al. (2022) also noted higher scarring rates in males and an overall decline in scar acquisition throughout life in both sexes for SR killer whales. This is somewhat different from the results presented in Robeck et al. (2019) which found a direct relationship in scar density and age for two of the same populations used in our analysis, however, this is likely due to the limitations of the data mentioned above. Although the absence of an interaction term in our final model prevents from statistically addressing inter-population variation in the effect of sex-age classes, similar rates of scar acquisition between sex and age classes across the three populations would suggest that most physical interactions causing scarring are likely driven by behaviours surrounding sexual selection. The higher scarring rates in adult males than adult females are consistent with scarring patterns in several other species of social mammal that have been attributed to reproductive competition between males (Chu and Nieukirk 1988; Tolley at el. 1995; Drews 1996; MacLeod 1998; Scott et al. 2005; Arlet et al. 2009; Rowe and Dawson 2009; Wright et al. 2017; James et al. 2022; Cords and Arguelles 2023). The negative relationship between scarring rates and age is similar to another dolphin species (Lee et al. 2019) but different from age related scarring trends in several other mammal species (Arlet et al. 2009; Crawford et al. 2015; Lanyon et al. 2021). This may be explained by the early life benefits of social play (Kuczaj and Eskelinen 2014) and establishment of dominance through sparring with peers (e.g. Rose 1992; MacCormick et al. 2012) as well as coercive behaviours by reproductive males who exhibit aggression towards offspring of potential mates, since this may induce cooperative behaviour from their mothers without the extreme of committing infanticide (Ebensperger 1998; van Schaik and Janson 2000; Towers et al. 2018; McEntee et al. 2023). This hypothesis is further supported by the finding that male killer whale calves have higher scarring rates than female calves since it may be expected that any aggression towards calves from adult males may be directed towards future competitors, rather than future mates. In this regard, it should be noted that the number of new conspecific scars acquired by calves may be underestimated since highly scarred calves may have died before being photographed and therefore would not have been included in this study. It is also important to consider that limited data availability for the CR population, particularly calves, increases the uncertainty of predictions of scar acquisition for this population. Additionally, this lack of image data compared to Bigg's and NR prevented the relationship between sex specific age class and population from being determined for the CR population, making general interpretations about these relationships less certain.

Scar healing

Scar healing rates varied between populations with NRs generally healing much faster than CR or Bigg's killer whales. We suggest this is due to original scarring events being less severe in NRs than the other populations because these differences cannot be explained by variations in environmental conditions such as salinity or sea surface temperature since NRs and Bigg's are sympatric. Furthermore, contaminant levels in these three populations do not align with scar healing rates given that CR killer whales have similar, but lower levels of pollutants than NRs, but heal at similar rates to Bigg's which are far more contaminated (Ross et al. 2000; Noël et al. 2009). Robeck et al. (2019) also noted more mild scarring in NR compared to Bigg's but did not attempt to quantify the age of scars based on appearance and therefore overlooked the possibility that variation in scarring may be affected by the intensity of the interaction. However, original scarring events may be less severe in NRs because this population is closed to immigration and emigration, whereas the CR and Bigg's populations are not (Towers et al. 2019a, 2020; Tixier et al. 2021). This indicates that aggression and subsequent scarring intensity could be positively correlated with interactions with unfamiliar conspecifics as seen in several other mammals (Dewsbury 1988; French et al. 1995; Barco-Trillo et al. 2009; Mirville et al. 2018). It is also possible that differences in diet between these killer whale populations may help explain healing rates considering that lipids are thought to promote skin healing (Chaudhary et al. 2024). However, if lipid intake is related to population health, scar healing is not correlated with the trajectories of these populations considering Bigg's and NRs were increasing in abundance over the time series of the study while CR killer whales were decreasing (Towers et al. 2019a, 2020; Tixier et al. 2021).

The results of this study also reveal that sex influences scar healing with males healing slightly faster than females. This may be due to differing levels of received physical interaction between sexes resulting in differing levels of scar severity. So, if scars are caused during sexually selected behaviours (e.g. Towers et al. 2018; Wright et al. 2023), this suggests that the physical impacts of sexual coercion on females are more severe than the effects of any retaliation by them or those of sexual competition between males, especially considering they have more scarring than females do overall. On the other hand, these differences in healing rates may be due to sex-based differences in vascular function (Costa and Tostes 2023) which could facilitate the process of healing. However, the only other study in which the scar healing process has been assessed at an odontocete population level that we know of showed contrasting results to ours in scar healing trends between sexes and indicated that females in their study may have healed faster than males due to the positive effects of estrogen on cellular regeneration (Lee et al. 2019).

Rates of scar healing were also influenced by age, with scars acquired by calves and juveniles healing faster than scars acquired by adults. Similar to differences in healing rates between sexes, these apparent differences in healing rates between age classes may potentially be due to differences in the severity of the scars acquired. Young killer whales for example are well known to engage in play more often than adults (Ford 1989; Rose 1992) so their scars may be more superficial and thus, prone to heal more quickly than these other age classes. Adult killer whales of both sexes on the other hand may be more commonly engaged in aggressive interactions with peers due to sexual coercion and reproductive competition (Wright et al. 2023). However, cellular aging may provide an alternative physiological explanation for why scars on adults heal slower than younger age classes since older cells are less able to divide and repair tissue (Borena et al. 2015; Tejada-Martinez et al. 2021).

The location of the scar on the body also appeared to significantly impact healing time. Scars on the dorsal fin healed slightly faster than those on the flanks despite both areas sharing the same black pigmentation. This may be due to functionally unique capillary networks between the connective tissue of the dorsal fin and the adipose tissue of the flanks which could facilitate angiogenesis required for wound healing differently (Arnold and West 1991). However, scars on the grey saddle patch took much longer to disappear than those off the saddle patch. This is likely because areas of the body with dark pigmentation (i.e. not the saddle, eye patches or underside) have a higher density of melanocytes closer to the surface of the skin and these cells accelerate wound healing and subsequent re-pigmentation (Hong et al. 2015; Su et al. 2022b; Gupta et al. 2023). The re-pigmentation of wounded skin on cetaceans is poorly studied though and differs both within (as highlighted by this study) and between species with scars on some odontocetes being permanently retained (Rosso et al. 2011; Corsi et al. 2022) while others heal without a trace (Lee et al. 2019; Su et al. 2022b). Similarly, some terrestrial mammals heal quicker on pigmented skin (Gupta et al. 2023) while others with differing levels of melanin heal at similar rates (Chadwick et al. 2013).

Study implications

The rates of scar acquisition being similar between all sex and age classes in the CR population in the Indian Ocean and the two populations in the northeastern Pacific has implications for our understanding of these threatened and endangered populations, and killer whales in general. First, when considered at a broader evolutionary scale our findings indicate that certain aspects of social evolution are shared by highly behaviorally, genetically, and geographically divergent killer whale populations. If our interpretation of results is correct in that many of the similarities we see in scarring rates between sex and age classes of these different populations is due to sexually selected behaviours rather than resource competition this suggests that reproductive activity and associated mating strategies have not diverged as strongly as ecological adaptations have evolved in this species. Second, through providing a robust analysis of data from multiple years and populations, some of our results differ significantly from those presented in a previous study. Our analysis has shown an inverse relationship between scar acquisition and age, and suggests that different sex and age classes may share similar scarring rates across populations. These findings both contribute to and change insights into sexually selected social behaviours of this species recently reviewed by Wright et al. (2023). Third, this study indicates that rates of scar healing differ between populations highlighting that scars may be caused by a variety of behaviours ranging from mild to intense play and aggression. Considering younger individuals are more heavily scarred and physically more vulnerable than older age classes they may especially be at risk of mortality following more aggressive interactions considering open wounds can cause a pathway for fatal infections in killer whales (Raverty et al. 2020; Burek-Huntington et al. 2023). Future work may include developing a scar severity index which could allow for insights into the wound healing process to be gained and the impact of conspecific attacks on individual survival and population dynamics to be examined.

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Data availability This scarring and healing data analyzed in this study are provided as Supplementary Tables with the manuscript.

Declarations

Ethical approval The photo-identification data of NR and Bigg's killer whales used in this study were collected under Fisheries and Oceans Canada issued marine mammal research licenses 01 and 42. Photo-identification data of CR killer whales was collected under the APAFIS permit 33165-2021092117135118.

Competing interests The authors declare no conflicts of interest.

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