

# Evidence of Variable Agonistic Behavior in Killer Whales (*Orcinus orca*) Based on Age, Sex, and Ecotype

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## Abstract

We used photo-identification catalogs to assess the occurrence of rake marks in northern resident (NRKW) and transient (TKW) killer whale ecotypes from the northeastern Pacific. Rake-mark coverage on visible surface areas, excluding dorsal fins, was grouped into four categories: (1) None (0%), (2) Mild (1 rake mark to < 25%), (3) Moderate (25 to 50%), and (4) Severe (> 50%). We conducted pairwise comparisons on density of rake marks with sex, age, and ecotype using mixed model, ordinal logistic regression. In NRKWs, rake marks increase with age in males ( $p = 0.0007$ ), and males had a higher frequency and density than females ( $p < 0.0001$ ) and juveniles ( $p = 0.02$ ), with no difference between females and juveniles. Male residents > 30 years had an 8-fold higher frequency of severe rake marks than any younger 5-year age group ( $p < 0.0001$ ), while no such relationship was seen in females ( $p = 0.30$ ). In TKWs, rake marks also increase with age in males ( $p < 0.0001$ ) and females ( $p < 0.0001$ ), though no difference was found ( $p = 0.1$ ) between males and females. NRKWs and TKWs had differences in rake-mark frequency and distribution ( $p = 0.004$ ) due mostly to an increase in density ( $p = 0.003$ ) in female transient vs female resident killer whales. While final confirmation will require behavioral observations, and based on our indirect results, we hypothesize that the increased aggression in older males from both ecotypes is due to sexual competition; and in transients, it is potentially due to prey competition. The increased aggression observed in transient adult females compared to resident females may be due to sexual coercion and/or an increased need to reestablish dominance in the more fluid social

hierarchy, while increases observed for transient senescent females may be due to an increased need for calf protection.

**Key Words:** aggression, agonistic behavior, killer whale, orca, *Orcinus orca*, rake marks, dominance hierarchy

## Introduction

Killer whale (*Orcinus orca*) lineages or ecotypes of the northeastern Pacific fluctuate between parapatry and varying degrees of sympatry. The evolution of these unique ecotypes is believed to have been primarily driven by differing feeding strategies (Baird et al., 1992; Ford et al., 1998). Of these ecotypes, *transient* and *resident* are the best known, and they feed primarily on mammalian and salmonid species, respectively. While there have been some accounts of behavior that occurs when different ecotypes cross paths (Baird & Dill, 1995; Ford et al., 1998), little information describing dyad interactions between animals of varying age and sex classes within each ecotype has been reported (Heimlich-Boran, 1988; Ford, 1989). The majority of intra-ecotype or even intra-pod behavior that has been described is functional in nature (e.g., group hunting) and spatially associative (Osborn, 1986; Heimlich-Boran, 1988; Ford, 1989) and has resulted from an emphasis on observing groups and not individuals (Baird, 2000). While these data have been essential in long-term field studies for describing feeding strategies, time budgets (for percussive foraging, feeding, traveling, resting, and playing) and the organizational structure of social systems within these ecotypes, they have failed to identify and quantify specific behaviors between individuals

or, more generally, “what goes on beneath the surface” (Heimlich-Boran, 1988, p. 576).

Killer whale societies, which have been universally described as hierarchal, matrilineal groups, have evolved into differing sizes and stabilities based on foraging strategies (Bigg et al., 1990; Ford et al., 1998; Ford & Ellis, 1999; Baird & Whitehead, 2000), yet no detailed descriptions of behaviors exhibited during the formation and maintenance of these socioecological structures exist. In killer whales, like all social mammals, circumstances such as defense, predation or foraging, caregiving, and competition for breeding are dynamic and may or may not require cooperation (Caraco & Wolf, 1975; Baird, 2001; Cavigelli & Pereira, 2000; Scott et al., 2005; Shen et al., 2011). The benefits of living cooperatively must outweigh the costs of living alone (Alexander, 1974). As such, successful outcomes occur when group leaders are clearly defined for each cooperative endeavor (Vehrencamp, 1983). Dominance may be fixed or fluid, adjusting to the situation or context of the motivational risk/benefit to the individual in the socioecological structure, and it is determined through the use of agonistic behaviors (Langbein & Puppe, 2004; Archie et al., 2006b). These agonistic behaviors appear to be critical for the formation of stable social groups among most mammalian species and are used for the formation of dominance hierarchy structures during competition for resources (both food and territory) and mate selection (Landau, 1951; Drews, 1993; Zumpe & Michael, 2001; Langbein & Puppe, 2004; Robbins, 2008).

*Agonism* is typically defined as all behavioral adjustments made between two animals of the same species when faced with the potential for fighting over resource access. It includes threat, attack, defense, retreat, and/or appeasement (Scott & Fredericson, 1951; Tuchscherer et al., 1998; Langbein & Puppe, 2004). In cetacean social groups, the agonistic behaviors of both winners and losers are often subtle in exhibition and out of view of observers, making them inherently difficult to record; killer whales are no exception (Baird, 2000; Connor et al., 2000). Two separate reports have been made that describe agonistic behaviors that occurred during dominance establishment in captive bottlenose dolphins (*Tursiops truncatus*) and killer whales (Samuels & Gifford, 1997; Graham & Noonan, 2010). The behaviors observed for bottlenose dolphins, some of which were defined for the first time, have since been incorporated into an ethogram and used during focal behavioral studies of aggressive interactions in wild bottlenose dolphins (Scott et al., 2005). For killer whales, unique acoustic patterns were described during the rare agonistic behaviors

exhibited by the captive individuals—acoustic markers that have yet to be incorporated into behavioral analysis of wild animal counterparts (Graham & Noonan, 2010).

For odontocetes, one of the most common expressions of agonism observed in the form of physical interaction between conspecific individuals involves various degrees of oral/body contact (McCann, 1974; Samuels & Gifford, 1997; MacLeod, 1998; Scott et al., 2005). When this type of activity includes teeth, the resulting wound and subsequent scar are characterized by a grouping of parallel lesions (in varying degrees of density) that are spaced at a distance equal to that between the apex of adjacent teeth in conspecifics (Norris, 1967; Lockyer & Morris, 1985; Samuels & Gifford, 1997; MacLeod, 1998; Kugler & Orbach, 2014). These groupings are referred to as *rake marks*. The biting or “raking” of an individual has been suggested to occur during playful interactions in juveniles (Norris, 1967; McCann, 1974; Jacobsen, 1986; Ford, 1989) that may or may not lead to what is considered aggression (Scott et al., 2005), or it has been associated with dominance behavior between conspecific adults (almost always males) that is unquestionably aggression (McCann, 1974; Lockyer & Morris, 1985; MacLeod, 1998). Thus, for field researchers, the immediate or latent observations of these scars following behavioral activity can provide evidence of which animals were the direct targets of these interactions (Norris, 1967; Chu & Nieukirk, 1987; Scott et al., 2005). Conspecific aggression among odontocetes, often assumed to have occurred retrospectively by the presence of these rake marks, has been reported for most odontocetes (McCann, 1974; MacLeod, 1998; Connor et al., 2000; Graham & Noonan, 2010; Luksenburg, 2014). As with other taxa, the function of such aggression is believed to involve practice for adulthood in juveniles, competition for sexual partners or food, or, more inclusively, the general management of the social hierarchy (Connor et al., 2000).

In killer whales, conspecific aggression in the form of actual physical contact, including rake marks, is considered extremely rare due to few documented direct observations (Ford, 1989; Rose, 1992; Visser, 1998). While limited in the variety of social interactions that would typically occur in a larger heterogenous group of animals, aggression between a pair of captive killer whales and its calf was observed to occur in < 1% of the observed interactions (Graham & Noonan, 2010). For wild animals, one observed occurrence involved a large pod of resident killer whales (greater than ten) chasing and attacking a small pod of three transient killer whales. Fresh rake marks were observed on the dorsal fin and flank of

two of the transients just after the initial encounter (Ford & Ellis, 1999). Bisther (2002) reported instances of agonistic behavior with “visitor” pods displacing “local” pods in herring feeding grounds off the Norwegian coast in seven out of 79 (~9%) of the observations when two pods were present contemporaneously over a 10-year period. However, this involved threatening behavior followed by immediate dispersal, and any contact could not be verified. Except for a recent report of intra-group infanticide (Towers et al., 2018), observations of physical aggression between ecotypes are few, and reports of it within ecotypes or pods are virtually non-existent. Additionally, anecdotal accounts also appear to be infrequent, perhaps because, if they are reported at all, they often appear in secondary sources making them difficult to track (e.g., see Shore, 1995). A similar lack of observations of real-time aggressive behavior also occurs in the bottlenose dolphin (Scott et al., 2005). However, in bottlenose dolphin and other cetacean societies, it is generally assumed that aggression occurs routinely (Connor et al., 1996; Mann & Smuts, 1999; Scott et al., 2005; Marley et al., 2013), while, uniquely for killer whales, the paucity of any type of observed agonistic behavior and specifically physical aggression is often equated with actual rarity. Therefore, conspecific aggression is hypothesized to play a minimal role in the social structure of killer whales (Jacobsen, 1986; Rose, 1992; Visser, 1998; Baird, 2000; Graham & Noonan, 2010).

Despite this assumption, observable rake marks in killer whales have been noted (Scheffer, 1969; McCann, 1974; Jacobsen, 1986; Ford, 1989; Visser, 1998), and visible scarring can be seen in many images of killer whales (McCann, 1974; Dahlheim et al., 1997; Baird, 2000; Ellis et al., 2007). Scheffer (1969) first reported this pattern of tooth marks on a killer whale. He measured the spacing of alveoli of the teeth of two killer whale skulls suggesting a method for estimating the scar length on a photographed animal with the assumption that they were from another killer whale. Other cetaceans show scarring in accordance with the dentition of conspecifics (McCann, 1974), but they also show rake and bite marks from other species, including those commonly attributed to killer whale predatory attacks (Rice & Wolman, 1971; Katona & Whitehead, 1981; Arnborn, 1987; Lowry et al., 1987; George et al., 1994; Sheldon et al., 2003; Laidre et al., 2006; Reinhart et al., 2013). As apex predators (Estes et al., 1998; Ford et al., 1998; Pitman, 2011), killer whales are unique in that they have this type of scarring as solely representative of a conspecific-inflicted wound. Other marks and injuries possibly resulting from such

things as defensive wounds from prey (e.g., pin-nipeds) or entanglements with long-line fisheries as described for false killer whales (*Pseudorca crassidens*; Baird & Gorgone, 2005) would not result in this distinctive pattern.

The observed rake marks in killer whales indicate that at least some form of conspecific aggression is occurring. However, the prevalence or degree of this aggression is not known, although Baird (2000) states that scarring occurs at a relatively high rate. Visser (1998) described “prolific” (p. 77) body scarring on two individuals among 30 adult males with no others meeting this criterion. This subjective assessment is difficult to replicate or compare to photographic analysis of other individuals. Moreover, visual accounts of this extent (the dorsum and head in their entirety) are not available for most killer whales. Other than these observations, and despite the use of rake marks in other species to improve the understanding of conspecific social interaction (Norris, 1967; Kato, 1984; Lockyer & Morris, 1985; Chu & Nieuwkerk, 1987; Scott et al., 2005), no attempt has been made to quantify the frequency and extent to which individuals in a population (ecotype) show evidence of rake marks.

Photo identification, a technique which relies on identifying unique variation in color patterns and other morphologic characteristics of individual animals, was first used as a method for studying killer whales off the Pacific Northwest coast in 1973 (Bigg, 1982). Development of this technique occurred independently around the same time period in humpback (*Megaptera novaeangliae*; Katona et al., 1979) and right (*Eubalaena* sp.; Payne, 1986) whales and four species of small delphinids (for review, see Würsig & Jefferson, 1990). Individuals can be identified by collecting images of their natural markings, each unique and permanent (Würsig & Jefferson, 1990), thus making long-term population studies possible. This methodology is particularly suited to killer whales because they show a striking contrast of greyish-white markings that straddles their dorsum just posterior to the dorsal fin against the otherwise black pigment. This “saddle” region is visible during surfacing for respirations and, thus, can be repeatedly photographed and identified with accuracy over the course of many years and theoretically throughout the lifetime of individuals (Bigg, 1982; Ford et al., 1994, 2000; Baird, 2000; Ellis et al., 2007). Longitudinal application of these methods in killer whales has allowed for an array of life history information to be directly collected or estimated from inference, including the sex and age of individual animals within each ecotype. Therefore, the objectives of this research were to evaluate the density of observable rake marks on individual animals in the most recently published transient (Towers et al., 2012) and northern resident

(Ellis et al., 2011) killer whale photo-identification catalogs to determine if (1) differences in the density of rake marks can be detected between males and females, (2) patterns of rake-mark occurrence change with age, and (3) differences exist in the pattern of rake-mark occurrence between transient and northern resident killer whale ecotypes.

### Methods

We used the 2010 northern resident (NRKW) killer whale photo-identification catalog (Ellis et al., 2011) and the 2012 transient (TKW) killer whale catalog (Towers et al., 2012) to quantify the distribution of visible rake marks in these killer whale populations. These catalogs contain high-resolution images of the area of the animal visible during surfacing, including the dorsal fin and the exposed or visible surface area (VSA) of the saddle region and dorsum surrounding the dorsal fin of each individual within the respective groups (NR:  $N = 264$ ; TKW:  $N = 57$ ; Figure 1). Details on the collection methods and photographic techniques as well as the sorting of this material can be found in Ellis et al. (2011) and Towers et al. (2012).

For each evaluation, the skin of all VSA (excluding the dorsal fin) was visually examined after digital magnification at a minimum of 400x of the source material photographs for the presence of rake marks. *Rake marks* were defined and identified as a grouping of at least two parallel lesions of scar tissue or lacerations observed on the skin surface (Norris, 1967; Scott et al., 2005). Other lesions or scars not matching this criterion were ignored. Dorsal fins were not evaluated due to differences in lighting in this region within single images that consistently made it difficult to detect rake marks without significant image exposure manipulation. Therefore, only the VSA below an imaginary line drawn across the base of the dorsal fin connecting the cranial (in relation to the dorsal fin) and caudal margins of the dorsum was evaluated (Figure 1). We estimated the extent of rake marks in terms of the percentage of visually observable VSA covered by these groupings.

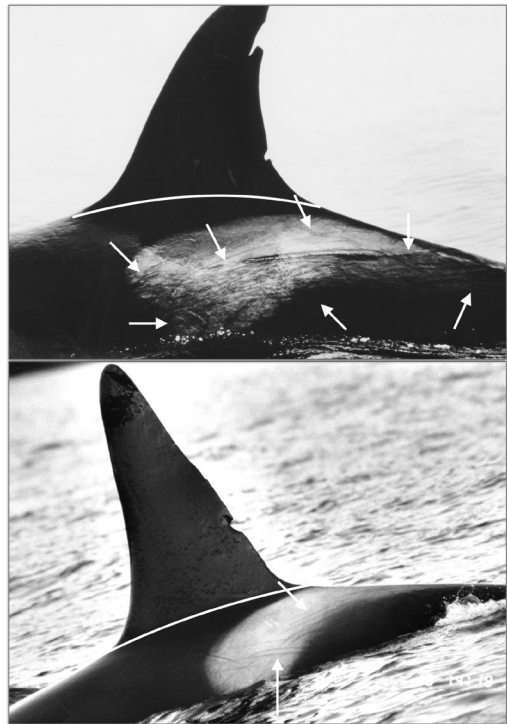
In the NRKW catalog, images were only presented from the left side of each animal, while both the right and left sides were included for the majority of the animals in the TKW catalog.

Rake marks were characterized into four groups based on the percentage of observable VSA affected as follows:

1. “None” = No observed rake marks
2. “Mild” = Greater than zero but less than 25% of observed surface area covered in rake marks

3. “Moderate” = Between 25 and 50% of observable surface area covered in rake marks
4. “Severe” = Greater than 50% of observable surface area covered in rake marks

While it is clear that the amount of total exposed surface area will be different for each animal depending on the angle from which the photograph was taken, as was the relative point during surfacing in which the animal was photographed as well as other factors, we could standardize for this inter-animal variation by relying on a percentage of total exposed surface area.



**Figure 1.** Illustration of how the percentage of rake marks covering the total visible surface area (VSA) was determined from photo-identification catalogs. Images were digitally magnified to a minimum of 400x for the evaluation. We ignored marks on the dorsal fin by delineating with an imaginary line (see white line above). Only the VSA was then evaluated for the presence of rake marks, and a percent coverage was estimated. In these example images from southern Alaskan resident killer whales (Ellis, 1987), we have highlighted areas (white arrows) with rake marks. The animal in the top image would be classified in the Moderate category (25 to 50% VSA covered with rake marks), while the animal in the bottom image would be classified in the Mild category (0 to 25% VSA with rake marks).

Categorization by the four observers was standardized by having each individual independently evaluate the same five photographs randomly selected from an earlier version (Ellis et al., 2007) of the catalogs. The results of these independent evaluations were then discussed among the group to gain consensus concerning the methodologic approach for dividing the VSA into the four percentage blocks (0%, < 25%, 25 to 50%, > 50%) for the analysis. Once methodological consensus was reached, each observer then independently scored the images, and the results from each individual were used for the analysis.

In addition, any animal whose photograph was considered too difficult to evaluate due to poor exposure or other limitations by two observers was eliminated from the study. If one observer could not evaluate the image and the remaining three were in agreement on the category, then the missing data point was replaced by the consensus value from the remaining three observers.

Both the NRKW and TKW catalogs identify animals by estimated or known age (based on year of first observation) and by sex. For the NRKW catalog, ages of animals first observed as adults were determined by the method described by Olesiuk et al. (1990, 2005), which corrects the date of first sighting of adult females with the age of possible offspring. TKW animals were assigned the date first observed as adults as a *maximum* age without any correction (Towers et al., 2012). Determination of the sex of each animal in both catalogs was accomplished by one of the following methods: Females were identified by the presence of a calf, with the majority presenting a first calf by age 14; while males are identified based on the dorsal fin height to width ratio—from 13 to 14 years (Olesiuk et al., 1990; Robeck & Monfort, 2006). Animals were also identified by sex if observational data (visualization of the genital region) was available, although this was not common. Thus, animals of unknown sex were typically less than 12 to 14 years of age and, therefore, were classified as juveniles. For comparisons to previous work on male–male group interactions (Rose, 1992), we further broke down age into three categories: (1) Juveniles (4 to < 12 y), (2) Subadult Males (12 to 25 y), and (3) Adult Males (> 25 y). For females, we used previous descriptions of age class groupings (Olesiuk et al., 1990; Ward et al., 2009) using the following categories: Calf (0 to 3 y), Juvenile (4 to 12 y), Adult (> 12 to 40 y), and Senescent (> 40 y).

#### Statistical Analysis

Unless noted, all statistical analysis was performed using *Stata* (StataCorp LP, College Station, TX, USA). The dependent variable “rake-mark categories” was coded (0, 1, 2, and

3) from least to most marks (None to Severe), and “sex” was coded (0, 1, and 2) as Juvenile, Female, and Male. In two separate analyses for differences within each sex, males were categorized as Juvenile, Subadult, and Adult (0, 1, and 2); and separately, females were categorized as Calf, Juvenile, Adult, and Senescent (0, 1, 2, and 3). To control for inter-replicate (observer) variation for each animal, we first determined whether or not a simple ordinal regression of a likelihood ratio test would adequately account for model variance or if a second-level mixed-effects ordinal regression model (“meolgit”) was needed using an “animal identification number (ID#)” as the random variable (Rabe-Hesketh & Skrondal, 2012). Hypothesis testing was then performed on the two fixed variables of “age” (continuous) and “sex” (as a factor) using a Wald test (Long & Freese, 2014) to determine if at least one was not equal to the null hypothesis or a value of no rake marks. We then used the predictive marginal means ( $\pm$  95% CI) for rake marks vs adult males and females at 5-year intervals for graphical comparison. Next, we used a separate mixed model to evaluate age group categories for males (Juvenile, Subadult, and Adult) and females (Calf, Juvenile, Adult, and Senescent). Finally, we used an additional mixed model to compare the overall frequency and distribution of each of the rake-mark categories between the NRKW and TKW populations, and then between males and females within these populations. The parallel assumptions for the fixed portion of the ordinal logistic regression in these analyses were evaluated using a Brant test for parallel regressions (Long & Freese, 2014). Significance for all comparisons was accepted at a level of  $p < 0.05$ .

## Results

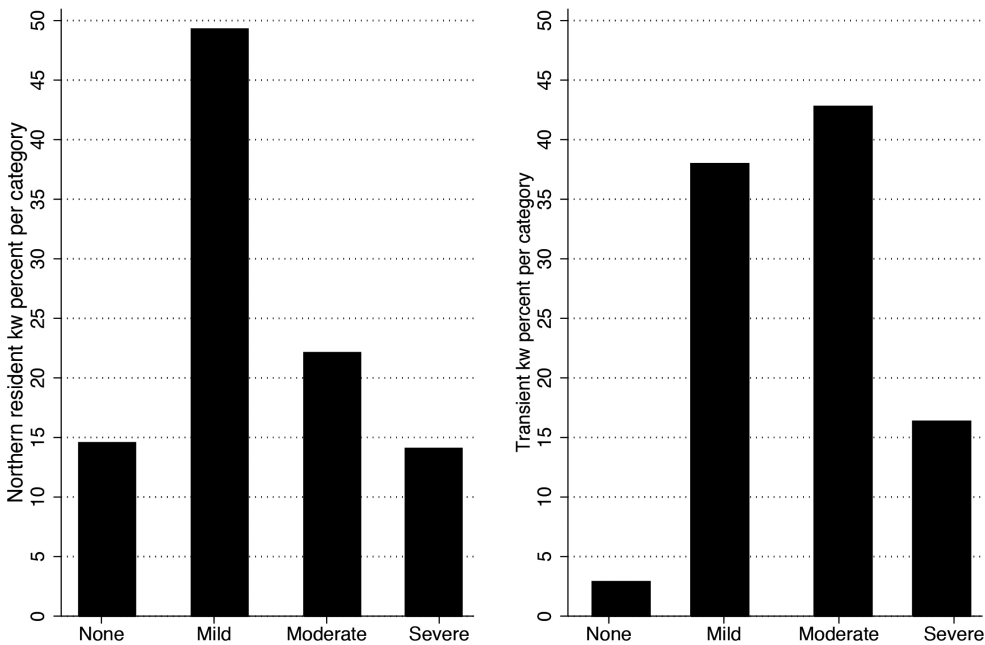
### *Northern Resident Killer Whales*

A total of 262 images (out of 267 possible) of northern resident killer whales from the 2010 catalog (Ellis et al., 2011) were considered of suitable quality to be evaluated by four different observers to classify the extent of rake marks (None, Mild, Moderate, and Severe) in the visible dorsal area (VSA) of the animals during surfacing (Figure 1). Rake marks were observed in 84% of all animal images (Figure 2).

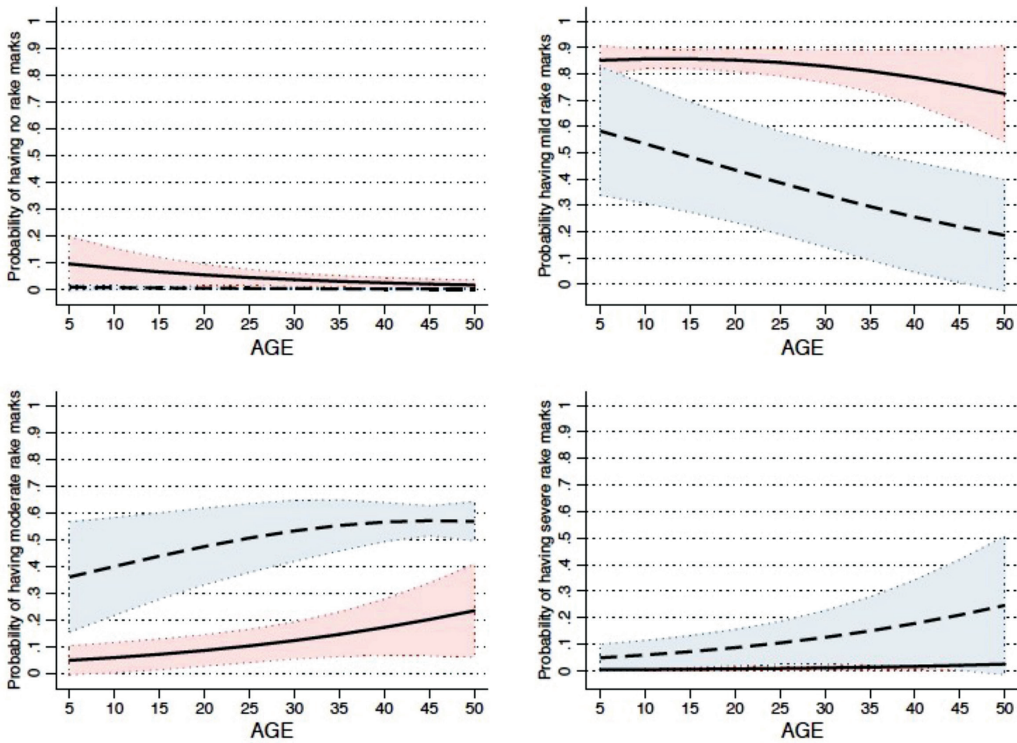
Accounting for model variance was significantly improved ( $\chi^2_{df=1} = 461.4, p < 0.0001$ ) using a two-level, mixed ordinal regression model with “animal ID #” as the random variable as opposed to simple ordinal regression. The full mixed model with the independent covariates of “sex” and “age” was significant ( $\chi^2_{df=1} = 18.6, p = 0.0003$ ). The proportional odds assumption for

the fixed portion of the model was not violated as determined by the Brant test ( $\chi^2_{df=4} = 7.48, p = 0.113$ ). There was no significant effect of Female ( $\chi^2_{df=2} = 2.4, p = 0.30$ ) or Juvenile ( $\chi^2_{df=1} = 2.2, p = 0.14$ ) and age on rake marks across all categories of rake marks, while a significant association between male ( $\chi^2_{df=2} = 14.5, p = 0.0007$ ) with age was detected. In addition, differences in the distribution of rake marks within the categories were detected between Male and Female ( $\chi^2_{df=1} = 16.7, p < 0.0001$ ) and Male and Juvenile ( $\chi^2_{df=2} = 5.3, p = 0.02$ ), while no differences were observed between Female and Juvenile ( $\chi^2_{df=2} = 1.9, p = 0.16$ ). Holding all other variables constant, the odds of having rake marks in the Severe category vs the combined, lesser categories of None, Mild, and Moderate are 3.7x higher for a male and 0.43x higher for a female than for a juvenile animal. Evaluating the average marginal effects of age on rake marks (across all sex categories), we find that for each 10-year increase in age, there is a 24 and 6.5% decrease in animals categorized as None or Mild, respectively, and a 21 and 31% increase of being categorized as Moderate or Severe, respectively. The predicted probabilities of being classified within each rake-mark category for male and female NRKW are illustrated in Figure 3.

For male age categories, we found no significant differences in rake-mark categories between Juvenile and Subadult ( $\chi^2_{df=1} = 0.02, p = 0.90$ ); however, differences were detected between Adult and Juvenile ( $\chi^2_{df=1} = 5.39, p = 0.02$ ) and between Adult and Subadult ( $\chi^2_{df=1} = 4.1, p = 0.04$ ). Holding all other variables constant, the odds of having rake marks in the Severe category for northern resident males vs the combined, lesser categories of None, Mild, and Moderate are 1.1x higher for a subadult male and 5.9x higher for an adult male than for a juvenile animal. The predicted probabilities of being classified in each rake-mark category are listed in Table 1. Further division of males and juveniles (unknown sex) into 5-year age brackets (0 to 4, 5 to 9, 10 to 14, 15 to 19, 20 to 24, 25 to 29, and > 30 y) revealed that adults older than 30 years of age had significantly more severe rake marks than any younger group of males ( $\chi^2_{df=1} = 24.9, p < 0.0001$ ). The predicted probabilities of being classified in each rake-mark category for each 5-year age bracket are listed in Table 1. The odds of reporting the next higher category of rake marks in animals 5 years and over when compared to animals between ages 0 to 4 years was between 11 and 33x higher; but in males over 30 years, it jumped to 563x.



**Figure 2.** Percentage of animals within the total population of northern resident (left; Ellis et al., 2011) and transient (right; Towers et al., 2012) killer whales classified as having rake marks on their VSA within the following categories: None = no rake marks observed on the VSA, Mild = 1 to < 25% of VSA with rake marks, Moderate = 25 to 50% VSA with rake marks, or Severe = > 50% of VSA with rake marks. Distribution frequencies of rake marks were significantly different ( $\chi^2_{df=1} = 8.1, p = 0.004$ ) between ecotypes.



**Figure 3.** Probability ( $\pm$  95% CI) of female (solid line) and male (dashed line) northern resident killer whales from 5 to 50 years of age having a None (no rake marks observed on the VSA), Mild (1 to < 25% of VSA with rake marks), Moderate (25 to 50% of VSA with rake marks), or Severe (> 50% of VSA with rake marks) classification of rake-mark coverage in the VSA in the northern resident photo-identification catalog (Ellis et al., 2011)

For female age categories, we found significant differences in categorical distributions of rake marks between Juvenile and Calf ( $\chi^2_{df=1} = 5.39$ ,  $p = 0.02$ ) and Juvenile and Adult ( $\chi^2_{df=1} = 6.78$ ,  $p < 0.009$ ) but not between Juvenile and Senescent ( $\chi^2_{df=1} = 3.27$ ,  $p < 0.07$ ). Differences were also detected between Adult and Calf ( $\chi^2_{df=1} = 8.05$ ,  $p = 0.005$ ) and Senescent and Calf ( $\chi^2_{df=1} = 4.1$ ,  $p = 0.04$ ) but not between Adult and Senescent ( $\chi^2_{df=1} = 0.01$ ,  $p = 0.94$ ). The odds of reporting a Severe category of rake marks in females vs the combined, lesser categories of None, Mild, and Moderate are 19.7x higher for a juvenile, 5.5x higher for an adult, and 5.2x higher for a senescent than for a calf, respectively. The predicted probabilities of being classified in each rake-mark category are listed in Table 2.

#### Transient Killer Whales

A total of 52 images (out of 57 possible) of the left side and 45 (out of 51 possible) of the right side of transient killer whales from the 2012 catalog (Towers et al., 2012) were considered of suitable

quality to be evaluated using the same methodology as for northern residents. However, unlike the NRKW catalog, images of both the right and left sides were provided. A comparison of the rake-mark categories between these two sides using a paired, two-tailed  $t$  test indicated no differences ( $t_{173} = 0.82$ ,  $p = 0.41$ ). Therefore, for consistency with the NRKW data, only rake-mark categories from the left side were analyzed. Rake marks were observed in 97% of all animal images (Figure 2). Accounting for model variance was significantly improved ( $\chi^2_{df=1} = 89.2$ ,  $p < 0.0001$ ) using a two-level, mixed ordinal regression model with “animal ID #” as the random variable as opposed to simple ordinal regression. The full mixed model with the independent covariates of “sex” and “age” was significant ( $\chi^2_{df=3} = 40.4$ ,  $p < 0.0001$ ). However, since only two animals (both calves) were in the None category, the proportional odds assumption could not be evaluated. Nevertheless, after the None category was eliminated, the proportional odds assumption for the fixed portion of the model was not violated ( $\chi^2_{df=4} = 7.48$ ,  $p < 0.11$ ); therefore,

**Table 1.** The predicted probabilities of the degree of rake marks observed on killer whale (*Orcinus orca*) male transient and northern resident ecotypes within each age group

Age groups	Predicted probability (%)				Significance <sup>1</sup> ( $p < 0.05$ )
	None	Mild (1 to 25%)	Moderate (> 25 to 50%)	Severe (> 50%)	
Male transient killer whales*					
Juvenile unknown sex (J: 5 to < 12 y, $n = 9$ )	--	77.5 ± 10.7	21.9 ± 10.0	0.6 ± 0.6	J ≠ S & A
Subadult male (S: 12 to 25 y, $n = 4$ )	--	6.5 ± 5.9	68.6 ± 12.1	24.7 ± 15.4	S & A ≠ J
Adult male (A: > 25 y, $n = 7$ )	--	6.6 ± 4.7	68.8 ± 10.2	24.4 ± 11.9	A & S ≠ J
Male northern resident killer whale*					
Juvenile unknown sex (J: 5 to < 12 y, $n = 58$ )	1.0 ± 0.5	61.5 ± 8.4	33.5 ± 7.4	4.0 ± 1.5	J ≠ A
Subadult male (S: 12 to 25 y, $n = 36$ )	0.9 ± 0.5	59.6 ± 11.4	35.2 ± 9.9	4.3 ± 0.5	S ≠ A
Adult male (A: > 25 y, $n = 16$ )	0.2 ± 0.1	21.7 ± 11.6	58.4 ± 3.8	19.7 ± 0.1	A ≠ J & S
0 to 4 y (1)	9.6 ± 4.6	86.1 ± 3.3	4.0 ± 2.1	0.28 ± 0.2	1 ≠ 1 to 7
5 to 9 y (2)	0.9 ± 0.5	64.3 ± 10.5	31.6 ± 9.5	3.2 ± 1.6	2 ≠ 1 & 7
10 to 14 y (3)	0.9 ± 0.7	64.2 ± 15.8	31.8 ± 14.2	3.2 ± 2.3	3 ≠ 1 & 7
15 to 19 y (4)	0.3 ± 0.3	41.7 ± 21.8	50.2 ± 15.8	7.8 ± 6.5	4 ≠ 1
20 to 24 y (5)	0.7 ± 0.8	58.6 ± 25.7	36.7 ± 22.1	4.1 ± 4.3	5 ≠ 1 & 7
25 to 29 y (6)	0.3 ± 0.3	39.8 ± 23.1	51.5 ± 16.2	8.4 ± 7.6	6 ≠ 1
≥ 30 y (7)	0.01 ± 0.03	3.8 ± 4.7	35.3 ± 26.9	61.0 ± 30.6	7 ≠ 1 to 3, & 5

<sup>1</sup>Wald's  $\chi^2$  test was used to test for equivalents of categorical distributions

\*No differences were detected in the distribution of rake marks across all age groups within each rake-mark category between the two ecotypes ( $\chi^2_{df=1} = 0.25, p = 0.62$ ).

all further analysis of transient data was conducted without the None category. With these two animals eliminated, the full mixed model was similarly significant ( $\chi^2_{df=3} = 35.6, p < 0.0001$ ).

There was a significant effect of Juvenile ( $\chi^2_{df=1} = 16.7, p < 0.0001$ ), Female ( $\chi^2_{df=1} = 31.8, p < 0.0001$ ), and Male ( $\chi^2_{df=2} = 33.6, p < 0.0001$ ) with age on rake-mark categories. Differences in rake marks were detected between male and juvenile animals ( $\chi^2_{df=1} = 4.7, p = 0.03$ ), while no differences were observed between male and female ( $\chi^2_{df=1} = 2.88, p = 0.09$ ) or female and juvenile ( $\chi^2_{df=1} = 1.2, p = 0.27$ ) animals. Holding all other variables constant, the odds of having rake marks in the Severe category vs the combined, lesser categories of Moderate and Mild are 8.9x higher for a male and 2.8x higher for a female than for a juvenile animal. Evaluating the average marginal

effects for age on rake marks (across all sex categories), we find that for each 10-year increase in age, there is a 46% decrease in animals categorized as Mild, and a 42 and 180% increase in animals categorized as Moderate or Severe, respectively. The predicted probability of being classified in each rake-mark category for male and female TKW is illustrated in Figure 4.

For male age categories, analysis omitting the None category resulted in regression that did not violate the proportional odds assumption ( $\chi^2_{df=1} = 0.84, p = 0.36$ ). With this model, there was significant differences between Juvenile and Subadult ( $\chi^2_{df=1} = 11.4, p = 0.0007$ ) and Adult and Juvenile ( $\chi^2_{df=1} = 14.9, p = 0.0001$ ). However, no differences were observed between Adult and Subadult ( $\chi^2_{df=1} = 0.0, p = 0.98$ ). Holding all other variables constant, the odds of having rake marks in a Severe



**Table 2.** The predicted probability of the degree of rake marks observed on a killer whale female transient and northern resident ecotypes within each age group

Age groups	Predicted probability (%)				Significance <sup>1</sup> ( $p < 0.05$ )
	None	Mild (1 to 25%)	Moderate (> 25 to 50%)	Severe (> 50%)	
Female transient killer whales*					
Calves unknown sex (C: 0 to 3 y, $n = 7$ )	8.2 ± 7.0	89.7 ± 6.2	2.0 ± 2.1	0.04 ± 0.06	1 ≠ A & S
Juvenile unknown sex (J: 4 to < 12 y, $n = 8$ )	0.8 ± 0.9	81.4 ± 11.3	17.2 ± 11.3	0.5 ± 0.5	J ≠ A & S
Adult females (A: 12 to 39 y, $n = 14$ )	0.1 ± 0.1	33.5 ± 12.9	62.4 ± 11.3	4.1 ± 2.5	A ≠ C, J & S
Senescent females (S: ≥ 40 y, $n = 12$ )	0.01 ± 0.01	6.1 ± 4.0	69.3 ± 9.3	24.6 ± 11.7	S ≠ C, J & A
Female northern resident killer whale*					
Calves unknown sex (C: 0 to 3 y, $n = 37$ )	21.2 ± 8.4	75.9 ± 7.1	2.5 ± 1.3	0.3 ± 0.2	C ≠ J, A & S
Juvenile unknown sex (J: 4 to < 12 y, $n = 71$ )	1.3 ± 0.6	61.9 ± 8.0	30.6 ± 6.4	6.2 ± 2.2	J ≠ C & A
Adult females (A: 12 to 39 y, $n = 80$ )	4.7 ± 1.71	81.4 ± 3.3	12.2 ± 3.7	1.8 ± 0.7	A ≠ C & J
Senescent females (S: ≥ 40 y, $n = 21$ )	4.9 ± 3.1	81.7 ± 4.9	11.6 ± 6.4	1.7 ± 1.1	S ≠ C

<sup>1</sup>Wald's  $\chi^2$  test was used to test for equivalents of categorical distributions.

\*Differences were detected in the distribution of rake marks across all age groups within each rake-mark category between the two ecotypes ( $\chi^2_{df=1} = 8.75, p = 0.003$ ).

category in transient males vs the combined, lesser categories of Mild and Moderate are 48x higher for a subadult and 47x higher for an adult male than for a juvenile animal. The predicted probability of each age group being classified in each rake-mark category is listed in Table 1.

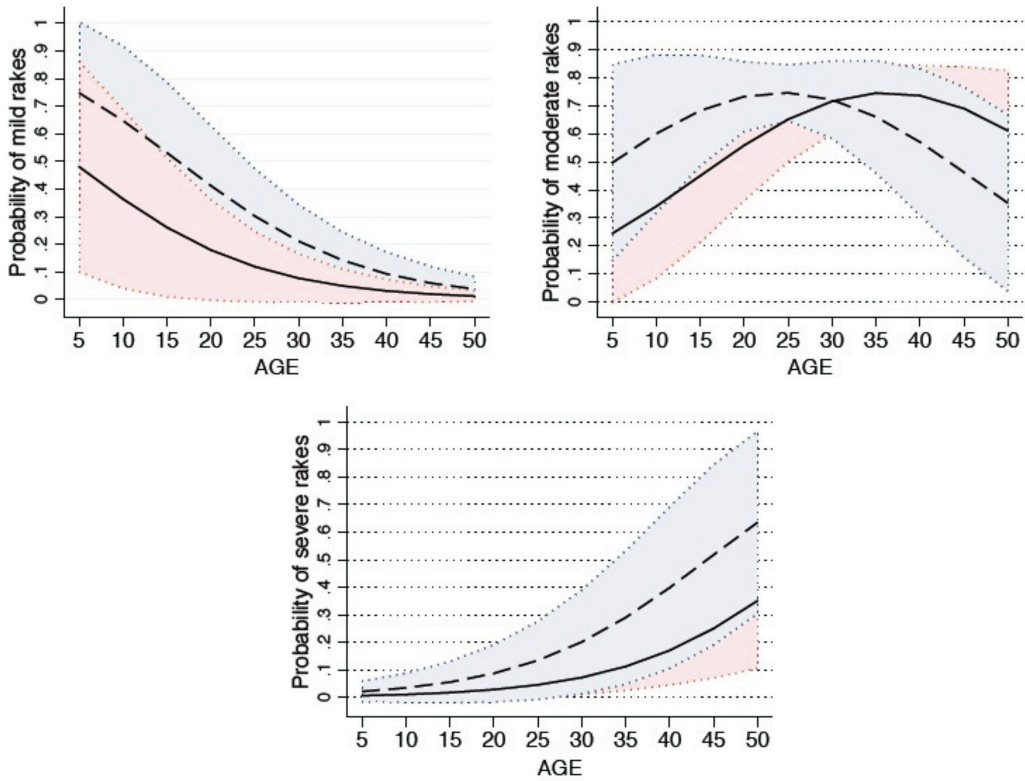
For female age categories, we found significant differences in categorical distributions of rake marks between Calf and Adult ( $\chi^2_{df=1} = 14.3, p < 0.0002$ ) and Calf and Senescent ( $\chi^2_{df=1} = 25.5, p < 0.0001$ ) but not between Calf and Juvenile ( $\chi^2_{df=1} = 3.6, p = 0.06$ ). The fixed portion of this model using all rake-mark categories did not violate the proportional odds assumption ( $\chi^2_{df=2} = 1.3, p < 0.52$ ). Differences were also detected between Juvenile and Adult ( $\chi^2_{df=1} = 5.0, p < 0.03$ ) and Juvenile and Senescent ( $\chi^2_{df=1} = 5.7, p = 0.02$ ). Holding all other variables constant, the odds of having a Severe category in transient females vs the combined, lesser categories of None, Mild, and Moderate are 10.0x higher for a juvenile, 92.6x higher for an adult, and 712.8x higher for a senescent female than for a calf. The predicted probability of each age group being classified in each rake-mark category is listed in Table 2.

### Transients vs Northern Residents

For the overall population of transient and northern resident killer whales, significant differences ( $\chi^2_{df=1} = 8.1, p = 0.004$ ) were observed in the distribution of rake marks across the four categories (Figure 2). The results from the mixed ordinal regression model odds ratio indicated that transient killer whales were 3.8x more likely to have rake marks in the Severe category than resident killer whales. For females, a significant difference was observed ( $\chi^2_{df=1} = 8.75, p = 0.003$ ) in the frequencies of rake marks in each category, with transients 4.8x more likely to have rake marks in the Severe category than female resident killer whales. For males, no differences were detected between transient and resident killer whales ( $\chi^2_{df=1} = 0.05, p = 0.83$ ) in the frequencies of rake marks across all categories.

### Discussion

Based on the high incidence of individuals with at least one observed rake mark within the transient and northern resident killer whale communities



**Figure 4.** Probability ( $\pm$  95% CI) of female (solid line) and male (dashed line) transient killer whales from 5 to 50 years of age having a Mild (1 to < 25% of VSA with rake marks), Moderate (25 to 50% VSA with rake marks), or Severe (> 50% of VSA with rake marks) classification of rake-mark coverage in the VSA in the transient killer whale photo-identification catalog (Towers et al., 2012)

of the northeastern Pacific (97 and 85%, respectively), it is apparent that the behavioral aggression required to create rake marks represents a normal and frequent method of social communication and, thus, an important component of social structure maintenance. These findings provide indirect evidence that is in direct contradiction to the prevailing notion in the literature that aggression among killer whales is rare (Jacobsen, 1986; Ford, 1989; Rose, 1992; Visser, 1998; Baird, 2000), despite easily visible rake marks in countless photographs of wild animals (Towers et al., 2018). Additionally, these results should not be surprising when viewed within the context of Odontoceti as other species of odontocetes have been documented to use biting as a form of social interaction as part of the agonistic behavior repertoire (Norris, 1967; Kato, 1984; Lockyer & Morris, 1985; Samuels & Gifford, 1997; MacLeod, 1998; Connor et al., 2000; Scott et al., 2005; Kugler & Orbach, 2014). When our results are compared to those of previous studies in other cetaceans,

also quantifying animals with at least one observable rake mark (Luksenburg, 2014), killer whales have a frequency similar to bottlenose dolphins (93.4%), almost twice that of false killer whales (49.3%), and three times that of Atlantic spotted dolphins (*Stenella frontalis*; 29.1%).

It is unclear whether the ubiquity of rake marks in killer whales has not previously been realized or, instead, that there is disagreement and/or dissonance as to whether this form of social interaction should be viewed as aggressive behavior. *Aggression* is generally considered a component of agonistic behaviors during which one conspecific threatens or actually causes bodily damage of any degree to another (McGlone, 1986; Zump & Michael, 2001). Unquestionably, rake marks, as obvious bodily damage in the form of lacerations, meet the threshold of this definition. For bottlenose dolphins in particular, it is well accepted in the literature that rake marks represent aggressive behavior (Samuels & Gifford, 1997; Scott et al., 2005; Rowe & Dawson, 2009; Marley et al., 2013;

Nekolny et al., 2013). Yet, for killer whales, a similar association has not been made even when accompanied by direct observation, which is often discounted as inconsequential.

Certainly, it appears that some of the discord around “aggression” in killer whales is in part due to semantics. For example, a review of the following description by Ford (1989) illustrates this apparent disconnect with respect to the definition of *excitement*:

Conditions of intense arousal or excitement were observed occasionally in all activity categories. Most cases involved sudden physical interactions between animals, often subadults, both at the surface and underwater. Individuals chased or lunged at each other, and collisions and slapping were also noted. Many of the fresh body wounds and healed scars that appeared to be made by killer whale teeth likely resulted from such apparent altercations or rough play. (p. 737)

Clearly, this description concerns agonistic behaviors, including aggression, which have resulted in rake marks. It is also surprisingly similar to agonistic behaviors observed among bottlenose dolphins (Samuels & Gifford, 1997; Scott et al., 2005). Ford (1989) and other scientists have described high intensity behavior observed at a distance as simply a form of play (Jacobsen, 1986; Rose, 1992). Most social mammals have been shown to engage in play (McFarland, 1987); however, it is apparent that agonistic and play behaviors are not mutually exclusive. Play in subadult animals, especially males during male-only social interactions, is often believed to be important for development of social and breeding skills—all of which require the ability to, at least temporarily, dominate another animal for attainment of the required resource. However, as observed with bottlenose dolphins (Scott et al., 2005), “play” behavior among subadult males can sometimes lead to aggressive behavior and, in odontocetes, rake marks (Jacobsen, 1986; Scott et al., 2005).

In killer whales, all spectral aspects of agonistic behavior from regular avoidance to rare aggressive attacks have been documented between different ecotypes (Baird et al., 1992; Ford et al., 1998; Ford & Ellis, 1999; Baird, 2000; Bisther, 2002). When transients are on an intersecting course, resident killer whales will typically avoid them by moving to a different area or altering their course if in transit (Baird & Dill, 1995; Bisther, 2002). This habitual behavior has led Baird (2000) to speculate that mammal-eating transients, in some circumstances, may represent a predatory threat toward lone, injured, or

young resident killer whales. Therefore, under Baird’s (2000) hypothesis, it is not surprising that residents would demonstrate agonistic behavior toward transients, possibly motivated by defense of juvenile pod members. Likewise, transients, who in all observations of these encounters or near encounters are vastly outnumbered by residents (Morton, 1990; Baird & Dill, 1995), would choose to avoid contact.

While it is clear that agonism occurs between ecotypes, the occurrence of agonistic behavior within pods remains controversial (Baird, 2000). Rose (1992) provides an account of an obvious aggressive interaction between siblings yet suggests that since she observed this behavior only once, it is evidence that it seldom occurs. Rose also suggested that subadult males (from 12 to 25 y of age) participate in male-only social interactions (MOSI), which she describes as play, in part because these interactions did not appear to result in obvious cutaneous injury. However, our rake-mark analysis of resident subadult males indicated that this age group had a significantly greater chance (3.6x) of having an increased density of rake marks compared to juveniles, but less than adults, and all ages of males had a significantly greater number of rake marks compared to females. Therefore, rake marks do occur in the age classes associated with MOSI but not at levels observed in adult males.

Jacobsen (1986) describes rake marks as possibly the result of sexual aggression and not the result of agonistic behavior, although most animal behaviorists do not make such a distinction. Aggression in any form, regardless of the motivation, is a type of agonistic behavior, and sexual aggression is one of the most common agonistic behaviors observed within social groups of mammals (Cavigelli & Pereira, 2000; Connor et al., 2000; Zumpe & Michael, 2001; Muller & Wrangham, 2009). In bottlenose dolphins, sexual aggression has been documented by the correlation of focal observations, rake marks, and presumed sexual receptivity in females based on calving intervals (Scott et al., 2005; Connor & Vollmer, 2009) or implied by differences in rake marks between the sexes (Rowe & Dawson, 2009; Marley et al., 2013). Similarly, we found significant differences in the occurrence and density of rake marks between sexes in the resident ecotypes, with males having a higher density. A plausible assumption is that the observed increase in rake marks among males is a result of inter-male competition for access to breeding females.

Additionally, when grouping resident males into 5-year age blocks, we found that males over age 30 had significantly greater probability of having rake marks in the Severe category than animals

in any younger age group. These data, along with our finding that rake marks significantly increase with age in adult males in both ecotypes, provide evidence that adult males (specifically 30 y and over for resident males) are either competing for access to breeding females or simply attempting to breed non-receptive females and, therefore, exhibiting or experiencing sexual aggression. These results are in accordance with those of recent efforts to elucidate paternity in northern residents where it was found that reproductive success was positively correlated with male age and size (Ford et al., 2011). Taken together, this further supports the argument that rake marks in killer whales are the result of aggressive behavior and serve as an important tool for the establishment of dominance.

While the small numbers of animals within the transient ecotype and the indirect evidence of aggression used in this analysis must temper our interpretations, it appears that differences in frequency and degree of rake marks between the transient and northern resident killer whale ecotypes probably reflect their differing social structures. While both ecotypes exhibit matrilineal hierarchies, transients have pods that are smaller and more fluid in structure (Bigg et al., 1990; Baird & Whitehead, 2000) in contrast to residents, which are more philopatric (Bigg et al., 1990; Baird, 2000). This fluidity would result in novel members, either adult male or female, attempting to join “new” pods for breeding or resource sharing purposes (Baird, 2001) and could be considered a fission–fusion system similar to bottlenose dolphins (Connor & Volmer, 2009) and African elephants (*Loxodonta africana*; Archie et al., 2006a). As a result, dominance structures within the “new” pod would need to be realigned more frequently, thus increasing the occurrence of agonistic behaviors (Samuels & Gifford, 1997). In fact, further investigation indicates that the observed differences between the two ecotypes were due almost exclusively to a higher density of rake marks in transient females vs resident females.

We hypothesize that this higher degree of rake marks in adult female transients, in the absence of behavioral observations, is indirectly reflective of an increased occurrence of sexual coercion between male and female transient killer whales. Sexual coercion has been documented in the more dynamic fission–fusion bottlenose dolphin societies (Connor, 2000; Connor & Vollmer, 2009), and our results indicate that the transient killer whale social system might be more similar to this system, lending support to the notion that transient and resident ecotypes are quite different (Baird & Dill, 1995; Baird & Whitehead, 2000; Morton, 1990).

While the increase in rake marks within adult females may be explained by sexual coercion, this cannot explain the dramatic increase in the odds of severe rake marks observed in post-reproductive or senescent transient females. This increase in rake marks in older, non-reproductive transient females may indicate an increased need, when compared to resident females, for older females to be involved in calf protection and/or in direct competition with conspecifics for food resources. It is worth noting that no evidence for improved calf survival was detected when a post-reproductive female was found within the pod in resident females (Ward et al., 2009). However, the fluid social dynamics and smaller pod size of the transients may provide increased opportunities for older females to provide protection for related calves. And, in support of this calf protection hypothesis, infanticide was recently documented among transient whales in the North Pacific (Towers et al., 2018).

The rake-mark differences observed in females between ecotypes may also suggest a transition from *egalitarian* residents (typically found in species with abundant resources and little need for conspecific competition) to a linear age and/or *nespotic* (Vehrencamp, 1983; Archie et al., 2006b) dominance structure in transients. Nespotic societies are ones that contain well-differentiated social relationships with strong age- or linear-based hierarchies and are typically found in species with limited resources (Archie et al., 2006b). In this organization, older transient females would be responsible for enforcement of group hierarchy, protection from conspecific males or females in other pods, and competition for prey. In residents, with more abundant prey resources and stable social groups, less competition between females is evident, resulting in reduced conflict and fewer rake marks. Residents may reside between egalitarian and nespotic where relatives are important for dominance status, depending on the situation or need. Without direct evidence for the results of dyad interactions, we cannot with certainty predict which type of dominance structure predominates in the various killer whale ecotypes.

Typically, many researchers rank aggressive behaviors based on investment or risk vs potential payoff, with “threats” considered at the lowest end of the spectrum of investment and physical contact or confrontations at the highest end (Robbins, 2008). While threatening behavior has been documented in bottlenose dolphins in a captive situation or in the field where environmental conditions allow for increased underwater observations (Samuels & Gifford, 1997; Scott et al., 2005), it would typically go undetected in the field observational conditions found in most wild killer whale habitats. Therefore, as in bottlenose dolphins (Scott et al., 2005), the

physical contact created by biting represents an elevated level of aggression over non-physical threats. However, as is the case in most mammalian intraspecies aggression (Zumpe & Michael, 2001; Link et al., 2009), the high frequency of occurrence of biting between pod members probably indicates that it should be considered a low intensity aggressive behavior not designed to cause serious physical harm. As evidence toward its mild intent, this behavior can be contrasted with that exhibited during more elevated aggressive attacks or during predatory aggression during which killer whales and other cetaceans often rely on ramming and/or tail fluking actions that would generally not leave any cutaneous lesions (Greenwood & Taylor, 1985; Dolphin, 1987; Jefferson et al., 1991; Rose, 1992; Connor et al., 2000). Thus, solely relying on rake marks to quantify aggressive behavior would most likely underestimate the actual frequency of its occurrence (Connor et al., 2000).

Unlike Scott et al. (2005), we did not attempt to quantify the age of the scars based on their appearance and, as such, we made the assumption that resolution of the scars would be consistent across age and sex classes. This assumption ignores the real possibility that variation in observed scarring across age classes is also affected by the intensity of the aggressive encounter. Thus, rare but intense aggressive encounters may result in higher accumulation of visible marks than more frequent, minor, less intense encounters. While final characterization of these interactions would require behavioral observations, this premise agrees with previously published observations made by Bigg (1982) in which he states that if a scar is severe enough and lasts for more than 2 years, it is considered permanent; and scars that are less severe will be gone in less than a year. Visser (1998) claims that rake-mark scars observed on one of two killer whales appeared to be healed due to the discoloration of the scar as compared to the background pigmentation. Further, in examining the nature of scarring in the images of the killer whales in this study, we found that the wounds could be easily fit into the categories of "new" or "obvious" used in Scott et al. (2005) for bottlenose dolphins.

In bottlenose dolphins, and similar to what has been described for killer whales (Bigg, 1982), superficial wounds generally heal in 2 to 20 mo, eventually appearing the same color as the background pigment unless the injuries penetrate deep into the epidermis (or further into the dermis or blubber), damaging the melanocytes (Lockyer & Morris, 1990). Therefore, the absence of light rake-mark scar tissue in black pigmented portions of killer whale skin or, conversely, off-coloration in white patches in wild as well as captive

populations (pers. obs.) indicates that killer whales are similar to bottlenose dolphins as well as false killer whales (Baird & Gorgone, 2005) in that rake marks will not leave a long-term visible scar unless severe damage has occurred.

Furthermore, as killer whales, like bottlenose dolphins, use their teeth for predation, it would not be predicted that they would accumulate scarring over time as is the case in other odontocetes (Risso's dolphins [*Grampus griseus*], narwhals [*Monodon monoceros*], and most species of Ziphiidae). In these species, where the maintenance of teeth was no longer selected for due to dietary specializations, some remaining teeth evolved as weapons used in male-male combat. In addition, MacLeod (1998) hypothesized that retention of non-pigmented scarring coevolved as an indicator of male dominance. This hypothesis, combined with our observations in captive animals and those reported for animals in the wild, provides support for the supposition that most rake marks represent incidences that have occurred for no more than 2 years prior.

Our study probably represents an underestimation of rake-mark occurrence due to several factors. In bottlenose dolphins (Scott et al., 2005, Figure 1), the anterior and posterior peduncle areas of the body (not included in the images of killer whales collected for the photo-identification catalogs) had the highest percentage of visible rake marks; they were present in > 70% of the images and almost twice of those found in the area analogous to the "saddle" region surrounding the dorsal fin, the area examined in this study. Similarly, the majority of very severe wounds documented on two killer whales from New Zealand (Visser, 1998) occurred in the dorsal and lateral cranial half of the body and the peduncle region, areas also not included in the catalog images. Additionally, a few animals had an extensive web of overlapping lesions on the saddle region in what appeared to be scratch marks that potentially obscured rake marks. These scratches, distinct in character from rake marks and not observed in the transient population, may possibly result from the well-documented behavior of northern resident killer whales rubbing their bodies on shallow rocky beaches (Jacobsen, 1986; Ford, 1989).

The results of this study provide evidence for the effect of sex and age on aggressive social interactions resulting in rake marks in killer whales and demonstrate differences in ecotype societies. The evidence suggests that male competition may play a role in reproductive success or failure in both ecotypes. However, females in the probable fission-fusion transient society may be the subject of sexual coercion and/or are required to reestablish dominance more often in these more plastic

societal organizations. Evidence suggests dominance structures in transient killer whales are more closely aligned with a despotic system, while northern resident killer whales display a more egalitarian system. Future research should involve the identification of intraspecific agonistic behaviors in captive killer whales for use with focal observational data of wild populations in an attempt to define how dominance hierarchies are established in wild populations.

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