Aquatic Mammals 2013, *39*(2), 107-115, DOI 10.1578/AM.39.2.2013.107

Using Tooth Rakes to Monitor Population and Sex Differences in Aggressive Behaviour in Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

This study investigated intraspecific tooth rake scarring, an established indicator of received aggression by conspecifics, on bottlenose dolphins (*Tursiops truncatus*) to gain knowledge of aggressive interactions. The differences in tooth rake scarring between male and female dolphins on the east coast of Scotland were examined, and overall levels of scarring were compared with dolphins on the west coast of Scotland (Sound of Barra and Hebrides). Photographs were examined for evidence of tooth rake scarring using four different methods. East coast males displayed significantly higher scarring percentages (i.e., body area covered by tooth rake scarring), numbers of dorsal fin rake directions (i.e., whether tooth rake scars were vertical, horizontal, diagonal, or curved), and nick percentage (i.e., amount of the dorsal fin missing due to nicks) than females. Differences also existed between the three areas, with bottlenose dolphins around the Sound of Barra showing significantly lower levels of dorsal fin rake directions than those on the east coast or Hebrides. Observed sex differences are likely the result of intrasexual conflict between males over access to females. However, other factors such as sex- or age-specific behaviours or sexual coercion of females may also be involved. Such information could potentially be used to differentiate between the sexes. The differences in dorsal fin scarring between these populations suggests differences in aggressive interactions, possibly indicating differences in social structure. The lower scarring levels seen in the Sound of Barra group may support the suggestion that bottlenose dolphins on the west coast belong to two communities. However, this variability in conspecific aggression may also be the result of different social behaviours, age or sex ratios, habitat, resources, or individual behavioural differences.

Key Words: social behaviour, social structure, cetacean, intraspecific aggression, tooth rake scarring, bottlenose dolphin, *Tursiops truncatus*

Introduction

Aggression is found throughout the animal kingdom, in both solitary and group-living species, and can occur for a number of reasons, most commonly as a response to intrasexual competition or intersexual conflict. For cetaceans, however, which spend the majority of their lives submerged, aggressive events are difficult to observe.

Much of our knowledge regarding dolphin aggression has been gained through studies of captive bottlenose dolphins (*Tursiops* sp.) (Tyack, 2000). Bottlenose dolphins are known to employ a range of aggressive behaviour in their social interactions, including chasing, ramming, body slamming, sideswipes, tail slaps, and biting (Samuels & Gifford, 1997; Weaver, 2003). Furthermore, other behaviours have been categorised as submissive (e.g., swimming ventral to an aggressor and affiliative rubbing), providing information about the winners and losers of such interactions (Samuels & Gifford, 1997). However, animals in one captive facility may not necessarily display the same behaviour as animals in a different facility. Additionally, and perhaps more importantly, data from captive studies may not show parallels with wild populations (Tyack, 2000).

Studies of aggression in wild bottlenose dolphins have generally used information from stranded animals (Patterson et al., 1998), from one or more direct observations (Parsons et al., 2003a; Cotter et al., 2011), or from interspecific interactions (Ross & Wilson, 1996; Herzing et al., 2003). Scars and natural markings have been used for individual identification of cetaceans (Würsig & Jefferson, 1990). These natural marks (e.g., tooth rake scars and nicks) are often inflicted during agonistic interactions with conspecifics. They can therefore be used as an indirect indicator of intraspecific aggression in the wild.

Tolley et al. (1995) investigated sexual dimorphism in wild bottlenose dolphins (*Tursiops truncatus*) using photographs to compare the frequency

and degree of dorsal fin scarring between the sexes. They found that the proportion of males possessing scars was greater than that of females, although there was no difference in the overall amount of scarred tissue between the sexes. However, this analysis focused exclusively on scarring to the dorsal fin and therefore a bottlenose dolphin with extensive scarring to the body, but relatively little damage to the dorsal fin, could give a misleading depiction of the presence of aggression. Similarly, Scott et al. (2005) used photographs to analyse the prevalence of tooth rake scars and found that wild Indo-Pacific bottlenose dolphin (*T. aduncus*) males had more scarring than females. In Scott et al.'s study, the occurrence of scarring on different parts of the dolphins' bodies was explored, but not the extent of scarring on each body section. Thus, a dolphin with one rake mark on each body section was considered to be as heavily scarred as an animal with dozens of rake marks in each section. The analysis of cetacean scarring levels is a research technique that can be developed and standardised to examine sex and population differences in aggressive intraspecific interactions that may be difficult to directly observe.

Herein, we investigated intraspecific body scarring in bottlenose dolphins in Scottish waters to gain information on aggressive interactions and social ecology. We used photographs from photo-identification studies and four different techniques to quantify scarring levels, examining not only the occurrence of natural marks on various body parts but also the extent of such scarring. We examined the differences in tooth rake scarring between males and females on the east coast of Scotland to investigate possible differences in social behaviour and to establish whether differences in scarring could be used to determine the sex of individuals. To investigate area or population level differences in aggression, we compared the overall degree of scarring of this east coast population with bottlenose dolphins on the west coast of Scotland.

Methods

We examined the degree of scarring or scarring levels (i.e., prevalence and severity of tooth rake scars and nicks) of bottlenose dolphins on the east and west coast of Scotland (Figure 1). The

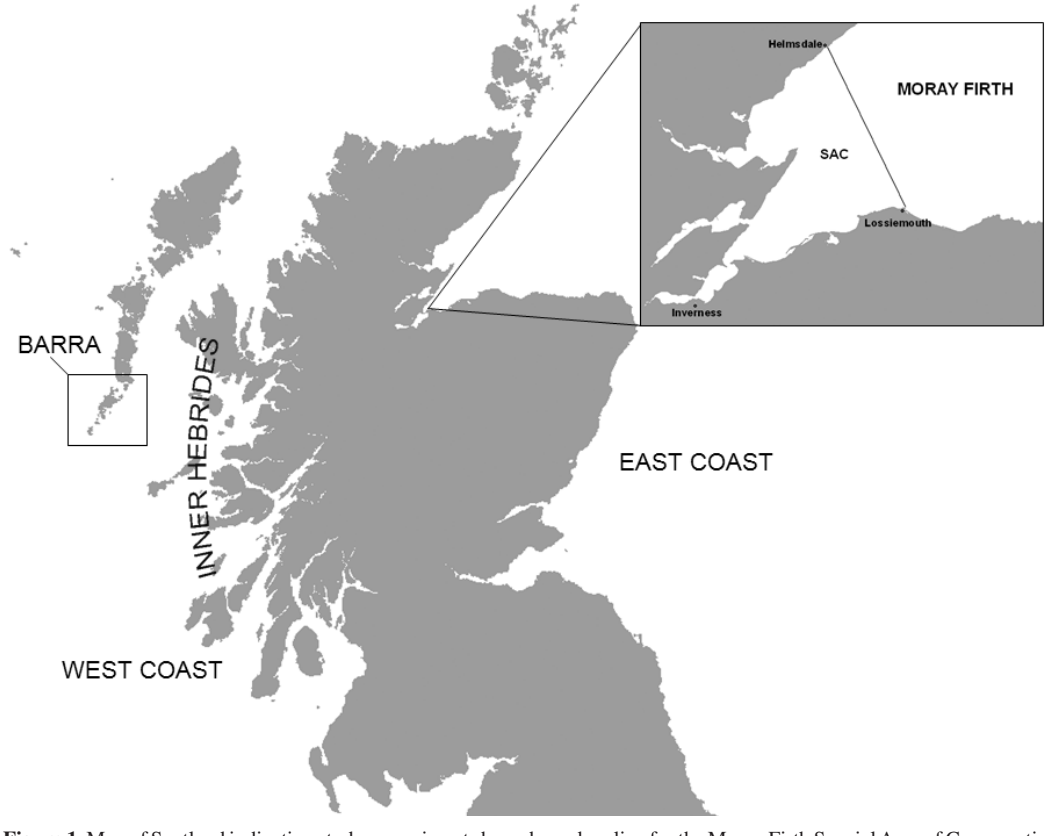

Figure 1. Map of Scotland indicating study areas; insert shows boundary line for the Moray Firth Special Area of Conservation (SAC).

east coast of Scotland has a resident population of *ca.* 195 bottlenose dolphins (Cheney et al., 2013). These animals have been studied for over two decades, and a photographic catalogue of identified individuals sighted since 1989 has been produced (Wilson et al., 1997; Cheney et al., 2013). The dolphin population on the Scottish west coast (population size *ca.* 45; Cheney et al., 2013) is less well studied; however, a catalogue of identified individuals has been produced of animals sighted in 1995, 1998, and from 2001 onward (Grellier & Wilson, 2003; Cheney et al., 2013). For both of these populations, individual dolphins were identified using standard photo-identification techniques (for details, see Wilson et al., 1997; Cheney et al., 2013). In the east coast catalogue, the sex of the individual is indicated if known; however, the sexes of individuals have not yet been confirmed for the majority of the west coast population.

Bottlenose dolphins continue to acquire marks and scars throughout their lives. We focused analysis on tooth rake scars: long, thin, parallel scratches on the skin, resulting from contact with the teeth of another dolphin. Rake scars are very distinctive, and easily identifiable in comparison to other sources of scarring (e.g., those resulting from bycatch, ship strike, or predation attempts). This type of scarring tends not to damage deep tissue; thus, the scars eventually fade over time (Scott et al., 2005). For bottlenose dolphins in Scotland, minor rake marks were visible on average for approximately 13 mo (Wilson et al., 1999). Therefore, photographs of individual dolphins were restricted to those taken over a 1-y period, either during 2004 or 2006.

Four methods of recording scarring were applied to a dataset of 112 bottlenose dolphins (east coast: $n = 77$; west coast: $n = 35$). Photographs of the east coast individuals were all taken within the Moray Firth Special Area of Conservation (SAC) (Figure 1) and included 27 known-sex animals (9 males and 18 females). Since major rake marks in this area can take an average of 22 mo to heal (Wilson et al., 1999), the two years were combined to give an overall view of scarring levels in the east coast population. For the west coast population, all data were sourced from the 2006 records. Previous studies have suggested that the west coast population is actually composed of two discrete communities (groups of dolphins who are not known to overlap, despite geographical proximity, but with no information on interbreeding) (Grellier & Wilson, 2003; Cheney et al., 2013). These include (1) a community of *ca*. 15 individuals seen around the Sound of Barra and (2) a community of *ca*. 30 animals seen near the Inner Hebrides and mainland coasts (Cheney et al., 2013) (herein termed *Hebrides*). Therefore, for some analyses, the west coast population was divided to represent these two communities. Calves (animals which were seen closely associated with a known mother) were not included in this dataset.

One of the authors (SM), blind to sex and age of individuals, classified the extent of scarring for 1,384 and 297 photographs for the east and west coast populations, respectively. Multiple photographs of each individual (minimum = 1; maximum = 68; mean = 13) were used as each photograph of an animal varied in picture quality and proportion of the body exposed. Four techniques were used and applied to each photograph:

1. *Overall Rake Direction (ORD)* – The number of tooth rake directions on each dolphin in each photograph was recorded. Directions were defined as tooth rake scars which ran in different directions to each other. For example, if there were three parallel tooth rake scars running anterior to posterior, four scars running ventral to dorsal, and three curved/oblique angle scars, this would equal three directions. The bottlenose dolphin's body was divided into 12 areas (Figure 2), and the number of rake directions in each area was counted. The total number of rake directions was then divided by the number of body areas visible in the photograph to create an average number of rake directions for each body area. This was applied to all photographs of an individual, and an average was taken of the scores for each body area per dolphin.
2. *Average Dorsal Fin Rake Direction (DFRD)* – The technique described above for ORD was applied to only the dorsal fin, left and right side.
3. *Scarring Percentage (SP)* – This was an estimation of the percentage of the bottlenose dolphin's body observed in each photograph that was obscured by tooth rake scars. This was then averaged for each individual to give an overall scarring percentage.
4. *Dorsal Fin Nick Percentage (DFNP)* – The dorsal fin often has nicks and tears from aggressive interactions. The length of each nick and total height of each dorsal fin was measured for each photograph of each individual. The total length of all nicks in each photograph was divided by the height of the fin to calculate the percentage of the fin missing, and an overall average was taken for each individual.

All data were analysed using the statistical package *Minitab*, Version 14.1. An unpaired *t*-test was used to investigate sex differences for known-sex individuals from the east coast population. This was applied to ORD, DFRD, and SP data. The data for DFNP were not normally distributed; therefore, a Mann-Whitney U-test was used for this analysis.

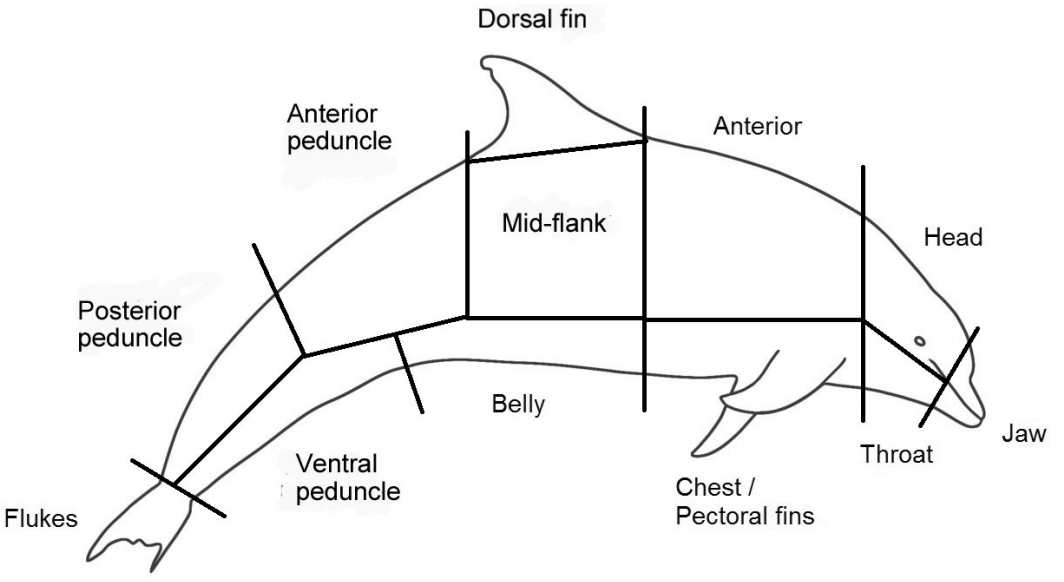

Figure 2. The bottlenose dolphin's body was divided into 12 areas (modified from Scott et al., 2005).

A comparison of the east and west coast populations was conducted using a Mann-Whitney U-test, and each technique was analysed separately. To examine whether any difference exists between the east coast, Sound of Barra, and Hebrides groups, a Kruskal-Wallis test was applied to each technique; if a significant difference was found, a Mann-Whitney U-test was used to determine which populations were exhibiting a difference.

Results

All bottlenose dolphins used in this study had tooth rake scars. Known-sex individuals (9 males and 18 females) from the east coast population were tested for sex-based differences in degree of scarring (Figure 3). Analysis of ORD showed no significant sex-based difference in degree of scarring (t-value = -1.70; df = 21; $p = 0.104$); however, SP (t-value = -2.53; df = 16; $p = 0.022$), DFNP (U = 206.5; $p = 0.021$), and DFRD (t-value = -2.55; df = 19; $p = 0.019$) all showed a significant difference between the sexes (Figure 3). Examination of the mean SP (males = 10.95; females = 7.70), median DFNP (males = 10.00; females = 4.50), and mean DFRD (males = 12.22; females = 7.56) suggested that male bottlenose dolphins had more scarring and dorsal fin nicks than females.

The east coast and west coast bottlenose dolphin populations were examined for differences in degree of scarring (Figure 4). There was no significant difference in the amount of scarring between these two populations when using three of the techniques (ORD [U = 4,065.5; $p = 0.228$], SP [U = 4,190.0; $p = 0.696$], or DFNP [U = 4,316.5; $p = 0.695$]); however, bottlenose dolphins on the east coast showed a greater number of rakes with different directions on their dorsal fins (DFRD) ($n = 76$; median = 9) than those on the west coast ($n = 35$; median = 6) (U = 4,582.0; $p = 0.039$).

As Sound of Barra dolphins have never been reported interacting with Hebrides animals, the original west coast population was separated into these two groups. The ORD (H = 11.02; df = 2; $p = 0.004$) and DFRD (H = 13.89; df = 2; $p = 0.001$) techniques showed significant difference between these populations (Table 1), but these differences were not evident using the SP (H = 1.41; df = 2; $p = 0.494$) or DFNP (H = 0.61; df = 2; $p = 0.722$) methods. There was a significant difference in ORD between the Hebrides dolphins and both of the other groups, with the Hebrides animals displaying the highest median number of ORD in both cases. Also, a significant difference was observed in DFRD between the Sound of Barra dolphins and both of the other groups, with the Sound of Barra animals displaying the lowest number of DFRD in both cases (Table 1 & Figure 5).

Discussion

All the bottlenose dolphins examined in this study had evidence of tooth rake scars, which were assumed to be from conspecifics, suggesting intraspecific aggression is a common occurrence. There appeared to be sex differences in degree of scarring, with male animals more heavily scarred than females. This suggests differences in aggressive

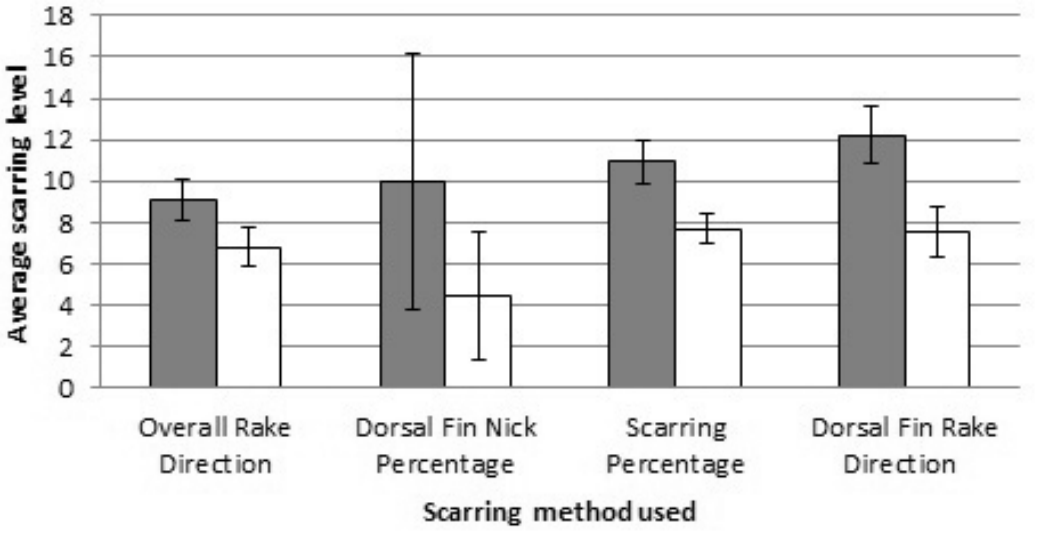

Figure 3. Average degree of scarring for known-sex individuals (n = 27) from the east coast of Scotland bottlenose dolphin population: males (n = 9; dark grey) and females (n = 18; white)

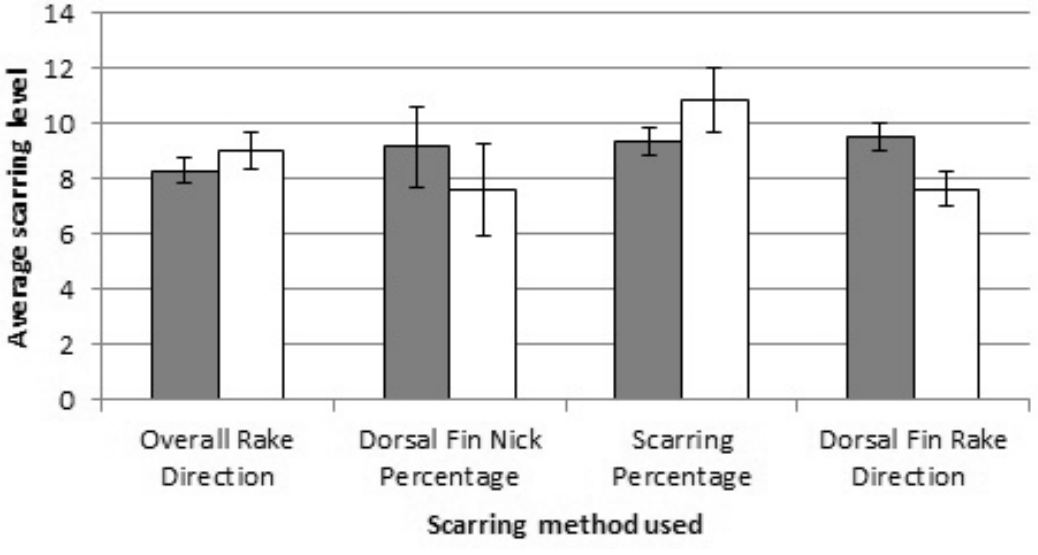

Figure 4. A comparison of average degree of scarring between the east coast (n = 76; dark grey) and west coast (n = 35; white) populations

behaviour between the sexes and indicates that scarring could potentially be used to determine the sex of individuals. Differences also exist between the three groups, with bottlenose dolphins seen around the Sound of Barra, the smallest group, exhibiting the lowest levels of scarring. This suggests there are also differences in intraspecific aggression between these different populations and areas.

Differences in Scarring Quantification Techniques

As demonstrated in this study, the application of different methods for quantifying tooth rake scarring can produce different results. The dorsal fin appears to be a likely body part to show scarring during aggressive interactions, possibly as bottlenose dolphins may turn their dorsal side (a less vulnerable area) to attacks. Similarly, SP perhaps signifies the intensity of such interactions; a few rakes

Table 1. A summary of the differences in Overall Rake Direction (ORD) and Dorsal Fin Rake Direction (DFRD) between the east coast, Hebrides, and Sound of Barra bottlenose dolphins; the upper diagonal denotes ORD and the lower diagonal DFRD, with median values in parentheses and significant results in bold.

	East Coast	Hebrides	Sound of Barra
East Coast		***p = 0.0119*** (EC = 7.60, HB = 10.80)	*p = 0.084* (EC= 7.60, SoB = 6.04)
Hebrides	*p = 0.788* (HB = 9.00, EC = 9.00)		***p = 0.003*** (HB = 10.80, SoB = 6.04)
Sound of Barra	***p = 0.000*** (SoB = 4.25, EC = 9.00)	***p = 0.001*** (SoB = 4.25, HB = 9.00)	

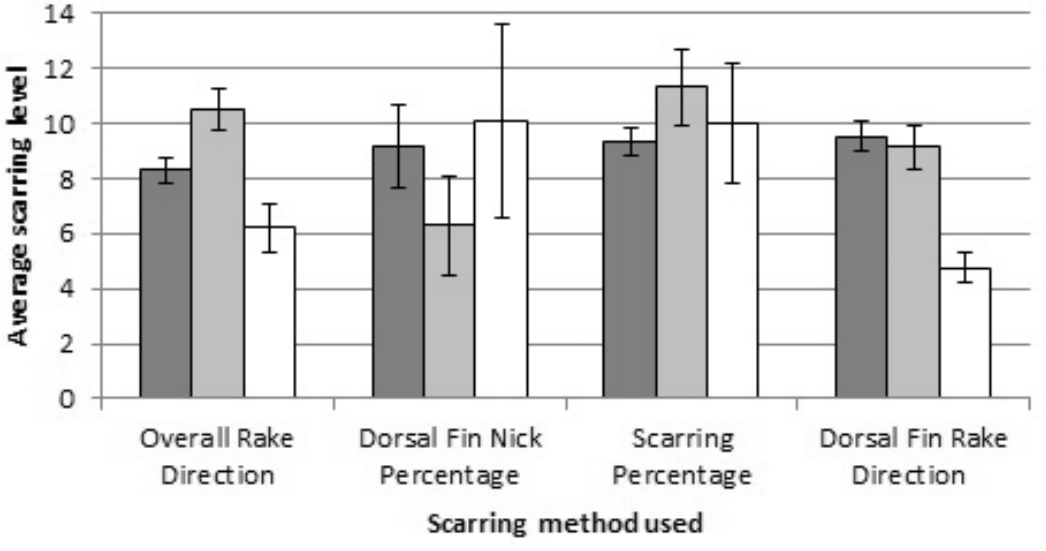

Figure 5. A comparison of average scarring levels between the east coast (n = 76; dark grey), Hebrides (n = 23; light grey), and Sound of Barra (n = 12; white) bottlenose dolphins

could be the result of a nip, whereas several parallel rakes could be the result of a more intense level of aggression. If this is the case, dorsal fin nicks could indicate an even higher level of aggression. Although nicks may be the result of a non-conspecific event (e.g., entanglement or predation), there were no other marks on the bottlenose dolphins investigated that conformed to fisheries interactions or predation attempts. Therefore, we suggest that in these areas, nicks are likely the result of a bite or tear being taken out of the trailing edge of the dorsal fin by another bottlenose dolphin and, thus, may only happen in severe agonistic situations. It is also possible that some of these tooth rake scars and nicks are the result of play as using these indirect methods of assessing behaviour does not allow us to differentiate between agonistic interactions and play behaviour. However, when classifying behaviour patterns of several odontocete species, "bites" have been found to be closely associated with apparently aggressive interactions, with many such encounters resulting in distinctive tooth rake

scars (Slooten, 1994; MacLeod, 1998; Parsons et al., 2003a; Silva-Jr et al., 2005). Furthermore, there have also been instances when play behaviour turns aggressive (Scott et al., 2005). Thus, we suggest that more nicks and tooth rake scars result from aggressive interactions, and the majority of the marks are likely from this source. While scarring from predation attempts or fisheries interactions can be clearly differentiated from tooth rake scars, it is not always possible to identify the species responsible for tooth rake scars. Although we cannot discount that tooth rake marks could be a result of interactions with similarly sized delphinid species, reports of interspecific interactions around the UK typically only reveal tooth rake marks of bottlenose dolphins on other cetacean species (Ross & Wilson, 1996; Barnett et al., 2009).

Sex Differences in Degree of Scarring

Male dolphins from the east coast population showed significantly higher amounts of scarring than females. Other studies have also found evidence of this distinction in scarring levels between the sexes (Tolley et al., 1995; Scott et al., 2005; Rowe & Dawson, 2009). In Sarasota Bay, Florida, although the proportion of male bottlenose dolphins possessing scars was greater than that of females in the population, there was no difference in the area covered by scarring (Tolley et al., 1995). In comparison, our study found sex differences in both the number of scars (DFRD) and the proportion of the body scarred (SP and DFNP). One possible cause of this disparity is a difference in breeding behaviour. Studies in Sarasota Bay revealed the existence of male alliances (Wells et al., 1987); and at other sites, dolphins in a male alliance work together to sexually coerce females (Connor et al., 2001; Parsons et al., 2003b; Scott et al., 2005). These long-term male alliances have never been observed on the east coast of Scotland (Wilson, 1995). This lack of alliances could result in greater intrasexual competition for access to females and therefore an increase in male-male aggression, explaining the greater overall male body scarring compared to females in this area. Comparison of this metric in another population of bottlenose dolphins without long-term male alliances—for example, Doubtful Sound, New Zealand (Lusseau, 2007)—could provide further evidence.

There was no sex difference in the ORD on the body as a whole. However, when only the DFRD was considered, there was a significant difference between the sexes with respect to rake directions, with males more heavily scarred. This suggests that female dolphins may be more heavily scarred in other body areas. As female aggression is described as rare to non-existent in other bottlenose dolphin studies (Tolley et al., 1995; Samuels & Gifford, 1997; Mann & Smuts, 1999; Scott et al., 2005), it is reasonable to assume that the majority of female scars are the result of male aggression. This hypothesis could be confirmed by examining whether scarring levels increase in females when they are in oestrous. In particular, the change in scarring degree on an adult female's body prior to and following the birth of a calf could be investigated. An increase in scarring would suggest sexual coercion in the form of forced copulation or harassment. However, this may vary between females, depending upon how compliant they are to male advances. Also, levels of aggression received as different sexes mature could also be investigated by examining different aged individuals or changes in individuals over time. While male intrasexual competition for mates is considered the most likely cause of the observed sex bias in scarring levels, other factors such as sex- or age-specific behaviours, individual reproductive status, inter-group aggression, sexual coercion of females, or other individual behavioural differences may also be important.

Population Variation in Degree of Scarring

Our results suggest that there is a difference in degree of scarring between the east and west coast populations, with east coast dolphins showing higher numbers of different DFRDs. This may suggest that individuals from the east coast population engage in more frequent, or more intense, agonistic interactions than those on the west coast. However, the significance of this analysis was not particularly strong ($p = 0.039$); thus, these results simply could be due to the larger sample size available from the east coast population. There were also differences between the two groups on the west coast, with the Sound of Barra group showing lower numbers of rake directions than either the east coast or Hebrides dolphins.

These population differences in scarring could indicate differences in intraspecific aggression between bottlenose dolphins in these different areas. However, the underlying cause of these differences is unknown. There are differences in population size between the east coast, Hebrides, and Sound of Barra groups (Cheney et al., 2013), and their social structures are thought to vary. The east and west coast populations are composed of two communities (Lusseau et al., 2005; Cheney et al., 2013). However, unlike the bottlenose dolphins on the west coast, the east coast communities do have limited interactions and overlapping home ranges (Lusseau et al., 2005). The high DFRD on the east coast may be the result of increased aggressive interactions when the two communities mix, either as a result of conflict or reaffirmation

of social bonds. Bottlenose dolphins seen around the Sound of Barra have not been known to interact with the other bottlenose dolphins on the west coast, and this group contains the smallest number of bottlenose dolphins (Grellier & Wilson, 2003; Cheney et al., 2013). This small group may have more stable social bonds or, as they do not mix with other groups, may have less inter-group conflict. However, differences in scarring could also be a result of different age or sex ratios, habitat, resources, or individual behavioural differences between these groups that could affect aggressive interactions and/or the degree of scarring.

Conclusion

As aggressive events are difficult to observe in dolphins in the wild, the use of tooth rake scars as indicators of intraspecific aggression among bottlenose dolphins may be a good source of information. The type of scarring exhibited by an individual may indicate the degree of aggression to which a particular individual might be involved. Thus, examining differences in scarring prevalence and type may highlight differences in social behaviour and in other aspects of ecology among different sexes or populations. East coast males appear to be more heavily scarred than females. This sex bias suggests that individuals could potentially be provisionally sexed according to their scarring levels. These scarring differences also suggest differences in social behaviour; however, the exact cause is yet to be determined. Two techniques (ORD and DFRD), which both examine rake direction, repeatedly highlighted dividing factors between the populations. Despite the fact that the three groups of dolphins around Scotland are the same species, there are significant variations in scarring levels, implying social differences between these populations.

Acknowledgments

The core bottlenose dolphin photo-identification study was conducted in collaboration with the Sea Mammal Research Unit at the University of St Andrews. We thank Susan Lusseau, Simon Ingram, Ross Culloch, and many other colleagues who contributed to the challenging fieldwork required to collect these data. The success of photo-identification on the west coast of Scotland depended upon collaboration with the Scottish Association for Marine Science, the Hebridean Whale and Dolphin Trust, and all the members of the public that reported bottlenose dolphin sightings. Many aspects of this study have also benefited from close integration with related projects that have been funded from a variety of sources. In particular, we thank the Scottish Government, Scottish Natural Heritage (SNH), the Whale and Dolphin Conservation Society, Talisman Energy (UK) Ltd, Chevron, the European Union, and the Natural Environment Research Council. Thanks also to SNH for granting Animal Scientific Licences to carry out this work.

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