Identifying Signature Whistles from Recordings of Groups of Unrestrained Bottlenose Dolphins (*Tursiops truncatus*)

Vincent M. Janik[1], Stephanie L. King[1], Laela S. Sayigh[2], Randall S. Wells[3]

[1] *Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews, Fife, KY16 8LB, U.K.*

[2] *Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.*

3 Chicago Zoological Society, Sarasota Dolphin Research Program, c/o Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA.

ABSTRACT

Bottlenose dolphins (*Tursiops truncatus*) have individually-distinctive signature whistles. Each individual dolphin develops its own unique frequency modulation pattern and uses it to broadcast its identity. However, underwater sound localization is challenging, and researchers have had difficulties identifying signature whistles. The traditional method to identify them involved isolating individuals. In this context, the signature whistle is the most commonly produced whistle type of an animal. However, most studies on wild dolphins cannot isolate animals. We present a novel method, SIGID, that can identify signature whistles in recordings of groups of dolphins recorded via a single hydrophone. We found that signature whistles tend to be delivered in bouts with whistles of the same type occurring within 1-10 s of each other. Non-signature whistles occur over longer or shorter periods, and this distinction can be used to identify signature whistles in a recording. We tested this method on recordings from wild and captive bottlenose dolphins and show thresholds needed to identify signature whistles reliably. SIGID will facilitate the study of signature whistle use in the wild, signature whistle diversity between different populations, and potentially allow signature whistles to be used in mark-recapture studies.

Keywords

methods, signature whistle, communication, *Tursiops truncatus*, bioacoustics, mark-recapture

Bottlenose dolphins (*Tursiops truncatus*) have individually-distinctive recognition calls that are unusual among animal signals. While most species use morphologically determined voice features in a call to recognize its sender (*e.g.*, Weary and Krebs 1992, Lind *et al.* 1996, Rendall *et al.* 1998), bottlenose dolphins use learned signature whistles in this context (Janik 2009, Sayigh and Janik 2010). Each dolphin develops its own unique frequency modulation pattern early in life to broadcast its identity (Caldwell *et al.* 1990, Janik and Slater 1998). Vocal learning appears to help in achieving novelty in signature whistle development (Janik and Slater 1997, Tyack 1997, Tyack and Sayigh 1997, Miksis *et al.* 2002, Fripp *et al.* 2005). The result is an individually distinctive signature whistle that encodes identity in the frequency modulation pattern even when voice characteristics are removed (Janik *et al.* 2006). Signature whistles account for roughly half of all whistles produced by wild bottlenose dolphins (Buckstaff 2004, Cook *et al.* 2004), but this can increase to 100% when animals are isolated from conspecifics (Caldwell et al. 1990). Bottlenose dolphin vocal repertoires remain flexible throughout their lives and the animals also use vocal learning in whistle matching, where one animal copies the signature whistle of another in a vocal interaction (Janik and Slater 1998, Janik 2000). Signature whistles, however, remain stable for long periods of time. In females, stability lasts for more than a decade and most likely for their entire lives (Sayigh *et al.* 1990, Sayigh *et al.* 2007). Males tend to change their signature whistles when forming an alliance with other males (Smolker and Pepper 1999) so that they sound more like their alliance partners (Watwood *et al.* 2004). However, alliance partner changes are relatively rare (Connor *et al.* 2000) and only single whistle changes have been observed for individual animals (Smolker and Pepper 1999).

Signature whistles have received much research attention due to the cognitive abilities required for their evolution. Vocal learning and vocal labelling with learned signals are rare and complex skills in animals and can only be found in humans, dolphins, and parrots (Janik 2009). Non-human primates are skilled at labelling objects with learned gestures, but appear unable to copy novel acoustic signals (Janik and Slater 1997). The fact that these skills have evolved in three different clades could help us to understand how complexity evolves in communication systems. It is thus of great interest to study signature whistle development and usage in delphinids.

Identifying signature whistles is a major challenge, however, because each dolphin produces its signature whistle and a variety of non-signature whistles. Since each individual develops its own signature whistle type, there appears to be no common acoustic feature that makes signature whistles recognizable as such. Caldwell and Caldwell (1968) defined the signature whistle as the most common whistle type produced when an animal is isolated. This definition has been used successfully for more than four decades, but it also restricts research opportunities to locations where animals can be captured or temporarily restrained. Studies on whistle usage would greatly benefit from a method that would allow the identification of signature whistles in wild, unrestrained dolphins. Furthermore, such a method would allow us to use signature whistles in mark-recapture studies to monitor habitat use and ranging patterns of individual animals through acoustic monitoring alone.

To address this issue, we developed the method SIGID (SIGnature IDentification), which reliably identifies signature whistles from single-hydrophone recordings of unrestrained bottlenose dolphins. While each signature whistle has a stereotyped frequency contour, bottlenose dolphins tend to incorporate time warping and frequency shifts (Buck and Tyack 1993) and change specific parameters in relation to context (Janik *et al.* 1994), which lead to variation in frequency and time parameters. Hence, the degree of stereotypy of single parameters is unlikely to be useful for distinguishing non-signature whistles from signature whistles. Instead, SIGID analyzes the temporal pattern of whistle production to identify signature whistles amongst all whistle categories in a recording.

METHODS

We use the term whistle to describe an uninterrupted tonal sound with a narrow-band fundamental frequency of more than 100 ms duration, following definitions by Lilly and Miller (1961) and Evans and Prescott (1962). A whistle type consists of all whistles of a particular frequency modulation pattern or contour. Thus, whistles of the same modulation pattern or contour belong to the same whistle type. We also use the term whistle category to describe the result of human whistle classification. Each whistle category is comprised of all whistles that are placed into the same group by an analysis method. We use these two terms to distinguish between categories that we create through signal pattern analysis and types that are units in the repertoire of the animal. Types and categories are not always identical, but categories can be shown to match types in the repertoire of animals through perception experiments (e.g. Weary and Krebs 1992) or by analyzing context-specificity of whistle usage, as demonstrated by Janik (1999) for signature whistles. Hence, after arriving at categories, we need to identify which ones represent signature whistle types and which ones represent non-signature whistle types. For this, we need to be confident that our categorization method discerns signature whistle types from non-signature whistle types with as little mixing as possible. In addition, each signature whistle type must be represented by a separate category. Two methods have been developed that are capable of such classifications even when animals are not isolated: one is the human observer method (Janik 1999, Sayigh et al. 2007) and the other is a neural network classification method called ARTWARP (Deecke and Janik 2006). Here, we first demonstrate that using the human observer method in combination with a bout analysis can identify signature whistles correctly from single hydrophone recordings of free-swimming animals. We call this identification method SIGID, for signature identification. Then, to test its accuracy, we compared the whistles that SIGID identified as signature whistles from single hydrophone recordings of groups of dolphins with recordings of the same animals in isolation, following the definition that the signature whistle is the most common whistle type produced in isolation (Caldwell et al. 1990, Sayigh et al. 1990, Janik and Slater 1998).

We used two different data sets for our comparisons. One consisted of recordings of wild bottlenose dolphins obtained during 28 focal animal behavioral follows (see Altmann 1974) of different groups with some overlap of individuals in Sarasota Bay, Florida, in 1994 and 1995. The total recording time was 47 h 42 min 16 s. Recordings were made using the system described in Sayigh et al. (1993), which included custom-made hydrophones, a high pass filter, and a Panasonic AG-6400 VCR (capable of recording frequencies up to approximately 30kHz). During focal follows we identified individuals with standard photographic-ID methods, using a photo catalogue of Sarasota dolphins initiated in 1970. Currently, the catalogue is comprised of more than 3,500 distinct individuals from the west coast of Florida, including about 160 dolphins that use Sarasota Bay on a regular basis. Within Sarasota Bay, at least 96% of the dolphins are individually recognizable (Wells 2003, 2009). All focal follow groups contained at least one calf of less than three years of age. Signature whistle types of wild animals were known from separations during capture-release events, in which bottlenose dolphins emit their signature whistle almost exclusively (Sayigh et al. 2007). All follows were used to investigate whether bottlenose dolphin signature whistles were emitted in bouts. Follows used in the method development and tests were on different groups of animals with only one individual occurring in both data sets. Eight follows were used to develop the SIGID method and another four were used to test it (Tab 1).

To further test the SIGID method on a different population, we used a second data set of five recording sessions taken over four days in 1996 from a captive group of four bottlenose dolphins at Zoo Duisburg in Germany. Two of these animals were captured in the Gulf of Mexico and two were born in captivity. Signature whistle types of these individuals were known from separations analyzed in a previous study (Janik and Slater 1998). In an earlier study on this group, it was demonstrated that human observers classified signature whistles of the same type (*i.e.*, from the same individual) into one category (Janik 1999). In that study, four signature whistle types were identified correctly and independently by five human observers. For this study, we analyzed different recordings from those used in Janik (1999). Captive recordings were conducted using two Dowty SSQ 904 sonobuoy hydrophones with custom-built preamplifiers and a Marantz CP430 tape recorder. The recording system had a frequency response of 1 - 20 kHz ± 3 dB (calibrated by Neptune Sonar Ltd, Kelk, U.K.).

Recordings from all wild and captive animals were digitized using an RME Fireface 800 Sound card sampling at 96 kHz controlled by Adobe Audition 2.0 on a Transtec PC computer. All whistles were categorized by one of two experienced human observers who have been shown to agree with the classification of groups of observers and the ARTWARP method (Janik and Slater 1998, Deecke and Janik 2006). For categorization, spectrogram displays were inspected using Adobe Audition 2.0 (FFT size 2048, 50% overlap, Hanning window). Some bottlenose dolphins use whistle types that consist of several loops (Sayigh *et al.* 2007). These are either repetitions of the same or different contours that almost always occur together but can be separated by short silent gaps. Esch *et al.* (2009) reported that the typical silent interval between loops of the same whistle is shorter than 250 ms. Since few whistles have such short inter-whistle intervals, we considered all whistles with silent inter-whistle intervals of less than 250 ms to belong to the same multi-loop whistle. All intervals between whistles of the same type were measured by subtracting the end time of the first whistle from the start time of the second whistle in the recording file. After this analysis, spectrograms of each type identified in the group recordings were compared to spectrograms of whistles of the same individuals when in isolation. The signature whistle types, the most common whistle type in isolation of each individual, were then visually identified in the categories from the group recordings. For the bout analysis, inter-whistle intervals of signature whistles of the same type for 11 individuals during 26 separate follows were plotted on a logarithmic scale to identify a bout criterion (Slater and Lester 1982). For the SIGID method, inter-whistle intervals within signature whistle types and within non-signature whistle types were compared to investigate what temporal criterion could be used to distinguish them. Once a criterion was determined, it was applied to the test data sets from Sarasota and Duisburg to investigate how well it could identify signature whistles. We analyzed each recording session or follow separately to document how often a signature whistle could be identified in separate recordings.

RESULTS

The analysis of whistle sequences produced by 11 different individuals showed that the most common interval between signature whistles of the same type is within 5 to 10 s (Fig 1A). The log survivorship plot of the data shows that signature whistles were produced in bouts (Fig 1B). This was reflected in two distinct parts to the log survivorship plot of signature whistle intervals. The bout criterion interval lies at around 15 s (the point at which the linear extensions of both parts of the graph intersect). We wanted the SIGID method to be as conservative as possible, so that it created no false positives in signature whistle identification. We therefore used 10 s as the maximum interval between two signature whistles of the same type to consider them to belong to the same bout. The longest signature whistle inter-whistle interval in our sample was 89.5 min.

From eight follows in the wild, we extracted a total of 529 whistle contours (Tab 1) to determine whether there was a percentage of whistles of one type being part of a bout that would allow us to identify signature whistles with no false positives. Sixteen individuals in our follows were also recorded during capture-release events where signature whistles could be determined by isolating each animal and recording its most common whistle type. Seven of these individuals produced their signature whistles four times or more in the follows. Thus, the whistles of these seven animals could be used to develop a SIGID method. Three of the individuals were present in more than one follow.

We found that signature whistle categories were those in which at least 75% of all whistles in the category belonged to a bout using a bout interval criterion of 1-10 s. Applying these cut-off points, we identified 4 out of 7 signature whistles (Fig 2A, 3A). One of these 4 was correctly identified in two separate follows. We did not include inter-whistle intervals of less than 1 s in our criterion (grey bars in Fig. 2A). Such short intervals were common between brief whistles (Fig 3B) that are often described as chirps (Caldwell et al. 1990). Including inter-whistle intervals of less than 1s would have led to seven false identifications of chirp whistles as signature whistles. Similarly, lowering the percentage threshold by 5% to a value of 70%, would have identified one non-signature whistle as a signature whistle (Fig. 2B). Thus, a bout-interval criterion of 1-10 s and a cut-off of 75% are the most appropriate criteria to use in the SIGID method. It is important to note that the 1-10 s interval was applied in both directions. For a whistle to be counted as part of a bout, it had to either be followed or preceded by another whistle of the same type within the time window of 1-10 s. Any other whistle types that occurred in between two whistles of the same type were ignored.

We tested the SIGID method with these parameters on two data sets, five recording sessions from a captive population and another four follows from Sarasota Bay. In the captive facility up to four signature whistle types could have been identified by

SIGID. We conducted the SIGID analysis with the same settings as in the previous data set. One captive recording session had no signature whistles in it. In three recording sessions, SIGID did not succeed in identifying any of the signature whistle types. One of these sessions had only non-signature whistles in it, another only six renditions of signature whistles (C1 in Fig. 4), but the third one had a total of 196 renditions of the four signature whistles (C3 in Fig. 4). In the fourth session (C4 in Fig. 4), there were 286 renditions of the four signature whistles, two of which could be identified by SIGID. The last session (C5 in Fig. 4) had 482 renditions of the four signature whistles, three of which could be identified by SIGID. Whistle classification by a human observer has the advantage that one can go through a recording sequentially and document how the number of whistles in each whistle type changes as the recording is being analyzed. This allows monitoring of how the percentage of whistles in a category that have at least one other whistle of the same type occurring within 1-10 s of themselves changes over the recording time. Not surprisingly, this percentage goes up and down throughout a recording session. We found that a whistle category was a signature whistle type if it met the following criteria: (a) it had at least 4 whistles in it, and (b) at least once in our sequential bout analysis, 75% or more of the whistles occurred within 1-10 s of one other whistle of the same category. For example, if after the first 8 whistles 6 (i.e. 75%) were within 1-10 s of another whistle of the same category, but later on in the analysis the percentage went below 75%, the whistle category still represented a signature whistle. When we applied this whistle-by-whistle analysis, our method identified one additional signature whistle in session C5. In our sample, this type of analysis did not increase the false detection rate.

Using the total recording time of the additional four test follows from wild dolphins in Sarasota, we successfully identified 2 signature whistles of seven known ones produced by animals present in the follow, and an additional two if we used the sequential method described above. (Tab 1, Fig 4). Interestingly, the signature whistle of one animal that was included in the development and in the test data set was successfully identified in the development data set but not in the test set.

The parameters for the SIGID classification system were specifically chosen to be conservative. Therefore, one would expect a very low false detection rate, and a correspondingly moderate high missed identification rate. Taking all test follows into account, the false detection rate of SIGID was 0 %, the missed identification rate was 47 % for the sequential analysis, and 56 % when analysing all whistles in a session together. Thus, around half of the signature whistles present were correctly identified, and none of the non-signature whistles were incorrectly identified as signature whistles.

The overall number of signature whistles did not relate directly to whether a whistle was identified successfully as a signature whistle or not (Fig. 4). In several cases only five whistles were sufficient to identify a signature whistle, while in other cases more than 100 renditions of a whistle still did not result in its identification. This shows that bottlenose dolphins do not always follow the bout pattern that we defined. However, it is clear that if whistles of the same type occur primarily within 1-10 s of each other, they are signature whistles.

DISCUSSION

We demonstrated that it is possible to identify bottlenose dolphin signature whistles from single hydrophone recordings of wild and captive groups of animals. This method does not allow the allocation of signature whistles to individuals. For this, one would have to use passive acoustic localization of whistles (*e.g.*, Janik 2000, Janik *et al.* 2000, Quick and Janik 2008, Quick *et al.* 2008). However, even without this additional step, the identification of signature whistles in the wild allows us to address a variety of novel questions. We can use it to study the frequency and variation of signature whistles and their use within and between populations, or in mark-recapture studies to assess habitat use of specific individuals or population size.

Our analysis showed that signature whistle bouts have an inter-whistle interval of 1 to 10 s. Bottlenose dolphins rarely repeated their signatures with less than 1 s between renditions, giving other individuals a chance to reply to the first call (Nakahara and Miyazaki 2011). Generally, the production of recognition signals in bouts results in increased redundancy and allows for more effective information transmission when increasing inter-individual distances lead to signal degradation and attenuation.

The investigation of how the temporal production of whistles can be used to identify signature whistles has also revealed that bottlenose dolphins frequently produce stereotyped non-signature whistles that are delivered with much smaller inter-whistle intervals than signature whistles (Fig. 2B). Most of these whistles were brief and relatively simple in their frequency modulation pattern. Given that all of the wild groups contained at least one young calf, it is possible that these whistles are typical for infants, and perhaps form part of the process required to arrive at a more stereotypic signature whistle later in life. However, further work on non-signature whistles is needed.

We were able to show that SIGID works successfully on animals from two different populations. We therefore think the same settings can be used for studying additional populations. We tuned the method to be extremely conservative, so that it missed about half of the signature whistles in the sample. Hence, a whistle that was not identified as a signature whistle may still be a signature whistle. However, if using SIGID in mark-recapture studies or to investigate how signature whistles are used, we think false negatives are a minor problem as long as the investigator is aware that they exist. It is much more important to avoid false positives. For studies that would not suffer from a small number of misidentifications, threshold values could be changed. However, one needs to be cautious if no other verification of signature whistles is available.

Several errors could occur when using SIGID on other populations. For example, we may need to be cautious when inter-whistle type variability is small. In theory, SIGID should not be able to identify any signature whistles in such cases, since it is tuned to be conservative. If inter-whistle type variability was low, several discrete whistle types would be lumped together in one category during classification. It is unlikely that these whistles would then fulfill our criteria for signature whistles, requiring that 75% of the whistles in a category have to occur within 10 s of at least one other whistle of the same category. Thus, SIGID may not work in some populations and will not work in species that do not have signature whistles. Using the sequential version of SIGID or including very small categories in cases may also introduce some error to the results. Such an error would perhaps not matter when comparing many different signature whistle types and their diversity, but it may be more of a concern when studying whistle usage of animals in small groups.

The use of SIGID is also influenced by the number of whistles analyzed. In an analysis of recordings from a very large group, with perhaps several hundred whistles, there is an increased chance that categories will include more than one whistle type, simply because of the higher probability of similar whistle types in large data sets. To counter this effect, one should limit the number of whistles put into each analysis. This means that even for small group sizes, one should run a separate classification analysis for each recording session. Since the same animals may have been present in more than one recording session, whistle categories must be compared across sessions to identify signature whistles that occurred in more than one session.

In very large or very vocal groups, the lumping together of whistles within 250 ms of each other into one whistle type may not prove fruitful. In small groups like those considered here, it is unlikely that a lot of animals call at the same time. However, the number of short inter-whistle intervals might go up if many animals are around. In this scenario, a lumping of whistles with short inter-whistle intervals may combine two whistles of different individuals into one. However, the average group size of bottlenose dolphins is generally below 10 (Connor et al. 2000) and individuals tend to decrease their vocal output when group size increases (Quick and Janik 2008). Furthermore, lumping of whistles from different individuals into one would lead to fairly unique whistle types with very few renditions. Hence, the method would still be conservative if used on larger groups. Generally, it is best to use many recordings of the same individuals for SIGID. This would help to identify the same signature whistles in different follows and hence increase one's confidence in their correct classification as signatures. In cases of many whistles, one can also analyse all whistle components separately (*i.e.*, not lump those within 250 ms of each other into one type), and then use a transition analysis to identify separate loops that belong to the same whistle (see Janik & Slater 1998).

Our results provide a second method for identifying signature whistles. Previously, a signature whistle was recognized by identifying the most common whistle type produced by an isolated dolphin. Now, SIGID can identify signature whistles from recordings of free-ranging dolphins, even if many dolphins whistle at the same time, since the inter-whistle interval is only measured between whistles of the same type. Dolphins can produce whistles of other types in between their signature whistles, but these are ignored in SIGID. This method will not identify signature whistles in cases when a dolphin whistles rarely or with a different bout structure than that identified in this study. Similarly, the method might not be able to resolve signature whistle types that are very similar in their contour. However, we can be confident that the signature whistles identified are not false positives. This new method should greatly enhance our ability to study signature whistles in a wide variety of populations. It will also allow us to use signature whistles in mark-recapture studies and enhance our ability to determine group composition even under conditions where animals are difficult to observe at night or in bad weather.

ACKNOWLEDGMENTS

We thank all of the Earthwatch Institute and other Sarasota Dolphin Research Program volunteers who helped with various aspects of the field work over the years. We especially thank A. Blair Irvine, Michael D. Scott, Jason Allen, Mandy Cook, Travis Davis, Sue Hofmann, Kim Hull, Stephanie Nowacek, Kim Urian, and Amy Weeks. We thank the staff of the Duisburg Zoo for the opportunity to work with their animals and for their support during this project, especially Roland Edler, Reinhard Frese, Manuel Garcia Hartmann, Kerstin Jurczynski, Ulf Schönfeld and Achim Winkler. We thank Jacqui King, Ashley King, Adam King, Martin Reynolds and Javier Echenique for acting as human judges for whistle similarities and Volker Deecke and Teresa Gridley for helpful comments on ARTWARP and SIGID. This work was supported by Dolphin Quest, National Oceanic and Atmospheric Administration (NOAA) Fisheries Service, Disney's Animal Programs and Mote Marine Laboratory (R.S.W.), Harbor Branch Oceanographic Institute (L.S.S. and R.S.W.), and a Royal Society University Research Fellowship (V.M.J.). Field work was conducted under NOAA Fisheries Service Scientific Research Permits 417, 655, 945, 522-1569 and 522-1785 (to R.S.W.). The manuscript was written by VMJ during his fellowship at the Wissenschaftskolleg zu Berlin.

LITERATURE CITED

Altmann, J. 1974.Observational study of behavior: sampling methods. Behaviour 48: 227-265.

Buck, J. R., and P. L. Tyack. 1993. A quantitative measure of similarity for *Tursiops truncatus* signature whistles. Journal of the Acoustical Society of America 94: 2497-2506.

Buckstaff, K. C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 20: 709-725.

Caldwell, M. C., and D. K. Caldwell. 1968. Vocalization of naive captive dolphins in small groups. Science 159: 1121-1123.

Caldwell, M. C., D. K. Caldwell and P. L. Tyack. 1990. Review of the signature-whistle-hypothesis for the Atlantic bottlenose dolphin. Pages 199-234 *in* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

Carpenter, G. A., and S. Grossberg. 1987. ART2: Self-organization of stable category recognition codes for analog input patterns. Applied Optics 26: 4919-4930.

Connor, R. C., R. S. Wells, J. Mann and A. J. Read. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. Pages 91-126 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds. Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, IL

Cook, M. L. H., L. S. Sayigh, J. E. Blum and R. S. Wells. 2004. Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society of London B 271: 1043-1049.

Deecke, V. B., J. K. B. Ford and P. Spong. 1999. Quantifying complex patterns of bioacoustic variation: use of a neural network to compare killer whale (*Orcinus orca*) dialects. Journal of the Acoustical Society of America 105: 2499-2507.

Deecke, V. B., and V. M. Janik. 2006. Automated categorization of bioacoustic signals: avoiding perceptual pitfalls. Journal of the Acoustical Society of America 119: 645-653.

Esch, H. C., L. S. Sayigh and R. S. Wells. 2009. Quantifying parameters of bottlenose dolphin signature whistles. Marine Mammal Science 24: 976-986.

Evans, W.E., and J. H. Prescott. 1962. Observations of the sound production capabilities of the bottlenose porpoise: a study of whistles and clicks. Zoologica 47: 121-132.

Fripp, D., C. Owen, E. Quintana-Rizzo, *et al.* 2005. Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. Animal Cognition 8: 17-26.

Janik, V. M. 1999. Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. Animal Behaviour 57: 133-143.

Janik, V. M. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289: 1355-1357.

Janik, V. M. 2009. Acoustic communication in delphinids. Advances in the Study of Behavior 40: 123-157.

Janik, V. M., G. Dehnhardt and D. Todt. 1994. Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*. Behavioral Ecology and Sociobiology 35: 243-248.

Janik, V. M., L. S. Sayigh and R. S. Wells. 2006. Signature whistle contour shape conveys identity information to bottlenose dolphins. Proceedings of the National Academy of Sciences of the USA 103: 8293-8297.

Janik, V. M., and P. J. B. Slater. 1997. Vocal learning in mammals. Advances in the Study of Behavior 26: 59-99.

Janik, V. M., and P. J. B. Slater. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56: 829-838.

Janik, V. M., S. M. Van Parijs and P. M. Thompson. 2000. A two-dimensional acoustic localization system for marine mammals. Marine Mammal Science 16: 437-447.

Lilly, J. C., and A. M. Miller. 1961. Sounds emitted by the bottlenose dolphin. Science 133: 1689-1693.

Lind, H., T. Dabelsteen and P. K. McGregor. 1996. Female great tits can identify mates by song. Animal Behaviour 52: 667-671.

Miksis, J. L., P. L. Tyack and J. R. Buck. 2002. Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. Journal of the Acoustical Society of America 112: 728-739.

Nakahara, F., and Miyazaki, N. 2011. Vocal exchanges of signature whistles in bottlenose dolphins (*Tursiops truncatus*). Journal of Ethology 29: 309-320.

Quick, N. J., and V. M. Janik. 2008. Whistle rates of wild bottlenose dolphins: influences of group size and behavior. Journal of Comparative Psychology 122: 305-311.

Quick, N. J., L. E. Rendell and V. M. Janik. 2008. A mobile acoustic localization system for the study of free-ranging dolphins during focal follows. Marine Mammal Science 24: 979-989.

Rendall, D., M. J. Owren and P. S. Rodman. 1998. The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. Journal of the Acoustical Society of America 103: 602-614.

Sayigh, L. S., H. C. Esch, R. S. Wells and V. M. Janik. 2007. Facts about signature whistles of bottlenose dolphins (*Tursiops truncatus*). Animal Behaviour 74: 1631-1642.

Sayigh L. S., and V. M. Janik. 2010. Signature whistles. Pages 553-561 *in* M. D. Breed and J. Moore, eds. Encyclopedia of animal behavior. Academic Press, Oxford, UK

Sayigh, L. S., P. L. Tyack and R. S. Wells. 1993. Recording underwater sounds of free- ranging dolphins while underway in a small boat. Marine Mammal Science 9: 209-213.

Sayigh, L. S., P. L. Tyack, R. S. Wells and M. D. Scott. 1990. Signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus*: mother-offspring comparisons. Behavioral Ecology and Sociobiology 26: 247-260.

Sayigh, L. S., P. L. Tyack, R. S. Wells, M. D. Scott and A. B. Irvine. 1995. Sex differences in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. Behavioral Ecology and Sociobiology 36: 171-177.

Slater, P. J. B., and Lester, N. P. 1982. Minimising errors in splitting behaviour into bouts. Behaviour 79: 153-161.

Smolker, R., and J. W. Pepper. 1999. Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). Ethology 105: 595-617.

Tyack, P. L. 1997. Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. Bioacoustics 8: 21-46.

Tyack, P. L., and L. S. Sayigh. 1997. Vocal learning in cetaceans. Pages 208-233 *in* C. T. Snowdon and M. Hausberger, eds. Social influences on vocal development. Cambridge University Press, Cambridge, UK

Watwood, S. L., P. L. Tyack and R. S. Wells. 2004. Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. Behavioral Ecology and Sociobiology 55: 531-543.

Weary, D. M., and J. R. Krebs. 1992. Great tits classify songs by individual voice characteristics. Animal Behaviour 43: 283-287.

Wells, R. S. 2003. Dolphin social complexity: Lessons from long-term study and life history. Pages 32-56 *in* F. B. M. de Waal and P. L. Tyack, eds. Animal social complexity: Intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA.

Wells, R. S. 2009. Learning from nature: Bottlenose dolphin care and husbandry. Zoo Biology 28: 1-17.

Table 1: Sample sizes and results for all analyzed follows. Sessions with a D were used for the development of SIGID. All others were used for testing it. Numbers in parentheses give results with sequential SIGID method.

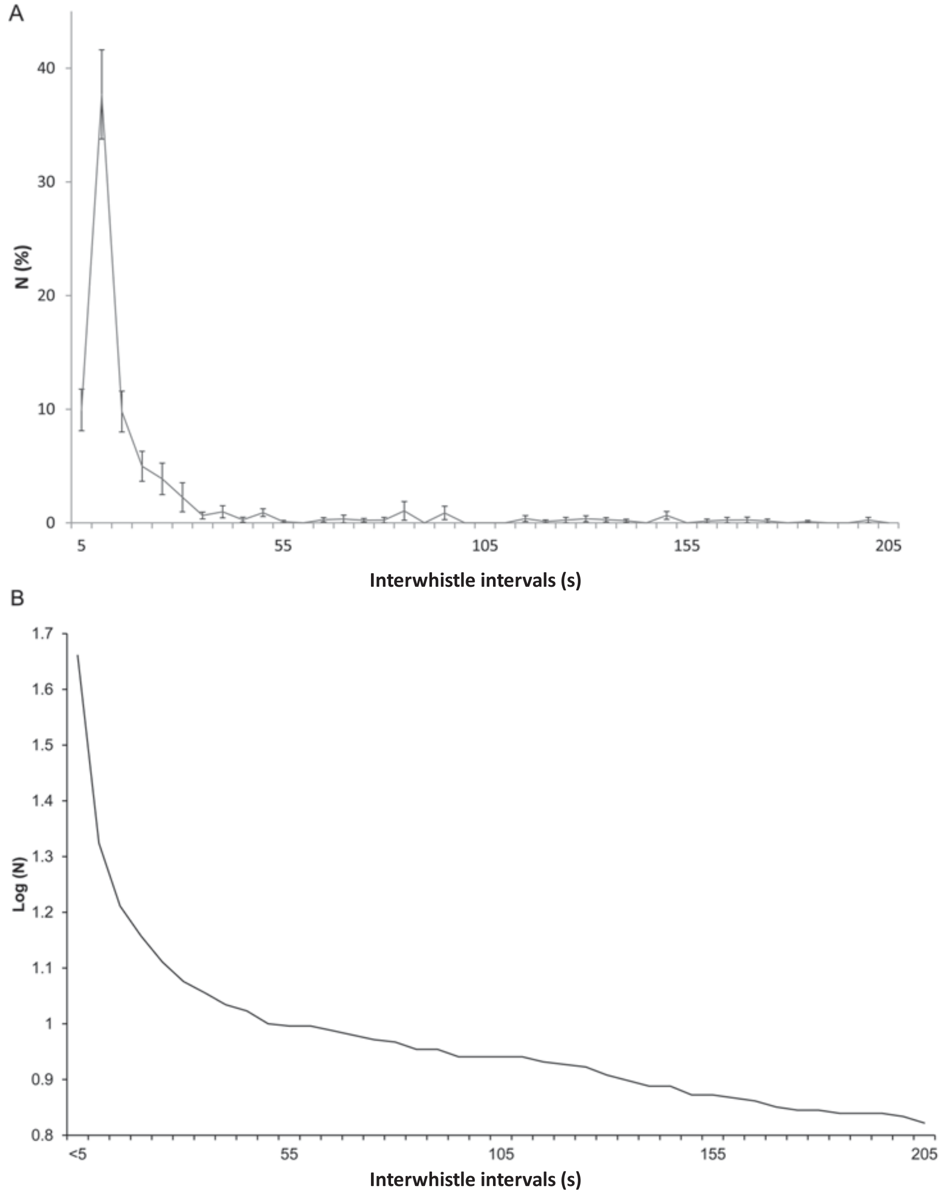
Recording period	*Duration (min:s)*	*Whistles (Signature & others)*	*Animals present*	*Animals with known signature*	*Known signature whistle types recorded*	*Signature whistle types identified by SIGID*	*SIGID False positives*
Wild1(D)	48 :06	192	7	5	2	1	0
Wild2 (D)	1 :48	19	6	5	2	1	0
Wild3 (D)	9 :56	65	7	6	2	2	0
Wild4 (D)	122 :11	53	2	1	1	0	0
Wild5 (D)	54 :27	21	2	1	0	0	0
Wild6 (D)	95 :19	14	2	1	1	1	0
Wild7 (D)	9 :32	32	4	4	2	1	0
Wild8 (D)	50 :00	133	9	8	3	3	0
Wild 9	107 :47	31	2	1	1	1	0
Wild 10	115 :07	22	5	3	1	1	0
Wild 11	123 :26	22	4	2	2	0 (1)	0
Wild 12	120 :09	113	6	3	3	0 (1)	0
Captive1	47:08	144	4	4	2	0	0
Captive2	15 :51	56	4	4	0	0	0
Captive3	46 :58	420	4	4	4	0	0
Captive4	46 :05	804	4	4	4	2	0
Captive5	46 :24	1031	4	4	4	2 (3)	0

Figure 1: Inter-whistle intervals of signature whistles of the same type. A) Average number of inter-whistle intervals (± SE) in percent from 11 individuals (431 intervals). B) Log survivorship plot of the same data standardized for sample size showing the pronounced difference in slope between the first part and the rest of the curve, indicating that signature whistles occur in bouts. In both graphs, numbers on the x-axis indicate the end time of each 5 s bin. The x-axis is limited to 205 s, but intervals between signature whistles were found to be up to 89.5 min long.

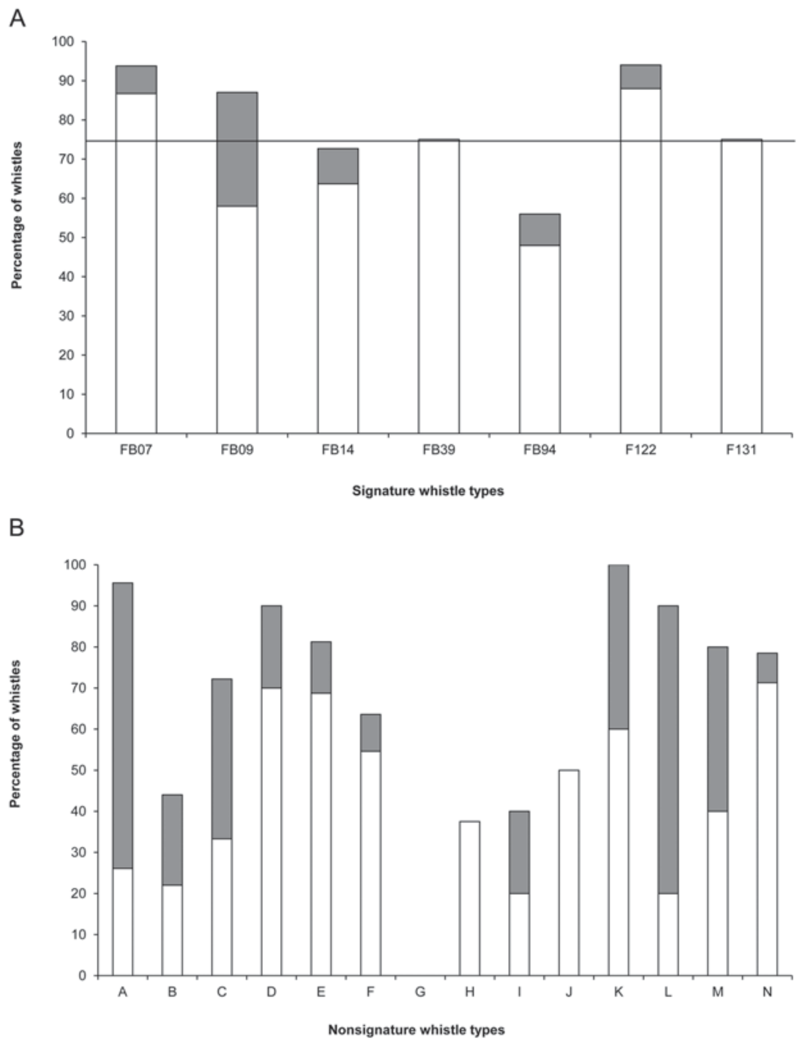
Figure 2: Bout information for identified whistle categories from wild follows. White bars indicate percentages of whistles that occurred within 1-10 s of another whistle of the same category. Grey bars indicate percentages of those that occurred within 0.25 to 0.999 s of another whistle of the same category. Whistles with inter-whistle intervals of less than 0.25 s were combined into single multi-loop whistles (see methods). The horizontal line at 75% shows the threshold used for SIGID. A) signature whistle types, only one bar is shown for FB122 even though its whistle was identified correctly in 2 different follows, B) non-signature whistle types.

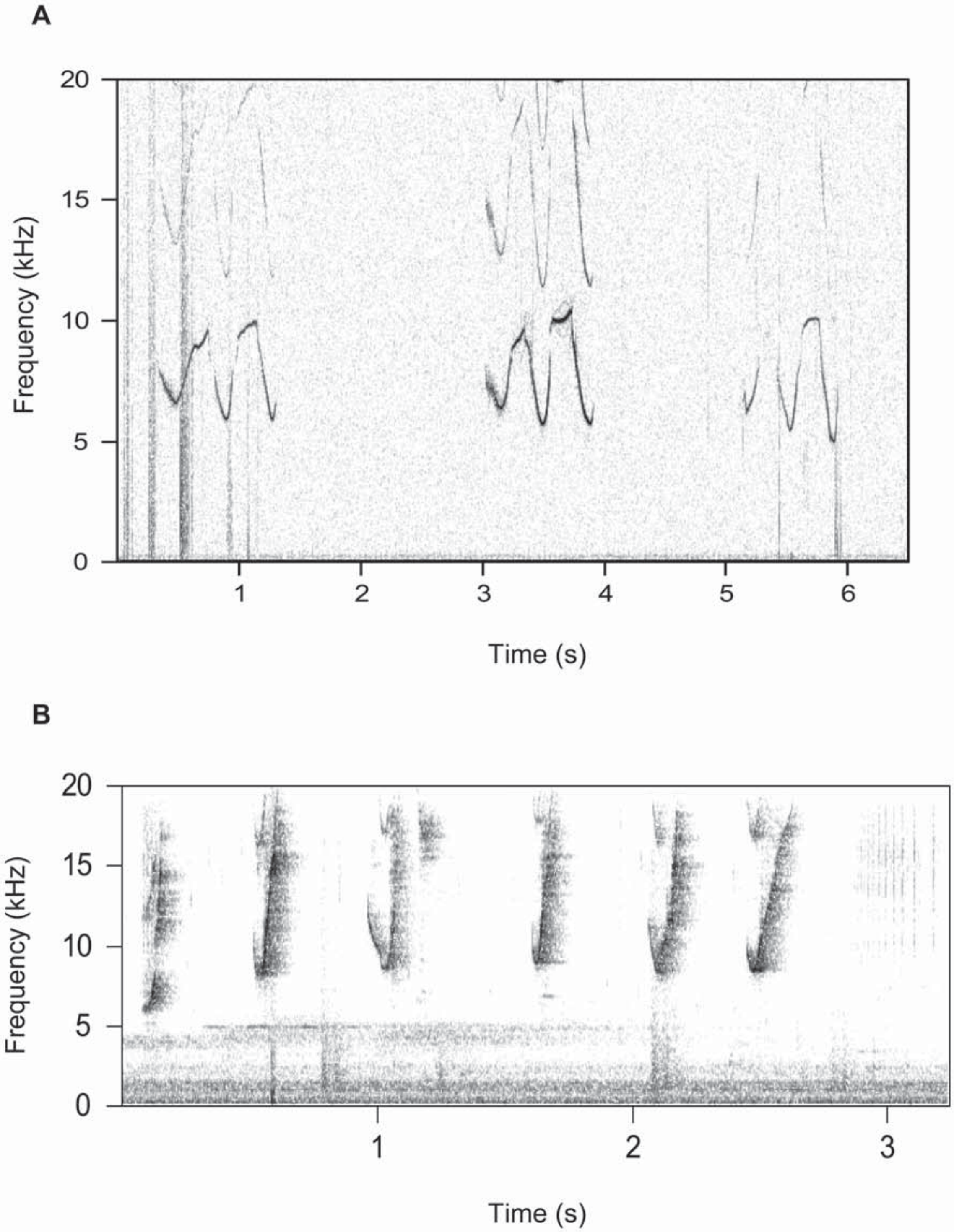
Figure 3: Spectrogram of a sequence of (A) a signature whistle type and (B) a non-signature whistle type. Note the different time scales. The inter-whistle interval in the signature whistle sequence is larger than 1 second while it is below 1 sec in the non-signature whistle sequence. FFT size 512, 50% overlap, Hanning window, sampling frequency 96 kHz

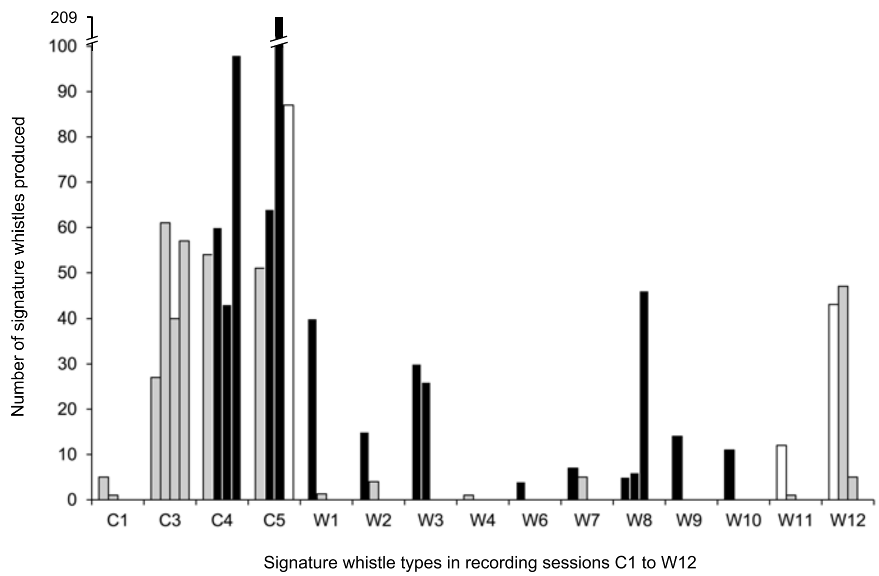
Figure 4: Number of signature whistles in our samples by recording session. Each bar represents one signature whistle type. Black bars indicate those identified successfully by the SIGID method while grey bars evaded identification. White bars indicate whistles that were identified correctly only if data were analyzed sequentially (see text) but not if all whistles in the session had been lumped into one analysis. Recording sessions C2 and W5 contained no signature whistles and were excluded from the figure.



A
N (%)
40
30
20
10
0
5
55
105
155
205
Interwhistle intervals (s)
B
Log (N)
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
<5
55
105
155
205
Interwhistle intervals (s)


A
Percentage of whistles
100
90
80
70
60
50
40
30
20
10
0
FB07
FB09
FB14
FB39
FB94
F122
F131
Signature whistle types
B
Percentage of whistles
A
B
C
D
E
F
G
H
I
J
K
L
M
N
Nonsignature whistle types


A
20
15
10
5
0
Frequency (kHz)
1
2
3
4
5
6
Time (s)
B
20
15
10
5
0
Frequency (kHz)
1
2
3
Time (s)


209
100
90
80
70
60
50
40
30
20
10
0
Number of signature whistles produced
C1
C3
C4
C5
W1
W2
W3
W4
W6
W7
W8
W9
W10
W11
W12
Signature whistle types in recording sessions C1 to W12