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Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls

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ABSTRACT

Studies on captive bottlenose dolphins, *Tursiops truncatus*, have shown that each individual produces a stereotyped, individually specific signature whistle; however, no study has demonstrated clear context-dependent usage of these whistles. Thus, the hypothesis that signature whistles are used to maintain group cohesion remains untested. To investigate whether signature whistles are used only in contexts that would require a mechanism to maintain group cohesion, we examined whistle type usage in a group of four captive bottlenose dolphins in two contexts. Individuals were recorded while they were separate from the group and while they all swam in the same pool. Separations occurred spontaneously when one animal swam into another pool. No partitions were used and no aggressive interactions between dolphins preceded separations. Calling animals were identified by an amplitude comparison of the same sound recorded in the two pools. Each dolphin primarily produced one stereotyped signature whistle when it was separated from the group. Similarly the remaining group in the other pool also used primarily their signature whistles if one animal was in a separate pool. If all animals swam in the same pool almost only nonsignature whistles were used. Signature whistle copying was rare and did not initiate reunions or specific vocal responses. The results strongly support the hypothesis that signature whistles are used to maintain group cohesion.

All mobile species in which associating with particular conspecifcs is advantageous need a mechanism for maintaining group cohesion. This is particularly obvious if mothers and their dependent offspring frequently separate (e.g. during foraging trips), but even among adults it can be at a premium. Group-living animals in which social bonds exist need to be able to locate specific partners or must simply stay in their social group. There are two ways to locate an individual after separation. First, spatial cues can be used to find the location when the last interaction occurred. This method becomes less and less reliable, however, as mobility or local population density increases. Second is the possibility of a recognition system, based on cues given by one individual that another can home in on. Like many other signals, recognition signals give information on the location of an individual as well as its identity. Both of these are important for the maintenance of group cohesion.

Individual recognition of vocal signals is often possible from general voice characteristics of an animal's calls (Cheney & Seyfarth 1980, 1988; Lind et al. 1996; Rendall et al. 1996). Individual variation in such characteristics is higher in species that live in noisy environments than in those living in quieter ones (Beecher 1991). If animals live in high background noise and are very mobile, however, genetic differences in vocal tract morphology that cause differences in voice characteristics could become insufficient to assure individual recognition, and specialized signals may be necessary.

Research on captive and temporarily captured wild bottlenose dolphins, *Tursiops truncatus*, has shown that each individual uses its own distinct, stereotyped signature whistle if it is isolated from conspecifics (Caldwell & Caldwell 1965; Caldwell et al. 1990; Sayigh et al. 1990; Janik et al. 1994). Researchers have distinguished between signature whistles by looking at their frequency contours, which are the unique modulation patterns of the fundamental frequency of the whistle. With this method it has been shown that signature whistles remain stable for up to at least 12 years (Sayigh et al. 1990). Caldwell et al. (1972) also showed that a bottlenose dolphin can be trained to distinguish between different

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signature whistles. Caldwell & Caldwell (1968) were the first to hypothesize that these whistles could be important for individual recognition and group cohesion. Recognition or isolation calls of other animal species often show a remarkable similarity in their overall contour in all individuals if compared with the variability of contours found in just one individual's call repertoire (e.g. Lieblich et al. 1980; Beecher et al. 1981; Stoddard & Beecher 1983). In contrast, dolphin signature whistles are unique frequency contours that are as dissimilar between individuals as are different nonsignature whistles in an individual's repertoire. Unlike recognition calls of other animals, they look like completely different whistle types to the human eye. Such enlarged variability increases resistance against interference tremendously (Beecher 1991). Furthermore, the development of signature whistles is influenced by vocal learning (Tyack & Sayigh 1997). Vocal learning in dolphins may have evolved to overcome problems imposed on individual recognition by high background noise levels and alterations in voice characteristics induced by changing water pressure (Janik & Slater 1997; Janik, in press a).

Even though individual recognition and group cohesion are considered the most likely functions of signature whistles today, however, there are some problems with this idea. Bottlenose dolphins can also produce copies of novel sounds at the first attempt (Richards et al. 1984; Sigurdson 1993). Tyack (1986) found that two captive bottlenose dolphins frequently copied each other's stereotyped whistles. He hypothesized that these whistles represented the subjects' signature whistles and that whistle copying could be used to address a specific individual in a group. This copying ability, however, could also work against individual recognition. If several animals produce the same signature whistle, then individual recognition could not work, assuming that other voice characteristics are not reliable indicators of identity. If signature whistles are identification signals it still remains to be shown how confusion with copying individuals is avoided.

Thus, to be able to assess the functional significance of signature whistles it is important first of all to investigate the contexts in which they are used, and we still know little about this. Because dolphins rarely provide any visible signs of sound production, many studies have focused on isolated individuals so that caller identification was not in question. Isolation, however, is just one very specific context and gives little information on whistle usage in other situations. Studies on whole groups of dolphins, on the other hand, have mostly not been able to identify the caller and so have given little information on the contextual usage of whistles. Therefore the hypothesis that signature whistles are used for individual recognition or group cohesion still remains to be tested.

Only two studies have been able to identify the caller and have looked at individual whistle usage in groups of dolphins at the same time. Tyack (1986) showed that each of two captive individuals primarily produced one stereotyped whistle type, but each also copied the other's stereotyped whistle frequently. In the other study, McCowan & Reiss (1995a) could not find any stereotyped whistle contours likely to have been signature whistles at all in their captive groups. It is somewhat puzzling that these two studies produced different results, but one reason for this may lie with the methods used as they differed in the way that a caller was identified and how whistles were categorized into types. Another reason for the different results could be the difference in recording context. While Tyack's group consisted only of the two animals that were wearing telemetry devices, McCowan & Reiss's groups were larger and undisturbed. Further study is needed to decide between these possibilities.

If the recognition/group cohesion hypothesis is right, signature whistles would occur mainly when animals were separated and out of sight of each other. We would also expect them to occur in novel and possibly threatening situations when group cohesion is of major importance for a cooperating animal such as the bottlenose dolphin. Studies on groups of dolphins that had been recently captured (Caldwell & Caldwell 1968), or were exposed to novel situations such as the lowering of the water level in the pool (Caldwell et al. 1990), have already demonstrated that stereotyped whistling can occur while animals are together. No study, however, has compared whistle production of the same individuals (after they have been well habituated to captivity) both while they were in isolation and in a group without any human intervention.

To investigate the hypothesis that signature whistles are used to maintain group cohesion, and are not just induced by stressful situations, we compared whistle usage in a group of four bottlenose dolphins while together and in isolation. Additionally, to address the question of individual specificity, we investigated the occurrence of whistle copying when the animals were in separate pools.

METHODS

Subjects and Facility

The study was conducted at the dolphinarium of the Duisburg Zoo in Germany. The subjects were four North Atlantic bottlenose dolphins: one adult male (Playboy, 23 years old) and one adult female (Pepina, 14 years old), both collected in the Gulf of Mexico on different occasions several years previously, and one subadult male (Duphi, 7 years old) and one juvenile female (Delphi, 3.5 years old) both born at the facility. They had different mothers but the adult male was possibly father to both of them. The adult female present in the pool was not the mother of either of the captive-born individuals, but was pregnant at the time of this study. Her calf was born 7 months after our study was completed. The dolphins used two connected indoor pools. The larger main pool was oval, 25 m long and 15 m wide; the smaller pool was a rectangle with side lengths of 10 and 9 m. Both pools were 5 m deep, and were connected by a gap 1.79 m deep and 1.23 m wide at the surface of the shared wall. Throughout the study all animals could use both pools at any time.

Data Collection

Data were collected over 10 days in January 1996. Each pool was equipped with a Dowty SSQ 904 sonobuoy hydrophone with custom-built preamplifiers. Both hydrophones were placed at 1 m depth and output from them recorded on two separate channels of a Marantz CP 430 tape recorder. Both channels were set at the same recording level. The recording system had a frequency response from 1 to 20 kHz ± 3 dB (calibrated by Neptune Sonar Ltd, Kelk, U.K.). This corresponds to the frequency range of whistle contours in bottlenose dolphins. We continuously noted the location (large or small pool) of each dolphin. Recordings were made either while all the animals were swimming together in the main pool or whenever one animal swam separately from the others in one of the pools. These separations were not induced but occurred spontaneously in the daily behaviour of the animals. No recordings were made during feeding or training sessions. Each session was started after the animals had been undisturbed for at least 10 min. Aggressive behaviours were sampled continuously to investigate whether separations were induced by aggressive interactions. Behaviours sampled corresponded to those investigated by Samuels & Gifford (1997). Observations were made from an elevated point 15 m from the pool.

Data Analysis

Frequency spectrograms of all recorded whistles were calculated using SIGNAL software (Engineering Design, Belmont, Massachusetts, U.S.A.) (FFT size: 1024, time resolution: 20.5 ms, frequency resolution: 48.8 Hz, number of FFT steps: 200, weighting function: Hanning window). In the first step, V.M.J. inspected the spectrograms by eye and classified them into separate whistle types without knowing the context in which they were produced or the identity of the dolphin. Sayigh et al. (1995) demonstrated the validity of this method by showing that human observers agree on which whistles look similar to each other on a frequency spectrogram. Furthermore, computer methods that have been used to classify dolphin whistles are still not able to detect some of the gestalt features of signature whistles and are therefore not suited to investigate signature whistle usage (Janik, in press b). Spectrograms were inspected twice. In the first run only very stereotyped whistle types were identified; in the second run all remaining whistles were categorized into more variable types which were defined by the shape of the frequency contour of a whistle (see Results). To test for interobserver reliability, however, a subset of 104 randomly chosen whistle contours was classified by five additional observers. No observer had any information on contexts of whistles or caller identity. The interobserver reliability of all six observers in the classification of what they considered stereotyped whistles was extremely high (Kappa statistic, Siegel & Castellan 1988: $\kappa=0.92$, $z=22.16$, $P<0.0001$) and corresponded closely to the initial classification.

Next we compared the amplitude of each whistle on the left and the right channel of the tape recorder to determine from which pool a whistle came (Janik et al. 1994). Whistles are omnidirectional since a dolphin's head does not focus low-frequency sounds such as whistles (Evans et al. 1964). Thus, the orientation of the animal has no influence on the amplitude comparison. We analysed whistle type production for each individual when it was swimming on its own, for the whole group swimming together, and for the remaining group if one animal was separate. Data on aggression were analysed for each 1-min period before a separation occurred.

RESULTS

Whistle Classification

All 2472 whistles were categorized into whistle types A, B, C, D_1, D_2, Rise, Wave, Sine, U-Shape, Fall and Residual (Figs 1, 2). Types A, B, C, D_1 and D_2 were the stereotyped whistle types identified in the first scan of the spectrograms. Figure 1 shows example spectrograms for each of these stereotyped whistle types. The classification of non-stereotyped whistles followed that of Tyack (1986) and Janik et al. (1994).

For further analysis, all types that occurred at least 80% of the time in close sequence (less than 500 ms apart) were considered one whistle. Such multiloop whistles have been described before and seem to represent one unit in the repertoire of a dolphin (Caldwell et al. 1990; Sayigh et al. 1990, 1995). The multiloop whistles found were types A, C and D (Fig. 1). In types A and C two very similar contours followed each other, while in type D the two contours were different (D_1 followed by D_2). Only 40 out of the 394 contours that made up type A in the total whistle sample of 2472 whistles recorded for this study occurred on their own. In type C it was 53 out of 391 contours, and in type D the first contour occurred 54 times on its own, the second one did so three times, and the two occurred together on 261 occasions. None of the less stereotyped whistle types formed multilooped whistles.

Whistle Usage

Whistle rates per individual did not differ significantly between isolation and group swimming (Kruskal–Wallis test: $H_4=6.335$, NS), but the distribution of whistle rates was different between contexts (Table 1). While the median whistle rate was lower in the group-swimming context, whistle rates of nil were rare. Conversely, in separations animals often did not whistle at all, except in a few separations when high whistle rates were apparent.

Figure 3 shows how whistle types were distributed between the different contexts. Each individual used a different stereotyped whistle type when it was separated from its group. In previous studies the signature whistle was the most frequent whistle type for each individual when it was in isolation. Thus, we termed these whistles the signature whistles of these individuals. Type A was the signature whistle of the adult male (68% of his whistles in isolation), type B belonged to the adult female

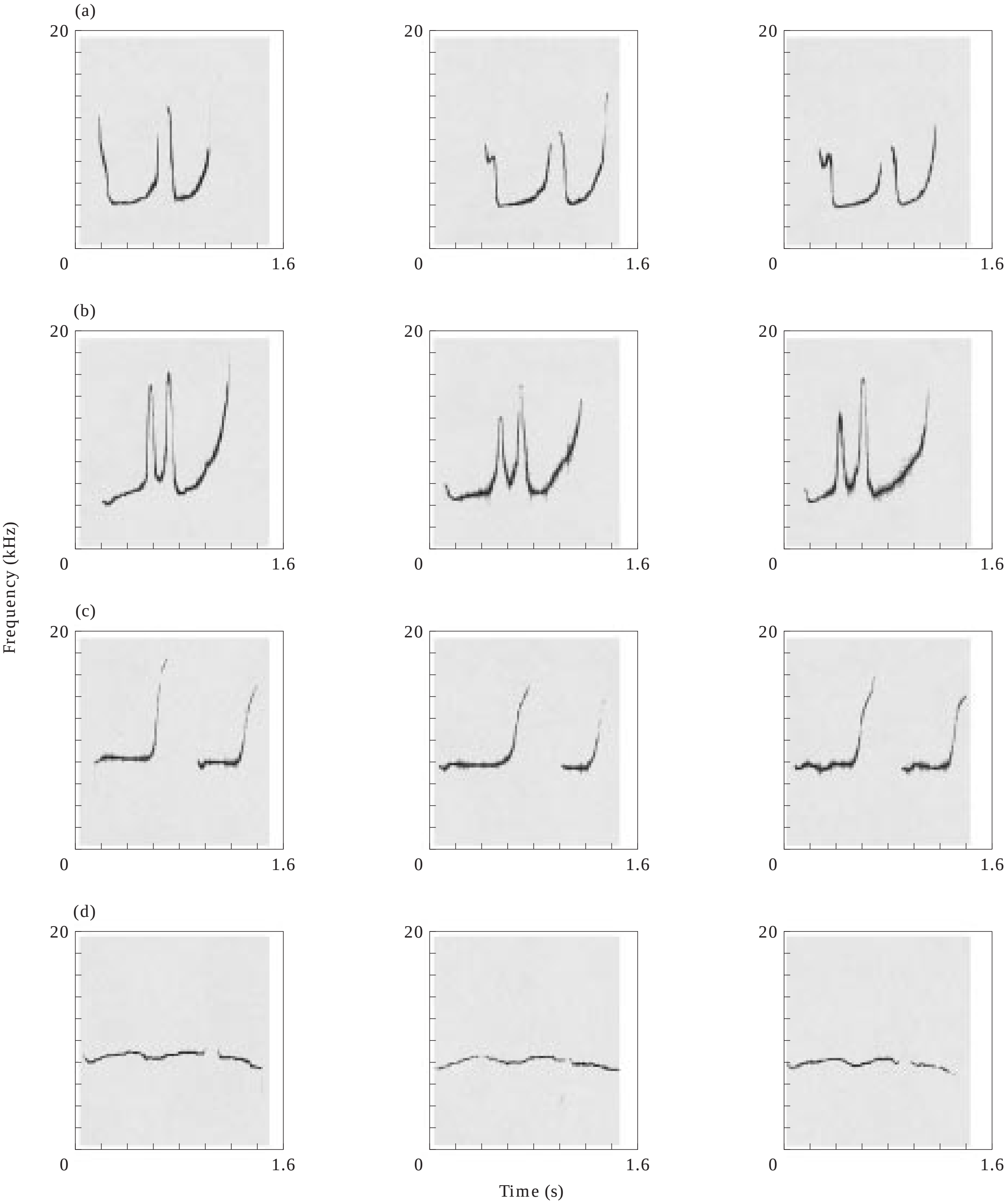


Figure 1. Three randomly chosen spectrograms of each of the stereotyped whistle types: (a) whistle type A, signature whistle of the adult male; (b) whistle type B, signature whistle of the adult female; (c) whistle type C, signature whistle of the subadult male; (d) whistle types D_1 and D_2. Contours D_1 and D_2 almost always followed each other and made up the signature whistle of the juvenile female. Background noise and harmonics have been removed on all spectrograms since the frequency response of the recording system was not sufficient to record complete harmonics.

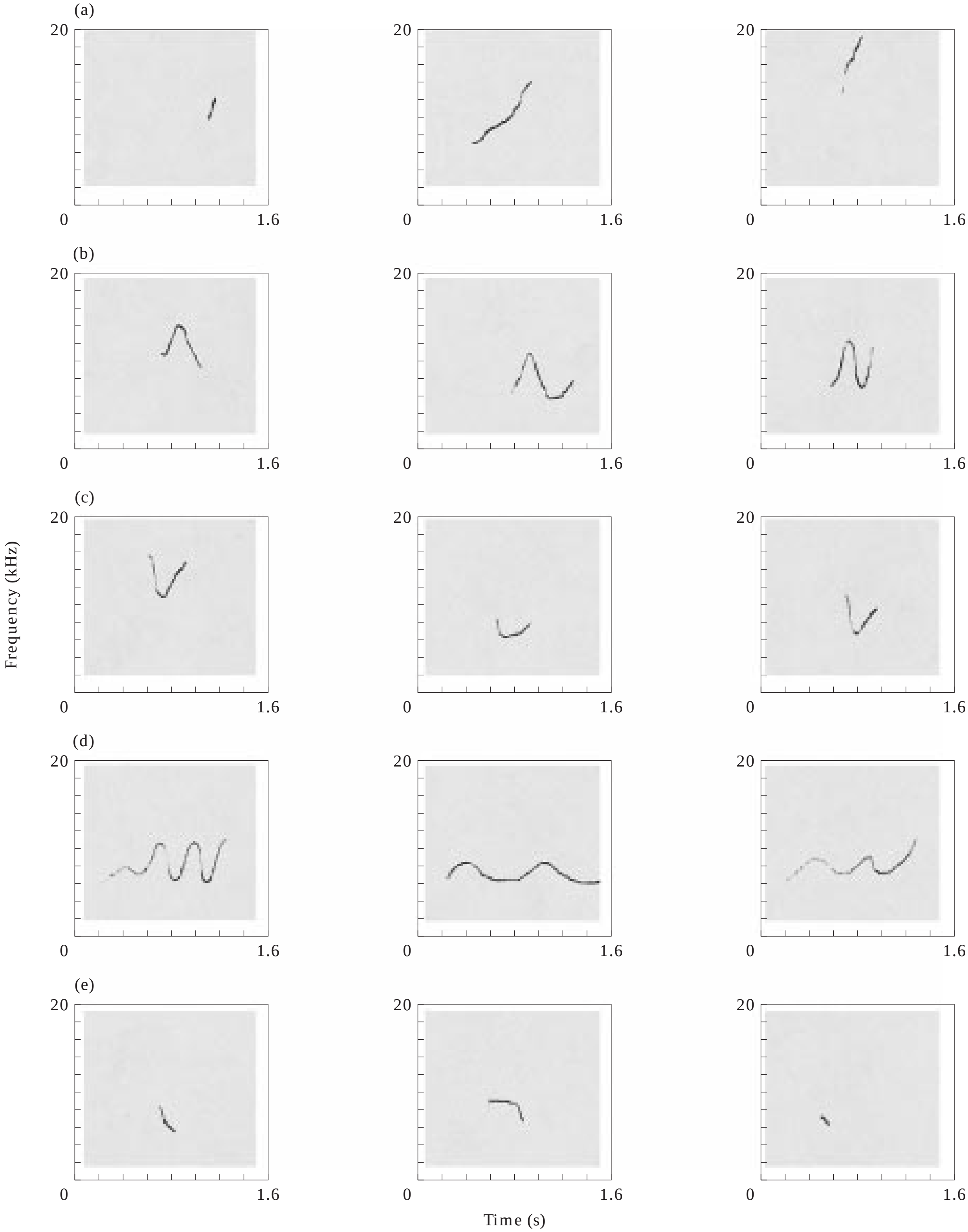


Figure 2. Three randomly chosen spectrograms of each of the more variable whistle types: (a) whistle type Rise; (b) whistle type Wave; (c) whistle type U-Shape; (d) whistle type Sine; (e) whistle type Fall. Background noise and harmonics have been removed on all spectrograms (see Fig. 1).

Table 1. Sample sizes and whistle rates for each individual in isolation and for the group swimming together

				Percentiles of whistles per individual per session per min†		
Individuals	Number of sessions	Total recording time (min:s)	Total number of whistles*	First quartile	Median	Third quartile
Adult male	38	60:55	128	0	1.73	3.67
Adult female	33	37:43	110	0	2.73	5.43
Subadult male	10	31:58	133	0	0	6.31
Juvenile female	21	47:40	238	0	2.05	9.28
Group swimming	37	219:00	714	0.13	0.79	1.54

*A further 1149 whistles were recorded from the rest of the group at times when one individual was separate. These were analysed separately since they are not independent from the data of the isolated individual.

†Note that percentiles describe the distribution of whistle rates from each separation or group swimming event. Thus, the median here is not equal to the overall whistle rate (total number of whistles/total recording time).

(31.8% of her whistles in isolation), type C to the subadult male (91.7% of his whistles in isolation) and type D to the juvenile female (72.7% of her whistles in isolation). Signature whistles were the most common whistles in the isolation context but did not occur during every separation. Short separations often did not involve any whistling or only nonsignature whistle types. The animals also used Rise, Wave, Sine, U-Shape, Fall and Residual whistles when in isolation, but almost never any of the other individuals' signature whistles. The only two such cases were when the subadult male produced parts of the juvenile female's signature whistle while he was in the separate pool (see below). The three animals that remained in the other pool together also used primarily their signature whistles if one animal was separated from them. Of the 1149 whistles recorded from these remaining individuals 56% were signature whistles. Given the total lack of signature whistles when all four animals were in the same pool, this is a particularly striking result.

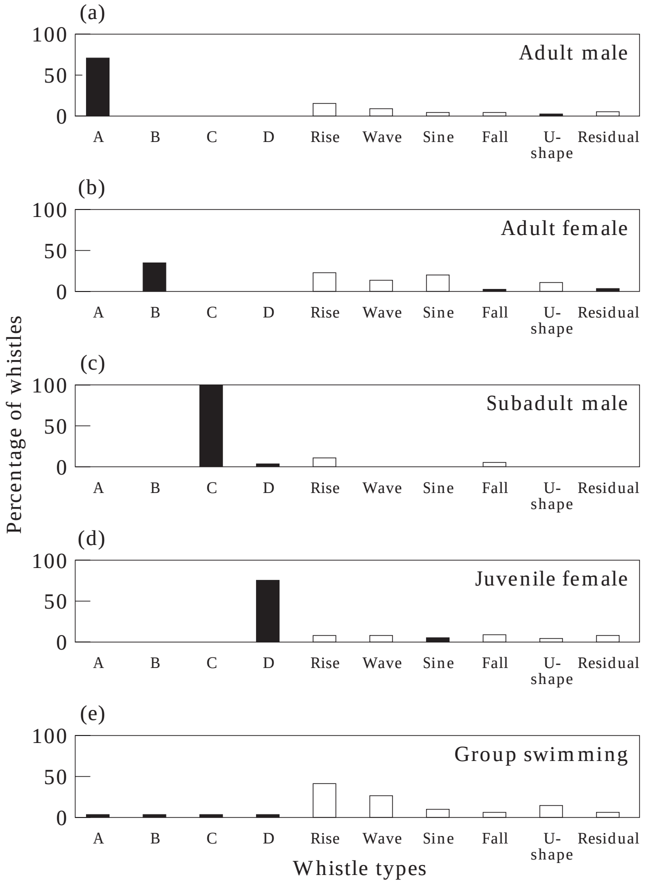


Figure 3. Whistle type usage in different contexts: (a) adult male in a separate pool; (b) adult female in a separate pool; (c) subadult male in a separate pool; (d) juvenile female in a separate pool; (e) all animals together in one pool. ■: Signature whistle types; □: nonsignature whistle types.

Almost all signature whistles used occurred when the whistling animal was separate from the rest of the group. Only 17 signature whistles were recorded during group swimming, representing 2.4% of all whistles recorded in that context, and 10 of these occurred in two bouts of five signature whistles each. When all four were together in a group the animals used almost entirely nonsignature whistles. This is only true for undisturbed animals however. We observed one incident in which all individuals produced almost entirely signature whistles while together in one pool. This happened when a feeding session was delayed. During this whistling bout the animals were often facing underwater windows where keepers were visible. This event was not part of the sample analysed in this study since the animals were not undisturbed at the time (several humans were present at the pool). It suggests, however, that signature whistles are sometimes used in contexts other than separation.

Separations were not induced by aggression, which was rare in this group and we observed only one case in which an aggressive act (a chase) preceded a 22-s separation.

Signature Whistle Copying and Whistle Matching

Signature whistle copying could be investigated only during separations since this was the only context in which one caller was known. If the signature whistle of the animal in isolation was heard from the pool where the rest of the group was swimming it must have been copied by an animal in that pool. In the total recording time of 397 min and 16 s that one animal was separated from the rest of the group, only five cases of signature whistle copying were found (Fig. 4). Signature whistle copying did not initiate the end of a separation and there was no consistent vocal response to copying. However, signature whistle copying occurred only after the copied whistle had been produced at least once within the preceding minute by the other individual. In all cases the copied whistle was also heard at least once in the minute after the copying from the other pool. For nonsignature whistles only direct matching of whistles could be analysed since all individuals used all nonsignature whistle types. A matching interaction was defined as an individual producing the same whistle type as another one within 3 s of the end of the first caller's whistle. Using the same strict criteria as for signature whistles we found no whistle matching involving nonsignature whistles. It could be, however, that the animals shared rarely used stereotyped nonsignature whistles but simply did not use them in matching interactions.

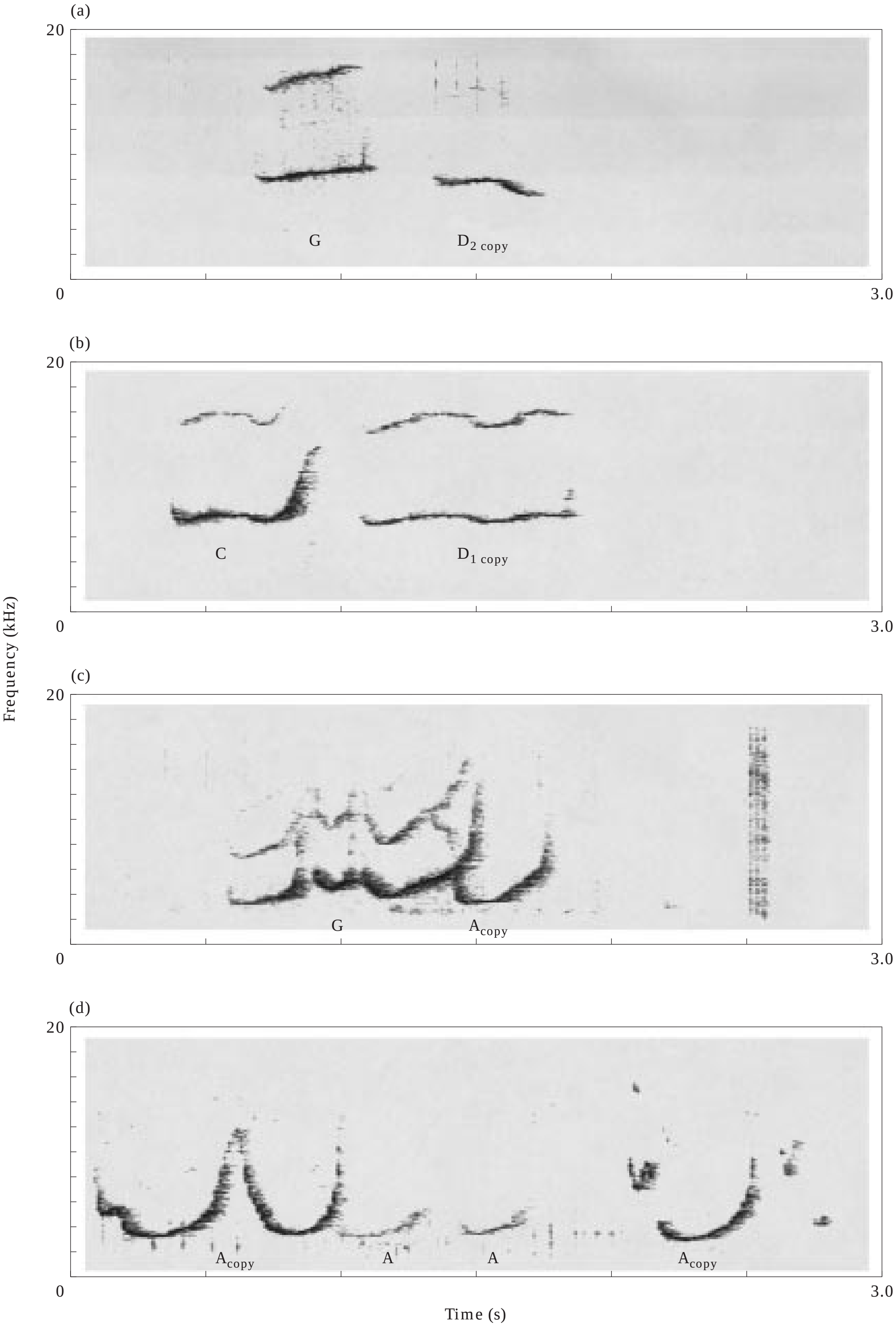
DISCUSSION

Previous studies on dolphin whistles did not find such clear differences in whistle type usage between contexts as those presented here. Some studies found signature whistles to be the most common whistle type in all contexts investigated (Caldwell et al. 1990; Janik et al. 1994), while others could not find any highly stereotyped whistling at all (Dreher & Evans 1964; McCowan & Reiss 1995a). This suggests that differences between studies were simply due to different methods (Herman & Tavolga 1980; McCowan & Reiss 1995a). Which methodology, however, is appropriate to investigate whistle types? Any classification method for animal signals involves decisions by humans on the parameters to be used. Further validation is needed to find out which method represents the best approximation to how dolphins themselves classify whistles. Without any data from perception experiments, one of the best methods to confirm the existence of a particular category found in one's data set is a test on an external variable (Aldenderfer & Blashfield 1984). This involves carrying out tests to compare the whistle types on variables that have not been used to define them (=external variables). In our study we followed this procedure by classifying whistles by eye and then looking at who used which whistle type in what context. Here, usage of whistles is the external variable. The results, showing that signature whistles occurred almost exclusively in the separation context but not in the group context and that they were very individually specific, confirmed that these whistle types are important units in the dolphin's repertoire. No such confirmation has been found for nonsignature whistles, however, in this or any other study. To draw conclusions on what represents a nonsignature whistle type, we shall need specific classification experiments, such as those done with birds (Horn & Falls 1996).

Our results also imply that differences between previous studies have been caused by differences in the contexts that were investigated. Studies that have looked at isolated individuals (Caldwell & Caldwell 1965; Caldwell et al. 1990; Sayigh et al. 1990; Janik et al. 1994), animals shortly after capture (Caldwell & Caldwell 1968; Caldwell et al. 1990), or in unusual situations such as a lowering of the water level in the pool (Caldwell et al. 1990), while many people were around the tank or while the animals were wearing telemetry devices (Tyack 1986), revealed that bottlenose dolphins almost only use signature whistles in such contexts. On the other hand, no stereotyped whistle types were found in studies in which animals well habituated to captivity and not exposed to any human intervention were recorded without being separated (Dreher & Evans 1964; McCowan & Reiss 1995a, b). Our study applied the same whistle classification method to the investigation of whistle usage in both context types, and suggests that the difference is not due to methodology, but that signature whistles are used only in the separation context (but also see Janik, in press b, for a discussion of discrepancies caused by different whistle classification methods). Thus, all results together show that signature whistles are primarily emitted in situations when behaviour helping to maintain group cohesion is likely to occur.

Researchers have used various terms to describe calls given in isolation. Infant calls that elicit an approach by the caregiver, for example, have been described as isolation or distress calls (reviewed in Maestripieri & Call 1996). Cohesion or monitoring calls, on the other hand, are used by isolated animals but do not elicit an approach and seem to help an animal to stay in touch with its group (Petter & Charles-Dominique 1979; Caine & Stevens 1990). The term contact call has been used for both of these categories (e.g. Pola & Snowdon 1975), and there is no clear-cut distinction between these two classes. Signature whistles could also be used by infants to elicit an approach by the mother, but whether they are is not known. Our results, and the fact that bottlenose dolphins can easily distinguish between different signature whistles (Caldwell et al. 1972), strongly support the hypothesis that these signals are used to communicate identity and maintain group cohesion. Further studies are needed to investigate their role in other contexts.

Our findings on whistle copying suggest that it is relatively rare. Similarly, low rates of signature whistle copying in captive animals have been reported by Burdin et al. (1975). Even though the results reported here are similar to those of some other studies, however, they differ markedly from what Tyack (1986) found in his group of two individuals. In his study stereotyped whistling was high while both individuals were in the same pool, independent of whether they were wearing telemetry devices or not, and whistle copying was common. His subjects were also well habituated to captivity so recent capture could not have caused these differences. All his recordings were made in one day, however. The increased activity around the pool and the wearing of the telemetry devices could have influenced the vocal behaviour of his subjects. Captive dolphins can be very sensitive to changes in their daily routines. Bottlenose dolphins produce higher rates of whistles in response to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novel situations (McBride & Heb 1948; Defran & Pryor 1980) and this could have been a factor influencing Tyack's results. Novel situations might lead not only to an increase in overall whistle rates but maybe also to an overrepresentation of particular whistle types in the expressed repertoire. Another explanation could be a delay in the normal feeding schedule. In the present study all individuals produced almost entirely signature whistles while together in one pool on one occasion when a feeding session was delayed. Thus, while Tyack's study was the first to draw attention to the occurrence of signature whistle copying, it was probably not representative of undisturbed vocal behaviour in bottlenose dolphins.

We still know very little about how wild bottlenose dolphins use whistles. One has to be careful in extrapolating results from studies on captive dolphins to wild ones. Data from captive individuals can give us some information on functions of whistles, but the pattern of occurrence of signature whistles and signature whistle copying may be very different in the wild. This is mainly because certain contexts do not appear in captivity. Thus in our study there were no other dolphins within hearing distance and the animals did not need to search for food. The visual range under water is low compared with the acoustic range. In the wild, groups spread out to feed or to socialize with other individuals, situations in which we would expect signature whistles to occur. Even in a group, however, wild dolphins may still be in contact with other dolphins that are out of sight. The situation in the wild seems to resemble that of a communication network (McGregor & Dabelsteen 1996) in which individuals constantly move into and out of acoustic range of each other. Thus, one could expect a much higher rate of signature whistling. It is difficult to make predictions about signature whistle occurrence in the wild, however, since both announcing and concealing one's presence could be of advantage according to the particular context (Janik, in press a). Smolker et al. (1993) showed that stereotyped whistling was common during separations and reunions of wild mother–calf pairs and that whistling usually stopped after infants returned to their mothers. This also supports the individual recognition/group cohesion hypothesis. Among mothers and their infants the advantage of giving information on identity and position is clear. Among adults it is more difficult to make predictions. There is a similar lack of data on the occurrence of signature whistle copying. The high rate of whistle copying in Tyack's (1986) study could have been stimulated by the method he used for caller identification. In the present study whistle copying was very rare. If Tyack's hypothesis that copying can be used to address specific individuals is right, however, we should expect it to occur more in the wild where many animals are within hearing range and the ability to address just one particular individual would be advantageous to cooperating animals. Whistle matching does occur in wild bottlenose dolphins (Janik 1997), but, unlike the duetting of gibbons or birds, not in long interactive sequences. Addressing a specific individual, however, could be used not only to initiate reunions but also in aggressive interactions comparable to the matched countersinging among birds. To assess other functions of signature whistles one of the next steps must be to look at how these learned cohesion signals are used in the wild.

Acknowledgments

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Figure 4. Spectrograms of all cases of signature whistle copying found in this study. (a) The subadult male copied the second loop of the juvenile's signature whistle. (b) The subadult male copied the first loop of the juvenile's signature whistle. (c) An animal in the remaining group copied one loop of the adult male's signature whistle. (d) An animal in the remaining group copied the adult male's signature whistle twice. The first and the last contour were produced by animals in the remaining group, the faint contours in the middle were produced by the adult male. Note that these spectrograms were produced from only one channel of the recording system. Whistles that are faint or seem interrupted are in fact complete and continuous versions of signature whistles from the other pool. A: Signature whistle produced by adult male; A_{copy}: whistle of adult male copied by remaining group; C: whistle of subadult male; D_{1copy}, D_{2copy}: signature whistle of juvenile female copied by subadult male; G: whistles of the remaining group of three.

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