Individual recognition in wild bottlenose dolphins: a field test using playback experiments

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We conducted playback experiments with wild bottlenose dolphins, *Tursiops truncatus*, to determine whether there is sufficient information in their individually distinctive signature whistles for individual recognition. We conducted experiments with members of a resident community of dolphins in waters near Sarasota, Florida, during temporary capture–release projects. We used a paired playback design, wherein the same two whistle sequences were predicted to evoke opposite responses from two different target animals. This design controlled for any unknown cues that may have been present in the playback stimuli. We predicted that mothers would respond more strongly to the whistles of their own independent offspring than to the whistles of a familiar, similar-aged nonoffspring. Similarly, we predicted that independent offspring would respond more strongly to the whistles of their own mother than to the whistles of a familiar, similar-aged female. Target animals were significantly (*P*<0.02) more likely to respond to the predicted stimuli, with responses measured by the number of head turns towards the playback speaker. In bottlenose dolphin societies, stable, individual-specific relationships are intermixed with fluid patterns of association between individuals. In primate species that live in similar 'fission–fusion' type societies, individual recognition is commonplace. Thus, when taken in the context of what is known about the social structure and behaviour of bottlenose dolphins, these playback experiments suggest that signature whistles are used for individual recognition.

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The study of individual recognition has encompassed a diversity of taxa and is well represented in the literature (e.g. see reviews by Marler 1960; Thorpe 1968; Falls 1982; Colgan 1983; Gould 1983). The majority of studies have focused on parent–offspring and neighbour–stranger recognition, although other studies have looked at recognition between mates (e.g. Beer 1970; White 1971; Berger & Ligon 1977), nestmates (e.g. Schimmel & Wasserman 1991), and fellow group or flock members (e.g. Mammen & Nowicki 1981; Clapperton 1987a, b; Biben & Symmes 1991). While the results of these studies are often described in terms of 'individual recognition', most of these studies did not actually test for discrimination between familiar individuals, but rather analysed differential responses between classes of individuals that differed in familiarity.

Many animals face recognition problems that do not require classifying conspecifics down to the level of each individual. For example, when a parent provides care to offspring, it usually needs only to differentiate its own

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offspring from the young of other parents. In general, helping behaviour that evolves through kin selection need not require individual recognition; rather, animals could classify conspecifics into kinship classes. With respect to competitive behaviour, some territorial songbirds may show less response when the songs of neighbours are played from their territories, but this does not require the bird to have an internal representation of each individual neighbour. Rather, a male may simply habituate to particular songs from particular locations.

Other recognition problems may require an animal to learn long-term representations of specific individuals and to perceive signature signals with enough resolution to allow each individual to be uniquely classified. As a theoretical example, in models of reciprocal altruism, individual interactants recognize one another and remember the history of how each individual has responded in the past (Axelrod & Hamilton 1981).

Human social behaviour relies upon individual-specific social relationships. Humans form concepts of other individuals that are stable over long periods and that are independent of sensory modality; the same individual can be recognized one time by voice, and the next time by facial features. It has been argued that other primates that interact repeatedly with one another throughout their lifetimes may also have this 'true' individual recognition, in which an animal forms long-term concepts of other individuals (e.g. Cheney & Seyfarth 1980, 1982, 1986; de Waal 1982; Dasser 1985; Essock-Vitale & Seyfarth 1986). '. . . [P]rimates can remember past interactions, seem able to predict the behaviour of others on the basis of prior observations (Kummer 1982), and discriminate among their own and other individuals' close associations' (Essock-Vitale & Seyfarth 1986, page 452). Although familiarity undoubtedly plays a role in these recognition systems as well, it is widely accepted that most, if not all, primate species display such 'true' individual recognition (Essock-Vitale & Seyfarth 1986; Snowdon 1990).

True recognition of individuals is a prerequisite for reciprocally altruistic behaviour (Trivers 1971), a capacity for which has been documented in vervet monkeys, *Cercopithecus aethiops* (Seyfarth & Cheney 1984), and bats (Wilkinson 1984). Connor & Norris (1982) suggested that dolphins display many of the characteristics presumed to be associated with reciprocally altruistic behaviour (e.g. long-term, close associations; care-giving behaviour). Individuals that interact repeatedly with one another over their lifetimes may need to track the history of these various relationships, in addition to classifying their associates into many categories (e.g. as individuals in their own group versus a neighbouring group).

Bottlenose dolphins, *Tursiops truncatus*, are a social species with long-lasting, close associations among individuals (Wells et al. 1987; Connor et al. 1992). These animals use acoustic communication extensively, indicating that this would be the most likely channel for individual recognition, if it were to occur. Their vision, although excellent (Dawson 1980), is of limited usefulness in many turbid, coastal habitats, and the olfactory lobe is absent in bottlenose dolphins (Herman & Tavolga 1980). Individual recognition through vocal whistle 'signatures' has been suggested by several authors (Caldwell & Caldwell 1965; Tyack 1986; Sayigh et al. 1990). However, so far only an ability to discriminate among whistles of different individuals (an important prerequisite to individual recognition) has been demonstrated experimentally (Caldwell et al. 1971, 1972).

Falls (1982) noted that features of a signal used for species recognition should show high interspecies variability along with low inter- and intraindividual variability, whereas features used for individual recognition should show high interindividual variability compared to intraindividual variability. Beecher (1982, see also Loesche et al. 1991) expanded this concept, and noted that selection for individual recognition could increase interindividual variability, decrease intraindividual variability, or increase perceptual sensitivity to signature traits. Many studies have demonstrated individual variability in vocalizations without testing whether this variability is perceived by conspecifics (e.g. Hafner et al. 1979 for humpback whales, *Megaptera novaeangliae*). As outlined by Beer (1970), demonstrating individual recognition should be a three-part process, where vocal variability is shown, evidence for individual recognition is noted in natural behaviour, and the ability to discriminate among individuals is confirmed through playback experiments. We explored the potential for individual recognition in free-ranging bottlenose dolphins using these three criteria.

Vocal Variability

Individual variation in bottlenose dolphins vocalizations has been thoroughly documented through analyses of individually distinctive signature whistles of captive and wild dolphins (Caldwell et al. 1990; Sayigh et al. 1990; Sayigh 1992). Several lines of evidence support the idea that the distinctive frequency contours of bottlenose dolphin signature whistles provide information on individual identity. First, interindividual variability is much higher than intraindividual variability (Buck & Tyack 1993). Second, Caldwell et al. (1971) demonstrated that one bottlenose dolphin was capable of extremely accurate discrimination of different exemplars of naturally occurring signature whistles, even when spectrograms of the whistles were visually similar. A later study (Caldwell et al. 1972) showed that the same dolphin was capable of distinguishing among signature whistles of at least eight different individuals, using many different exemplars from each individual. The ability to discriminate among many different whistle contours would be essential if signature whistles were used for individual recognition in fluid social groups. Third, studies on cognition have shown that dolphins are capable of discriminating among many different computer-generated whistle-like sounds (Herman et al. 1984; Richards et al. 1984; Herman 1986). Dolphins can learn to associate arbitrary sounds with arbitrary objects (Herman 1986), a skill that would also be necessary for association of specific signature whistles with particular individuals.

Observational Evidence for Individual Recognition

Observations of wild bottlenose dolphins provide compelling evidence for individual recognition. Extremely stable individually specific relationships have been extensively documented in wild communities of bottlenose dolphins (Wells 1991; Connor et al. 1992; R. S. Wells, unpublished data). For example, coalitions of two to three unrelated males can have coefficients of association that are close to 1.0, meaning that they are together in approximately 100% of all sightings for each individual. Mothers and calves remain in close association for 3–6 years, and one 10-year association was observed (Wells 1991); however, mothers and dependent calves frequently separate out of visual range and then reunite (Smolker et al. 1993).

In addition to these long-term, stable associations between individuals, dolphins interact repeatedly with many other individuals over the course of their long lives (free-ranging dolphins have been documented to live to at least 50 years of age (Hohn et al. 1989; A. A. Hohn, unpublished data). In environments where visibility of 30–50 m is exceptional, it is almost impossible to imagine how else these individually specific relationships could be maintained if not acoustically. Whistles can travel several kilometres and are omnidirectional. Furthermore, whistles are known to be used extensively in natural contexts (Sayigh 1992; Smolker et al. 1993).

Playback Experiments

As noted above, playback experiments have been used to test the ability of dolphins to distinguish between different signature whistles. In the present study we used playback experiments to test whether there is sufficient information in signature whistles for individual recognition. The primary target groups for these experiments were mothers and independent offspring that were no longer associating together continuously. During the period of close association between mothers and offspring, the signature whistle often appears to function as a contact call (e.g. McBride & Kritzler 1951; Sayigh et al. 1990), and to initiate reunions between mothers and calves that are out of visual contact (Smolker et al. 1993). Mother–offspring recognition could thus result purely from discrimination of familiar versus unfamiliar stimuli, based on how often the whistles are heard. Our experiments were designed to test whether mothers continue to recognize (i.e. respond differently to) signature whistles of independent offspring. Similarly, we tested whether independent offspring recognize signature whistles of their mothers. In these cases, the frequency with which the stimuli are being heard could not account for discrimination of whistles, because mothers and independent offspring tend to associate at low levels.

In our experiments, each target animal was presented with two familiar stimuli, with one predicted to elicit a stronger response than the other. In tests with mothers as target animals, we compared the mothers' responses to whistle sequences from an independent offspring and a familiar, similar-aged nonoffspring; in tests with independent offspring as target animals, we compared the offsprings' responses to whistle sequences from the mother and a familiar adult female. Offspring used as target and stimulus animals had been independent from their mothers for periods ranging from 1 month to 14 years. In each paired trial, each target animal (whether a mother or an independent offspring) associated at similarly low levels with both of the animals whose whistles were used as stimuli.

In a third set of experiments, we targeted females from different bands (Wells 1991), to test whether adult females preferentially respond to whistles of closely associated females, compared to whistles of familiar but less closely associating females. Not all females in a band are matrilineally related (Wells 1991), so recognition cannot be based on a simple matrilineal 'signature,' such as was found for pigtailed macaques, *Macaca nemestrina*, by Gouzoules & Gouzoules (1990). In addition, even the whistles of matrilineally related females are quite distinct from one another (Sayigh et al. 1990, 1995). Thus, it is of interest to determine whether females recognize signature whistles of their individual group members.

METHODS

Capture–release projects take place once or twice yearly in Sarasota, Florida, to obtain basic information about age, sex and genetic relationships for individual bottlenose dolphins (Scott et al. 1990; Wells 1991). We surrounded the animals using a large net in water approximately 1 m in depth, and then processed them on the deck of a boat for up to 1 h. We conducted playback experiments after the animal had been returned to the water but prior to its release. Although these temporary captures are artificial settings for wild animals, they are otherwise ideal for conducting playback experiments, because the animals' responses can be easily observed and the context easily controlled.

To control for any contextual cues that might be present in the whistle stimuli, we used a paired playback design. We predicted that pairs of target animals would respond differently (in opposite directions) to two playback stimuli, based on their relationships to the individuals that produced the stimulus whistles. If animals responded to whistles based on the level of arousal of the individual that produced them, or some other acoustic feature unrelated to the identity of the vocalizer, then both target animals should respond in a similar manner to a given pair of stimuli. Thus, this paired playback design also eliminated problems associated with pseudoreplication (Hurlbert 1984; Catchpole 1989; Kroodsma 1989a, b; Searcy 1989).

Experimental Design

The experimental design of mother–independent offspring playbacks consisted of paired trials, wherein we played the same two stimulus tapes (S1 and S2) to each of two target animals (T1 and T2, which were either mothers or independent offspring). These tapes consisted of

whistles of the respective independent offspring or mothers of the two target animals. For example, mother T1 would be predicted to respond more strongly to playback of whistles of her own independent offspring (S1) than to whistles of a familiar individual of similar age (S2). Similarly, mother T2 would be predicted to respond more strongly to playback of whistles of her own independent offspring (S2) than to those of S1.

In playbacks where T1 and T2 were females from different bands, stimuli consisted of whistles from a member of the target animal's own female band, and whistles from a member of another female band, which was known to the target animal but was not as close an associate.

We chose pairs of stimuli to control for familiarity. For example, in the mother–independent offspring playbacks, pairs were chosen such that mothers were from the same female band (Wells 1991). Where possible, we matched independent offspring for age in both target and stimulus pairs. In most cases, this ensured a fairly high level of association between the paired animals, because, within a band, mothers with similar-aged calves tend to associate together (Wells 1991, unpublished data). In addition, similar-aged independent offspring tend to associate together (Wells 1991, unpublished data). In all cases, the target animals were familiar with each of the animals whose whistles were used as stimuli. Coefficients of association between target and stimulus animals for 11 playback pairs are shown in Table 1. We calculated coefficients of association by dividing the number of sightings in which the two animals were together by the total number of sightings of each individual, either alone or together. Values for mother–independent offspring pairs encompass all sightings that occurred from the time the offspring became independent up until the time of the experiment. In most cases, coefficients of association between target and stimulus animals were similar across stimulus pairs. Coefficients of association between females in the same female band (calculated using data from all sightings up until the year of a given experiment) were somewhat higher than those between females of different bands (Table 1).

In total, 20 different individuals were used as target animals in the 11 paired trials. Two individuals were used as target animals in two different experiments in different years (Table 1: FB9 in trials 1 and 5; FB84 in trials 7 and 8) to increase the number of pairs of similar-aged animals.

Stimulus Preparation

We made recordings for use as stimuli in the experiments during temporary captures in previous years by placing a suction cup hydrophone directly on the head of each individual. This technique allowed us to obtain recordings of high quality with little background noise. We recorded whistle exchanges between two individuals on two separate channels of the same recorder.

We used the following procedure in preparing stimulus tapes.

(1) We monitored recordings of individuals whose whistles were to be used as stimuli on a Kay Elemetrics Corporation (Pine Brook, New Jersey) Model 5500 DSP sonagraph.

(2) We selected stimuli from recording sessions that involved whistle exchanges with another individual to preserve the natural timing of whistle exchanges in a capture situation.

(3) We selected a portion of an exchange that contained as little extraneous noise and/or feedthrough from the other channel as possible.

(4) We filtered out frequencies below the minimum frequency of the whistle, and stored a 47.5-s filtered section in the buffer of the sonagraph (this is the maximum buffer size when digitizing at 32 kHz).

(5) We then edited out any extraneous noise or feedthrough from the other channel, and inserted sections of typical ambient noise of the same length to preserve the original timing.

(6) To control the loudness of the stimuli, we constrained the loudest part of each stimulus sequence to a maximum amplitude.

(7) We then recorded the audio output of the sonagraph on a Marantz PMD-430 stereo cassette-recorder. We recorded all tapes at the same input level.

We selected the level on the amplifier that we used to power the playback speaker in the experiments after experimentation with a vocalight (Tyack 1985).
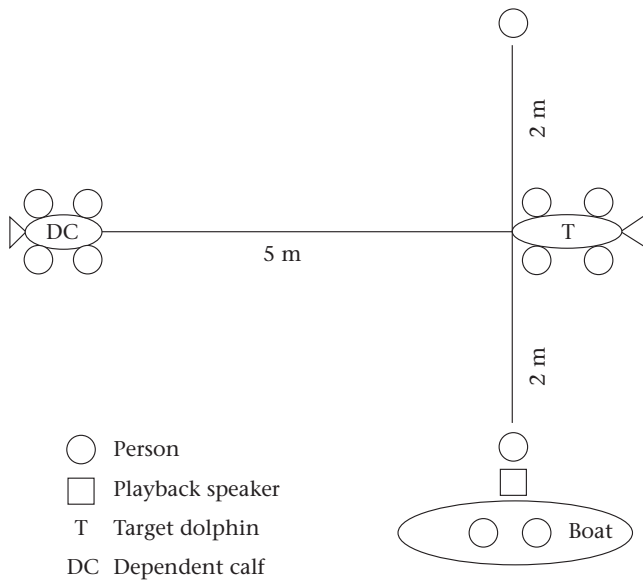
Table 1. Coefficients of association between individuals used as target and stimulus animals in 11 paired trials

Paired trial no.	Target animal ID (year born)	Stimulus animal 1	Stimulus animal 2
	Independent offspring		
1	FB6 (1984)	0.00*	0.00
	FB9 (1984)	0.08	0.23*
2	FB11 (1984)	0.08*	0.06
	FB7 (1984)	0.03	0.05*
3	FB93 (1985)	0.27*	0.03
	FB150 (1985)	NA	NA*
4	FB59 (~1974)	0.05*	0.06
	FB62 (1973)	0.05	0.06*
5	FB9 (1984)	0.17*	0.09
	FB55 (1986)	0.08	0.26*
6	FB92 (1988)	0.03*	0.00
	FB1 (1991)	NA	NA*
	Mothers		
7	FB19	0.08†	0.03
	FB84	0.06	0.05†
8	FB43	0.08†	0.03
	FB84	0.03	0.06†
9	FB5	0.25†	0.00
	FB63	0.16	0.16†
10	FB35	0.10†	0.00
	FB153	0.05	0.05†
	Other females		
11	FB57	0.20‡	0.03
	FB15	0.04	0.10‡

NA indicates that experiments were conducted shortly after the calf became independent; thus there are no available data.
*Independent offspring of the target animal.
†Mother of the target animal.
‡Member of the same female band as the target animal.

Figure 1. Schematic drawing of the layout for the playback experiments (not drawn to scale).

Vocalights contain light-emitting diodes (LEDs) which light up in proportion to the loudness of a sound. At the New England Aquarium, we held a vocalight at a distance of about 1 m from a dolphin whistling at typical levels, and observed the number of LEDs (2–4) illuminated. The level on the amplifier was set (before the experiments) when the same number of LEDs were illuminated at a distance of 1 m from the playback speaker. This approximates typical source levels of wild *Tursiops*, which have been measured at 150–173 dB re 1 μPa at 1 m (Fish & Turl 1976).

Protocol

Experiments consisted of five phases: (1) a 125-s pretrial period; (2) a 30-s playback; (3) a 305-s post-trial period; (4) another 30-s playback; and (5) another 305-s post-trial period. Playback apparatus included a University Sound underwater speaker, and a Marantz PMD-430 stereo cassette deck attached to a 90-W amplifier. The underwater speaker was the greatest constraint on the frequency response of the system, as it reproduced sounds faithfully only up to 11 kHz. However, because a great deal of the energy contained in most *Tursiops'* whistles is present below 11 kHz, and because the target animals did respond strongly (see Results), it appears that this speaker produced a satisfactory reproduction of the whistles. We made recordings of each playback with a Panasonic AG-6400 video cassette-recorder, and hydrophones designed for recording dolphin whistles (Tyack 1985). We videotaped all five phases for later analysis.

To facilitate measurements of head turns towards and away from the speaker, four people were stationed at each corner around the target animal and each held a measuring tape in the air, forming right angles above the target animal (Fig. 1). If the target animal was a female with a dependent calf, we positioned the calf directly opposite

(facing) the female (in the position marked 'DC' in Fig. 1). We held the female at a 90° angle to the playback speaker so that orientations of the target animal towards the speaker and towards the dependent calf could be differentiated. In one case, we caught a pair of target animals simultaneously with a third animal, which we then held in the dependent calf (DC) position for each of the playback experiments. This was done so that the paired experiments were conducted under as similar conditions as possible. Both experiments were conducted when the two target animals were not able to see or hear one another (one was being processed on the deck of a boat during playback to the other). In all other cases, only one member of a pair was caught at a time, and no animal was held in the dependent calf position unless it was a dependent calf of the target animal.

Within each pair, the order of stimulus presentations was the same, so the first stimulus was the one predicted to evoke a higher response for only one member of each pair. Thus, if either member of the pair showed a tendency to respond more strongly to the first stimulus (a 'surprise' effect), this would weaken the contrast between the two animals in each pair in the statistical analysis.

Analysis

We assessed the strength of the target animals' responses to playbacks by counting the number of head turns towards the speaker. Although we scored whistle production as a response to playback, there were no significant differences between the playback stimuli (Sayigh 1992). Head turns towards the playback speaker could represent efforts by the target animal to echolocate on the source of the whistles and/or to locate the source visually. Because echolocation is highly directional (approximately a 10° beamwidth; Au 1993), an animal must be oriented in the direction of an object of interest to 'visualize' it effectively. (We prevented target animals from echolocating directly onto the playback speaker by placing the speaker behind a person's body.) Thus, we counted head turns to determine whether target animals turned more in response to the predicted stimuli.

We scored head turns greater than 20° either towards or away from the playback speaker throughout the entire experiment. Anything less than 20° was not counted as a turn, because the animals frequently moved back and forth within a 20° turning radius.

The first author (L.S.S.) and a research assistant who was not familiar with any of the animals or their whistles scored the videotapes of four pairs of experiments completed between 1989 and 1991. Neither scorer knew which stimulus was predicted to evoke the stronger response while viewing the tapes. The two sets of scores were remarkably consistent. Out of 80 possible scores (8 experiments (4 pairs) × 5 'phases' each (pretrial, playback 1, etc.) × 2 scores for both turns towards and away from the speaker), 49% were exact matches, and 89% differed by two or fewer turns. Because seven additional pairs of experiments that were completed between 1992 and 1994 were scored only by L.S.S., we used only her scores for all 11 pairs of experiments for the sake of consistency.

She viewed the videotapes in random order without knowledge of the target animal or the order of stimulus presentation.

We combined head turns that occurred during the 30-s playback period with those that occurred during the ensuing post-trial interval for analysis. We compared turns towards the speaker in response to the two playback stimuli within each pair to test the hypothesis that the predicted stimuli would elicit a greater response (against the null hypothesis that there would be no difference in responses to the two stimuli). As an additional control, we analysed data on turns away from the speaker; we predicted that there would be no difference in the responses to the two stimuli. We analysed the data with the log-odds ratio for testing one-sided hypotheses (Everitt 1977; see Appendix).

To obtain an overall P value for the experiments, we set aside the paired design and performed a one-sample Wilcoxon signed-ranks test on the differences between the number of head turns that each dolphin made towards the predicted and the nonpredicted stimuli. We performed a similar test for head turns away from the speaker, and in this analysis we discarded difference values of zero and reduced the sample size accordingly (Pratt & Gibbons 1981).

RESULTS

Sample Size

From 1989 to 1994, we completed 38 playback experiments, which included 21 playbacks to independent offspring, 11 playbacks to mothers, and six playbacks to females from different bands (hereafter called 'other females'). However, the paired playback for 12 of these experiments could not be completed. Three target animals required to complete the pairs died, and three were not caught during the experiments. Six experiments were aborted after only half of the experiment had been completed because one of the stimulus animals died or disappeared, and playback of whistles of dead or possibly dead animals could have confounded our results. The remaining 26 experiments represent completed paired trials, although one was discarded due to equipment failure, and another was discarded due to difficulties in obtaining reliable scores of head turns. Thus, our results are based on 11 paired trials, consisting of six pairs of independent offspring, four pairs of mothers, and one pair of 'other females' (Table 1).

Analysis of Completed Pairs

The number of head turns towards the playback speaker was a strong indicator of an animal's response to the playbacks. Target mothers and offspring turned towards the speaker significantly more often during and after presentation of the predicted versus the non-predicted stimuli (Wilcoxon signed-ranks test: $S^+=162$, $N=20$, $P<0.02$; we excluded the paired trial involving 'other females' from this analysis; see Table 2). In

Table 2. Total head turns towards and away from the playback speaker in 11 paired trials

Paired trial no.	Target pairs	Pretrial (125 s)	Playback 1 (335 s)	Playback 2 (335 s)
	Independent offspring			
1	FB6			
	Towards	6	12*	8
	Away	5	13*	13
	FB9			
	Towards	1	1	9*
	Away	1	2	1*
2	FB11			
	Towards	1	6*	1
	Away	4	4*	2
	FB7			
	Towards	12	43	44*
	Away	6	17	15*
3	FB93			
	Towards	10	21*	7
	Away	5	7*	8
	FB150			
	Towards	4	22	18*
	Away	4	12	9*
4	FB59			
	Towards	6	14*	3
	Away	1	0*	1
	FB62			
	Towards	12	31	29*
	Away	8	23	23*
5	FB9			
	Towards	0	3*	7
	Away	0	5*	5
	FB55			
	Towards	1	3	6*
	Away	0	0	2*
6	FB92			
	Towards	5	15*	7
	Away	8	23*	15
	FB1			
	Towards	2	10	3*
	Away	2	5	2*
	Mothers			
7	FB19			
	Towards	2	18*	10
	Away	4	9*	7
	FB84			
	Towards	10	22	24*
	Away	13	18	24*
8	FB43			
	Towards	12	32*	23
	Away	9 (1)	24*	15
	FB84			
	Towards	11	29	45*
	Away	9	14	10*
9	FB5			
	Towards	12 (2)	27*	20
	Away	10 (4)	22*	20
	FB63			
	Towards	3	9	4*
	Away	1	11	8*
10	FB35			
	Towards	10 (2)	31*	28
	Away	7	7*	6
	FB153			
	Towards	11	44	40*
	Away	5	15	15*
	Other females			
11	FB57			
	Towards	1	3*	1
	Away	0	0*	0
	FB15			
	Towards	8	9	21*
	Away	0	1	0*

*Stimulus predicted to evoke a higher response.

Table 3. Log-odds ratio analysis of total turns towards the speaker in response to the predicted versus the other stimulus in 11 paired trials

Paired trial no.	Target pair	Predicted stimulus	Other stimulus	Log-odds ratio	P value
	Independent offspring				
1	FB6	12	8	13.5	0.01
	FB9	9	1		
2	FB11	6	1	6.1	0.05
	FB7	44	43		
3	FB93	21	7	2.5	0.05
	FB150	18	22		
4	FB59	14	3	4.4	0.02
	FB62	29	31		
5	FB9	3	7	0.9	0.56
	FB55	6	3		
6	FB92	15	7	0.6	0.71
	FB1	3	10		
	Mothers				
7	FB19	18	10	2.0	0.09
	FB84	24	22		
8	FB43	32	23	2.2	0.02
	FB84	45	29		
9	FB5	27	20	0.6	0.78
	FB63	4	9		
10	FB35	31	28	1.0	0.49
	FB153	40	44		
	Other females				
11	FB57	3	1	7.0	0.06
	FB15	21	9		

playbacks to mothers and independent offspring, the stimuli predicted to evoke a stronger response were the independent offspring and mother, respectively. There were no significant differences in turns away from the speaker (Wilcoxon signed-ranks test: $S^+=75$; $N=16$, $P>0.10$; we excluded four cases in which the difference in head turns between predicted and nonpredicted stimuli equalled zero, as well as the paired trial involving 'other females'; see Table 2).

In Table 3, the data are condensed to show only turns towards the speaker during the two playback periods. With these data, we calculated the log-odds ratio and its associated P value for each paired trial. Four of the six trials in which independent offspring were target animals were significant at a level of $P≤0.05$, whereas only one of the four trials in which mothers were target animals was significant at this level. Because only one paired trial was conducted with females from different bands ('other females'), we excluded these experiments from the Wilcoxon analysis; however, the log-odds ratio for this pair bordered on significance ($P=0.06$; Table 3).

Head turns that occurred during the pretrial period (Table 2) were not factored into the analysis. These turns probably resulted from the animals scanning their relatively unfamiliar surroundings. The playback design (Fig. 1) required that the target animals be held in place with people stationed at various positions nearby. In 10 of 24 playbacks, the number of head turns declined between the first and second minute of the pretrial period, indicating that the animals may have been acclimating to their surroundings. In five playbacks there was no change

in number of turns between the first and second minute, and there were increases in the other nine. Even if the animals were not yet acclimated to their surroundings, the paired design of these experiments would have corrected for any tendency of the animals to respond more strongly to the first stimulus (see Methods and Appendix).

DISCUSSION

These playback experiments demonstrate that bottlenose dolphins are capable of discriminating between whistles of different familiar individuals, and that they recognize the predicted individual in symmetrical paired experiments. Target animals in these experiments showed a significantly stronger head-turning response to the predicted stimulus, which was either the mother or an independent offspring.

All mothers used as targets and stimuli had had new calves since their association with the relevant stimulus or target offspring. Offspring used as targets and stimuli had been independent for periods ranging from 1 month to 14 years and most had formed close associations with other individuals. Since separation from their mothers, the independent offspring showed low rates of association with their mothers and with the other adult females used in the experiments. Thus, it is highly unlikely that discriminations were based strictly on a familiar versus unfamiliar basis, wherein individuals simply responded more strongly to frequently heard stimuli.

In the trial involving females from different bands ('other females'), discriminations also involved more

than a simple, dichotomous (i.e. familiar versus unfamiliar) classification. Both females whose whistles were used as stimuli associated with the target animals at similar rates. Both target animals had dependent offspring, yet both also responded preferentially to whistles of a member of their female band. More experiments such as these promise to provide even stronger evidence for individual recognition in bottlenose dolphins.

Overall, what is known of bottlenose dolphin behaviour and social structure supports the idea that individuals do have concepts of one another as individuals and that they track the history of their individual relationships. Many primate social relationships are based upon knowledge of the histories of interactions among individuals in their social group (e.g. Dasser 1985; Essock-Vitale & Seyfarth 1986). The long-term, individually specific bonds that characterize the fission–fusion societies of bottlenose dolphins provide parallels with many primate societies (e.g. in alliance formations; see Connor et al. 1992). Dolphins interact repeatedly with many different individuals over periods of many years. It seems likely that recognition of individuals is important in maintaining these long-term associations, and that signature whistles function in effecting this recognition.

Although it seems highly likely that the individually distinctive frequency contour of the signature whistle is providing information on individual identity, the possibility that other cues may provide this information cannot be ruled out. For example, Tyack & Sayigh (1997) pointed out that variations in the vocal tracts of animals may lead to vocal variability among individuals; these voice cues can lead to individual recognition in terrestrial animals such as humans. However, Tyack & Sayigh (1997) speculated that the gas-filled nasal sacs believed to be the source of vocalizations in dolphins (Cranford et al. 1996) may not provide reliable cues for individual recognition, because the shape of the nasal sacs is likely to be altered by pressure changes that take place during dives. In fact, Ridgway et al. (1997) documented changes in whistles produced by beluga whales, *Delphinapterus leucas*, at varying depths. Therefore, diving mammals may have to produce signals that are individually distinctive to reliably signal individual identity. Playback experiments utilizing synthetic and natural whistles are needed to test which acoustic features carry the individually distinctive information in whistles.

As in other studies of individual recognition (e.g. Cheney & Seyfarth 1980), there was a considerable amount of interindividual variation in responses in our study of bottlenose dolphins. This may relate to the immediate behavioural state and/or level of arousal of an animal. Also, because both playback stimuli in every experiment were recorded from living animals present within the community, it seems possible that recent experiences (e.g. aggressive or affiliative interactions) involving the target and stimulus animals could also affect responses. It is also notable that more paired trials involving independent offspring as target animals (four of six) were statistically significant than were trials with mothers as target animals (one of four). It is possible that a mother investing in a new calf may not be strongly motivated to respond to her independent offspring.

Thus, negative results from these experiments cannot differentiate between a lack of motivation to attend to kin or associates versus an inability to recognize them. However, positive results, in the form of head turns towards the speaker, suggest not only that dolphins recognize their kin or associates, but also that they are motivated to respond to them. The very fact that target animals did respond to playbacks of kin or associates implies that individually specific social relationships are important to dolphins. In fact, similar results for playbacks to unrelated vervet monkeys have been widely cited as evidence for reciprocal altruism (Seyfarth & Cheney 1984). Although it is premature to draw similar conclusions from these data, they do suggest that playback experiments would be a promising technique for further study of cetacean communication and behaviour. The results presented here provide a strong basis for integrating work on individually specific social relationships and communication of dolphins.

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Table A1. Format of two-by-two contingency table for each paired trial

	Stimulus 1	Stimulus 2
Target animal 1		
Target animal 2		

Appendix

Analysis of paired trials using the log-odds ratio (Everitt 1977)

The entries in Table A1 are the number of times target animal *i* responds to stimulus *j*. Suppose that stimulus 1 is the hypothesized favoured stimulus for target animal 1 and stimulus 2 is the hypothesized favoured stimulus for target animal 2. Let π_{ij} be the unknown true probability that animal *i* will respond to stimulus *j*. The odds that animal 1 will respond to stimulus 1 is defined as $\theta_1 = \pi_{11}/\pi_{12}$. Similarly, the odds that animal 2 will respond to stimulus 1 is defined as $\theta_2 = \pi_{21}/\pi_{22}$. The odds ratio ($\theta$) is defined as:

$$\theta = \theta_1/\theta_2.$$

The null hypothesis (H_0) is that $\theta = 1$; that is, that both animals will respond in the same way to both playbacks. This can be tested against the one-sided alternative hypothesis (H_1) that $\theta > 1$; that is, that target animal 1 will respond more strongly to stimulus 1 than to stimulus 2 and/or that target animal 2 will respond more strongly to stimulus 2 than to stimulus 1. An approximate test can be based on the estimate:

$$\theta = n_{11}n_{22}/n_{12}n_{21}$$

where n_{ij} is the observed count in row *i*, column *j*. The test is to reject H_0 in favour of H_1 at significance level α if:

$$\log\theta > z_\alpha\sigma$$

where z_α is the upper α-quantile of the standard normal distribution function and

$$\sigma = \left(\sum_i\sum_j\frac{1}{n_{ij}}\right)^{1/2}$$

If any n_{ij} equals 0, θ will equal 0 or ∞. This problem can be avoided by adding 0.5 to all of the observed counts in forming θ.