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Whistle Convergence among Allied Male Bottlenose Dolphins (Delphinidae, *Tursiops* sp.)

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Smolker, R. & Pepper, J. W. 1999: Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). *Ethology* **105**, 595–618.

Abstract

Dolphins are adept at learning new vocalizations (whistles) throughout life, an ability thus far demonstrated in few nonhuman mammals. In dolphins, this ability is well documented in captivity but poorly studied in the wild, and little is known of its role in natural social behavior. This study documents the previously unknown phenomenon of whistle convergence among habituated free-living male bottlenose dolphins (*Tursiops* sp.). Over a 4 yr study period, three male subjects formed an alliance, spending most of their time together and cooperating to herd females. Within individuals, whistle repertoires were more variable than expected based on previous studies, mostly performed with captive dolphins, but became less so during the course of the study. Among individuals, the distinctiveness of individual repertoires decreased such that the three males were virtually indistinguishable by the end of the study. Initially, some whistle types were shared. By the end of the study, the three males had formed a close alliance, and had all converged on one particular shared whistle form which they had rarely produced before forming the alliance. The results are discussed in terms of their implications for the prevailing ‘signature whistle’ hypothesis, as well as possible mechanisms and functional significance of whistle convergence among cooperating males.

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Introduction

Vocal learning is central to the question of how complex communication systems evolve and has a peculiar taxonomic distribution. It is well documented in many songbird species (for reviews, see Kroodsma 1982, Kroodsma & Baylis 1982 and Catchpole & Slater 1995) and is highly developed in humans. But among

nonhuman primates, the best-studied mammalian group in this regard, evidence is meager. Learning does seem to play a role in the development of comprehension and correct usage of vocalizations in some nonhuman primates (Seyfarth et al. 1980; Seyfarth & Cheney 1986; Hauser 1988), but production of appropriate species-specific calls appears to develop largely without learning (Talmage-Riggs et al. 1972; Winter et al. 1973; Leiblich et al. 1980; Seyfarth & Cheney 1986; Owren et al. 1992; but see Masataka & Fujita (1989) and a review in Snowdon & Elowson (1992)). Although vocal learning has rarely been studied in detail in other mammal groups, little evidence for it exists thus far (but see Esser (1994) with regards to bats; Boughman 1997). Mounting evidence for vocal learning abilities in dolphins is, therefore, of considerable interest.

Most studies of dolphin whistles (involving recordings of hundreds of dolphins where whistles could be attributed to individuals) have found that individuals possess unique 'signature' whistles, and that 60–100% of the whistles emitted by an individual are its signature (Caldwell & Caldwell 1965, 1968; Tyack 1986; Sayigh et al. 1990, 1995; Caldwell et al. 1990; Smolker et al. 1993; Janik & Slater 1998). Adult signatures are highly variable across individuals. Dolphins are not born with their signature whistles, but rather, infants produce unsteretyped whistles at birth and gradually develop a signature, usually by about 6 mo of age (Caldwell & Caldwell 1979; Caldwell et al. 1990; Smolker, unpubl. data, but see McCowan & Reiss 1995b). The structure of the whistle adopted by an infant is not heritable (Sayigh 1992) and appears to be learned.

In addition to learning their signatures, dolphins are capable of vocal imitation. Captive dolphins spontaneously imitate whistles to which they are exposed (Caldwell & Caldwell 1972; Reiss & McCowan 1993) and have been trained to imitate computer-generated whistles and to use these as 'labels' for objects in their tank (Richards et al. 1984; Richards 1986).

It is not clear what function vocal learning serves in dolphins. As noted above, the predominant hypothesis for the function of dolphin whistles is that they serve as 'signatures', to convey the individual identity of the caller. However, many mammals produce individually distinctive vocalizations that are not learned (e.g. Scherrer & Wilkinson 1993). Learning is not essential to the development of individually distinctive 'signature' vocalizations, and the possession of individual signatures does not explain the functional significance of the dolphin's vocal learning and imitation skills. Tyack (1986) suggested that dolphins may imitate the signatures of conspecifics as a way to establish contact. If so, this could account for at least some of the dolphins' learning and imitation skills.

A recent study by McCowan & Reiss (1995b) suggests that dolphin whistle repertoires may be more complex than previously assumed. They recorded 10 individuals from three different captive social groups and found that the dolphins did not appear to have individually distinctive signatures. Instead, they produced variable whistle repertoires (low levels of individual stereotypy), and one whistle type predominated in the repertoires of all individuals across the three different (isolated) social groups. Some older studies also reported more variable whistle repertoires (Dreher & Evans 1964; Lang & Smith 1965; Kaznadzei et al. 1976; Gish

1979). McCowan & Reiss attribute this discrepancy between their results and those of many other studies to the fact that the dolphins were less stressed. They attributed whistles to individuals by means of bubbles emitted from the blowhole during production rather than by separation or capture.

The drawback of captive studies, even where subjects are freely interacting, is that they may not reveal how whistles are integrated into the natural behavior of the animals. Vocal learning in birds, for example, often depends on patterns of social association and interaction, which are severely disrupted by captivity (Kroodsma & Pickert 1984; Baptista & Petrinovich 1984; Baptista & Morton 1988). Captive dolphin groups are generally small and stable, composed of a few individuals housed together for husbandry and display purposes, quite different from the fission–fusion social organization typical of most wild dolphin societies (Wells et al. 1987; Ballance 1990; Smolker et al. 1992).

To investigate how dolphins use whistles in their natural social behavior, it is essential to study freely interacting wild animals. It is, however, extremely difficult to attribute whistles to individuals in the wild. We took advantage of a unique situation in which several dolphins regularly entered shallow water at a campground called Monkey Mia, where they were provisioned with fish, but remained integrated into the larger (unprovisioned) population in the area. This situation provided a rare opportunity to attribute whistles to individual wild dolphins, and to collect detailed long-term data on their relationships and behavior.

Virtually all adult males in this population were members of ‘alliances’ of two to three males (in some cases more) that persisted for many years (Smolker et al. 1992). Alliances are characterized by very high levels of association and close behavioral synchrony. They also cooperate extensively in the contexts of herding females and competing with other males (Connor et al. 1992a,b). Herding of females is often aggressive and is presumably a strategy to monopolize mating opportunities (Connor et al. 1992a,b).

Herding typically begins with a ‘capture’, in which the males chase the female, followed by a period of association with her, lasting from an hour to several weeks. Males sometimes perform elaborate displays around herded females, mount the female, or ‘inspect’ her genital area, and they tend to swim in a rank formation behind her. Females sometimes attempt to escape from herding males by bolting at high speed away from them. Males enforce herding using a distinctive vocalization (‘pops’; Connor & Smolker 1996), thought to be an aggressive threat, as well as other forms of aggression, including head jerks, charging, hitting, and chasing.

We examined the changing patterns of social and vocal behavior among three males (Snubnose, Bibi and Sicklefins), who were the focus of intensive observation during 1985–1988. During the study the three subjects formed and solidified their relationship as an alliance and simultaneously converged on producing very similar whistles. These findings should be interpreted cautiously because they are based on one three-member alliance. However, they document a previously unknown phenomenon that may be crucial to understanding the function of vocal learning in dolphins.

Methods

Study Site and General Methods

The study was conducted at Monkey Mia, in Shark Bay, Western Australia, where several dolphins have come into very shallow (< 1 m) water at a 'provisioning area' on a daily basis since at least the early 1960s (Connor & Smolker 1985). During the study period, eight dolphins, including five females and three males, visited regularly. We collected data on the three males, Snubnose (Snu), Bibi (Bib) and Sicklefins (Sic), during four field seasons between 1985 and 1988. Snu and Bib had been visiting the provisioning area and accepting fish handouts for several years prior to the onset of this study (R. Smolker, unpubl. data). Bib was the offspring of a provisioned female who died just prior to this study. Sic first began routinely visiting the provisioning area and taking fish handouts in 1987. The three males were part of a larger nonprovisioned population with which they interacted extensively, and they spent much of their time away from the provisioning area (Smolker et al. 1992).

At the provisioning area the males engaged in a variety of behavior patterns, including taking fish handouts from people and interacting with each other. They also herded nonprovisioned females both at and away from the provisioning area (Connor et al. 1992a,b). The dolphins were never restrained, and interacted with nonprovisioned conspecifics and with each other in a manner similar to interactions occurring offshore. (For further details of the study site, animals, and general methods, see Smolker et al. 1992, 1993, Connor et al. 1992a,b, Richards 1996 and Mann & Smuts 1998.)

Behavioral Observations

Dolphins in Shark Bay form small groups or 'parties', the membership of which changes frequently as individuals join and leave. We estimated the amount of time dolphins spent in association with each other away from the provisioning area as per Smolker et al. (1992), using party sighting data collected from small boats. Party membership was assessed within the first 5 min of encountering dolphins. Dolphins were counted as party members if they were within 10 m of any other party member at any point during the 5 min interval. We excluded solitary dolphins and parties traveling rapidly, because it was difficult to identify dolphins in these contexts. We also eliminated foraging assemblages and parties sighted at or within 200 m of the provisioning area because these were likely to reflect attraction to food rather than to each other. To avoid nonindependence of data due to resampling the same parties, we also discarded from the dataset any parties in which any member had been recorded less than 1 h previously or in which the party composition had changed by less than 30% since an earlier sighting the same day. To estimate the proportion of time that each pair of dolphins spent together during each year, we used the 'half-weight' association index (Cairns & Schwager 1987).

We defined herding events as per Connor et al. (1992a), based on observing any of the following behavior patterns: 1. capture; 2. female bolts; 3. male producing 'pop' vocalizations; 4. aggressive charge, hit, bite or head jerk.

Recording Whistles

We recorded whistles while standing in shallow (< 1.5 m) water among the provisioned dolphins, using a Sony TCD5M cassette recorder with various hydrophones, all providing flat response (± 3 dB) to about 16 kHz. Because the water was shallow, the dolphins typically had their heads at or just below the water surface. This made it possible to localize the sound source by ear, and thereby attribute whistles to particular individuals. Most recordings were made using two observers. One person stood still and operated the tape recorder, describing dolphin behavior on one channel while recording dolphin sounds through a hydrophone on the second channel. A second observer moved among the dolphins locating the source of whistles and pointing these out to the tape-recorder operator. During four 6 mo field seasons over 4 yr, we recorded 1691 whistles attributed to the three male subjects on 139 different days.

Acoustic Analysis

Whistles were digitized at a sampling rate of 40 000 points/s using an IBM compatible microcomputer equipped with a DT2821 analog/digital board (Data Translation, Marlboro) and the SIGNAL version 2.2 digital sound analysis system (Engineering Design, Belmont). All acoustic analyses were also conducted using SIGNAL. For visual inspection, we generated spectrograms of each whistle using a 256 point fast Fourier transform, with a frequency resolution of 156 Hz and time resolution of 6.4 ms.

The problem of defining what constitutes a single whistle has received little attention. Dolphins sometimes produce whistles that include short gaps in the sound production. Using extrapolation, these are usually treated as single whistles (Lang & Smith 1965; Caldwell et al. 1990). However, in attempting to follow this procedure we found it difficult to reliably determine whether a given gap fell within a single whistle, or between two different whistles. Instead, we treated all gaps as terminating the preceding whistle, and defined whistles as unbroken lines on spectrograms.

Following the approach of McCowan (1995), our analyses were performed on whistle 'contours' rather than the original recordings. A whistle's contour was defined as its dominant frequency as a function of time. Contours thus retain information about the pattern of frequency modulation, while discarding any noise, harmonics, or amplitude fluctuations present in the original waveform.

To extract contours from digitized whistles we used a program written in the SIGNAL command language. The program displayed each whistle as a spectrogram, and allowed an operator to trace its contour using an on-screen cursor controlled by a mouse. The program divided the resulting digitized contour into 100 equal-length segments, and stored the mean frequency of each. These lower

resolution contours were imported into the SPSS statistics program for further analysis.

Quantifying Pairwise Whistle Similarity

It was not possible with this whistle sample to visually compare spectrographs due to a large and variable sample size with high degrees of graded variation. To quantify similarity among whistle contours, we modified the approach described by McCowan (1995). For each pair of contours, we generated a Pearson product-moment correlation across 100 pairs of frequency values. Dividing each whistle into an equal number of segments makes it possible to compare contours with similar shapes but different absolute durations. The Pearson correlations make it possible to compare whistles with similar shapes but different absolute frequency characteristics. This method measures similarity in contour shapes irrespective of absolute time–frequency characteristics. Because we considered negatively correlated contours to be no more dissimilar than those with zero correlation, we deviated from McCowan's method in converting negative correlations to zero. The resulting value, which we refer to as a 'similarity index', ranges from zero for a very dissimilar pair of whistles, to one for a pair of whistles with an identical contour shape.

To graphically illustrate patterns of similarity among whistles, we conducted multidimensional scaling (MDS) analyses of matrices of similarity indices. Because SPSS cannot perform MDS analyses on more than 100 cases, we randomly sub-sampled 100 whistles for these analyses. We calculated a matrix of similarity indices, transformed them into distances by subtracting them from one, and subjected the resulting matrix to MDS analysis using default parameters.

Quantifying Repertoire Similarity and Distinctiveness

In order to examine changes in the stereotypy of individual repertoires, we needed to quantify whistle similarity within repertoires. To do this we selected the subset of all whistles from a given individual in a given year and calculated the similarity indices for all possible whistle pairs. (For n whistles the result was a square half-matrix containing $n(n-1)/2$ values.) We used the average of these similarity indices as a measure of self-similarity or acoustic stereotypy.

To quantify acoustic similarity between individuals, we used a similar approach. We first selected two subsets of contours, representing all whistles produced by two males in the same year. We then calculated the similarity indices for all possible pairs of whistles consisting of one from each male. (For N and M whistles from the two males, respectively, the result was a rectangular matrix containing $N*M$ similarity indices.) We used the average of these similarity indices as our measure of acoustic similarity between the two individuals.

To quantify individual distinctiveness, we used a 'distinctiveness index' that reflected the difference between similarity to self and similarity to others in a given year. We first calculated the subject's self-similarity as described above. We then calculated its similarity to each of the other recorded males (one other male in

1985–1986, and two in 1987–1988), as described above, and averaged these values. Finally, we subtracted the subject's average similarity to others from its similarity to self. The resulting distinctiveness index is zero if an individual's whistles are as similar to those of others as they are to other examples from its own repertoire. As individual repertoires become more distinct the index becomes increasingly positive.

Categorizing Whistles

To sort whistles into categories, we used a clustering approach inspired by McCowan (1995). We analyzed the matrix of similarity indices among all 1691 whistle contours by hierarchical clustering analysis using the 'within-groups average' linkage method. To determine how many categories to use, we followed Podos et al. (1992) in using the 'moat index' (Wirth et al. 1966) to assess how well each possible level of clustering corresponded to natural categories in the data. The moat index is calculated by subtracting each cluster's longest within-cluster linkage distance from its shortest between-cluster linkage distance and averaging these differences. Thus, the higher the moat index, the more internally cohesive and externally isolated the clusters are. We entered the agglomeration schedule generated by the cluster analysis into a customized computer spreadsheet to automatically calculate the moat index for each possible number of clusters, and selected the cluster solution with the highest moat index¹. This solution had 101 clusters and we designated each of these as a 'whistle type'. Of the 101 whistle types, 18 contained at least 10 whistles, and together these accounted for 91.7% of the total sample. We designated these as 'major' whistle types, and the remaining 83 whistle types containing fewer than 10 whistles each, as 'minor' whistle types.

Although useful for summarizing large datasets, it is unlikely that this classification scheme resulted in 'natural categories' (those perceptually relevant to the dolphins). Note that our basic results on repertoire stereotypy, similarity and distinctiveness do not rely on classification results.

Statistical Analyses

To quantify changes over time in both acoustical and social proximity, we used Spearman rank-order correlations. We report *p* values to help evaluate trends,

¹Our use of hierarchical clustering had two advantages over the K-means technique used by McCowan. Hierarchical clustering can operate directly on a similarity matrix, eliminating the need to reduce similarity indices to a smaller number of variables through principle components analysis before clustering, which loses some of the available information. Hierarchical clustering also simplifies the process of choosing the optimal number of clusters. With K-means clustering this required a separate analysis for every possible number of clusters, followed by visual evaluation of plots from each analysis. This was feasible for McCowan's dataset of 20 whistles with 19 possible clustering solutions, but not for our sample of 1691 whistles with 1690 possible clustering solutions. Instead, a single hierarchical clustering analysis produced the agglomeration schedule needed to automatically calculate a moat index for each possible number of clusters, making it easy to select the optimal clustering solution.

but these should be considered cautiously given that pairwise proximities among the three males are not mutually independent. All statistical analyses were performed using SPSS for UNIX release 5.0 (SPSS Inc., Chicago).

Results

Alliance Formation

The defining features of male alliances are mutually high association levels and cooperative herding of females (Smolker et al. 1992; Connor et al. 1992a,b). Over the 4 yr of the study, the three male subjects increased both of these behavior patterns dramatically (Fig. 1).

In 1985 and 1986 Sic was often seen offshore in association with various other dolphins. He occasionally approached the provisioning area with Snu and Bib, but did not linger, accept fish handouts, or permit human contact. Starting in 1987 he became much more habituated to humans and began to associate frequently with Snu and Bib, both at the provisioning area and offshore. The three males substantially increased the amount of time they spent together across the 4 yr of the study. By 1987 they were together most of the time. The trend towards increasing association through time was highly significant (12 pair-years, $R_S = 0.756$, $p = 0.004$).

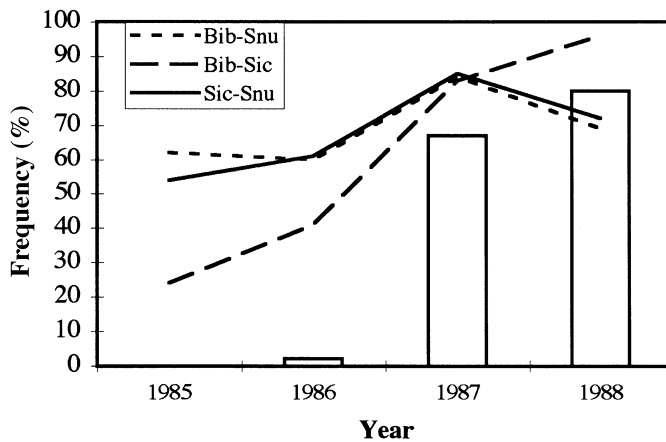


Fig. 1. Rates of association (lines) and herding (bars) by year. The lines represent the estimated proportion of time two individuals were together, based on half-weight association indices calculated using co-occurrence in parties. Party sighting data were collected away from the provisioning area 6 May–23 Aug. 1985, 18 May–23 Aug. 1986, 8 Mar.–11 Nov. 1987 and 28 Mar.–2 Dec. 1988. The bars represent the number of days in which at least two of the males were observed herding females together, as a proportion of the number of days in which any of them were sighted

Even in the first 2 yr of the study, the three males associated with each other at moderate levels, indicating that they had already begun to establish their alliance. Their association levels rose dramatically during the third and fourth years of the study. In all but one case (Snu in 1985), each male had one of the other two as his most frequent associate. In all but three cases (Bib in 1985 and Sic in 1985 and 1986), each male also had the remaining male as his second highest ranking associate. Thus, with some exceptions during the early years, these three males ranked mutually as each other's closest associates.

We first observed Snu and Bib cooperatively herding females on two occasions late in 1986. By 1987 and 1988, now accompanied by Sic, the three males together herded females frequently (almost daily), often bringing nonprovisioned females into the provisioning area with them.

Acoustic Behavior

The numbers of whistles attributed to each dolphin in each year are summarized by whistle type in Table 1. We were unable to record whistles from Sic in 1985 or 1986, before he began frequenting the provisioning area.

Because our classification procedure was based only on contour shape, the resulting whistle categories need not have differed in absolute time and frequency characteristics. To address differences in absolute characteristics, we used SIGNAL to measure whistle durations, and calculated the following five frequency measures from the stored contours: starting, ending, minimum, and maximum frequencies, and frequency range (maximum – minimum). We used an analysis of variance to examine variation among major whistle types in each of these absolute time and frequency measurements. All six measures showed highly significant variation among whistle types (ANOVA, $n = 1551$, $df = 17$, $p < 0.001$ for each measure).

The averaged contours of the 18 major whistle types (those clusters that contained at least 10 whistles) are illustrated in Fig. 2. The contours of most major whistle types appeared relatively similar in form. For comparison, Fig. 3 illustrates the contours of 18 randomly selected minor whistle types.

Decreasing Variation within Individuals

Over the course of the study, variability within the repertoire of each male fell steadily. This was demonstrated by the increasing average similarity between whistles produced by the same individual (10 individual-years, $R_s = 0.875$, $p = 0.001$; Fig. 4).

The decrease in variability within the repertoires of individual males was also evident in the falling proportion of whistles that fell into minor whistle types. From 1985 to 1988, minor whistle types comprised 29%, 13%, 8%, and 4% of the annual totals, respectively. This steady drop in the proportion of minor whistles, averaging 8.3%/yr, was more than twice as great as that shown by any major whistle type (Table 1).

Table 1: Number of whistles recorded of each type by individual and year

| Whistle type | 1985 | | | 1986 | | | 1987 | | | 1988 | | | Annual change |
|--------------|------|-----|--------|------|-----|--------|------|-----|--------|------|-----|--------|---------------|
| | Bib | Snu | Totals | Bib | Snu | Totals | Bib | Snu | Totals | Bib | Snu | Totals | |
| 1 | 6 | 2 | 8 | 1 | 3 | 4 | 5 | 6 | 11 | 31 | 92 | 123 | +5.4% |
| 2 | | 1 | 1 | | | 1 | 1 | 1 | 2 | 12 | 40 | 42 | +4.0% |
| 3 | 1 | 1 | 2 | 1 | 1 | 2 | 5 | 23 | 28 | 23 | 45 | 136 | +3.3% |
| 4 | 1 | 1 | 2 | | | | 8 | 19 | 27 | 20 | 22 | 91 | +2.2% |
| 5 | | 1 | 1 | 1 | 2 | 3 | 5 | 1 | 6 | 9 | 15 | 52 | +1.6% |
| 6 | | | | 2 | 23 | 25 | 23 | 23 | 46 | 8 | 12 | 20 | +1.4% |
| 7 | | 3 | 3 | 2 | 1 | 3 | 5 | 33 | 38 | 18 | 9 | 20 | +1.4% |
| 8 | | 4 | 4 | 1 | 11 | 12 | 17 | 13 | 30 | 9 | 17 | 23 | +1.2% |
| 9 | | 1 | 1 | 3 | 13 | 16 | 29 | 31 | 60 | 6 | 3 | 9 | +0.3% |
| 10 | | | | 1 | | 1 | 6 | 21 | 27 | 1 | | 3 | 0.0% |
| 11 | | | | | | | 1 | 7 | 8 | 1 | | 1 | 0.0% |
| 12 | 1 | 3 | 4 | | 3 | 3 | 3 | 1 | 4 | 1 | | 14 | -0.3% |
| 13 | 5 | 3 | 8 | 3 | 3 | 6 | 10 | 7 | 17 | 17 | 9 | 26 | -0.4% |
| 14 | | 6 | 6 | | | | 1 | 6 | 7 | | | 13 | -1.6% |
| 15 | 8 | 2 | 10 | 9 | 19 | 29 | 31 | 29 | 60 | 6 | 8 | 7 | -1.6% |
| 16 | 13 | | 13 | 2 | 6 | 8 | 48 | 25 | 73 | 9 | 3 | 142 | -2.4% |
| 17 | 12 | 1 | 13 | 16 | 8 | 24 | 25 | 13 | 38 | 4 | 6 | 97 | -2.9% |
| 18 | | 14 | 14 | | 12 | 12 | 1 | | 2 | 2 | 7 | 36 | -3.3% |
| Minor | 11 | 26 | 37 | 11 | 7 | 18 | 9 | 20 | 29 | 1 | 13 | 140 | -8.3% |
| Totals | 58 | 69 | 127 | 51 | 90 | 141 | 195 | 306 | 501 | 178 | 328 | 1691 | |

Annual change, mean year-to-year change in number of whistles of each whistle type as a proportion of the total; minor, all 83 minor whistle types pooled.

Whistles were recorded on 17 d between 4 Apr. and 14 Aug. 1985, on 27 d between 26 May and 20 Aug. 1986, on 55 d between 27 May and 12 Sep. 1987, and 40 d between 27 Mar. and 17 Aug. 1988.

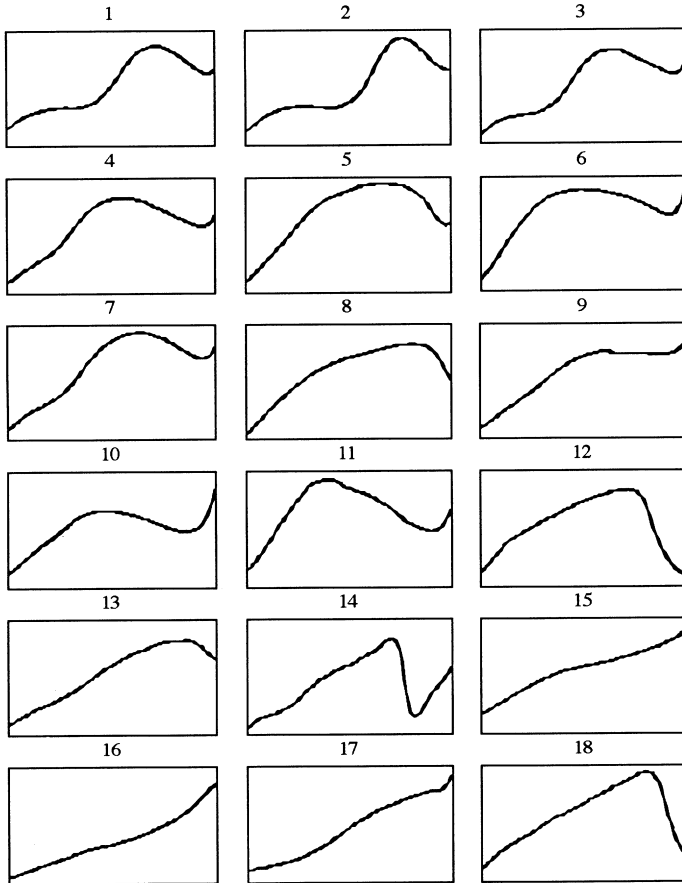


Fig. 2: Average contours of the 18 major whistle types. Average contours are plotted using the mean value for each of the 100 frequency measures

Convergence between Individuals

During the study the three males steadily converged towards a common whistle contour, illustrated by a steady increase in the average similarity between whistles produced by different males (8 pair-years, $R_S = 0.951$, $p < 0.001$; Fig. 5).

By 1988 the males had converged on a set of very similar whistle types as their most commonly produced whistles (types 1, 2, 3 and 7, see Table 1). These whistles shared characteristic patterns of frequency modulation, including two 'humps', or concave-downward segments, with the second containing the whistle's highest frequency. We refer to these four types collectively as 'two-hump' whistles. The increasing proportion of two-hump whistles is illustrated in Fig. 6.

Two-hump whistles were rarely heard in 1985 and 1986. In contrast, by 1988

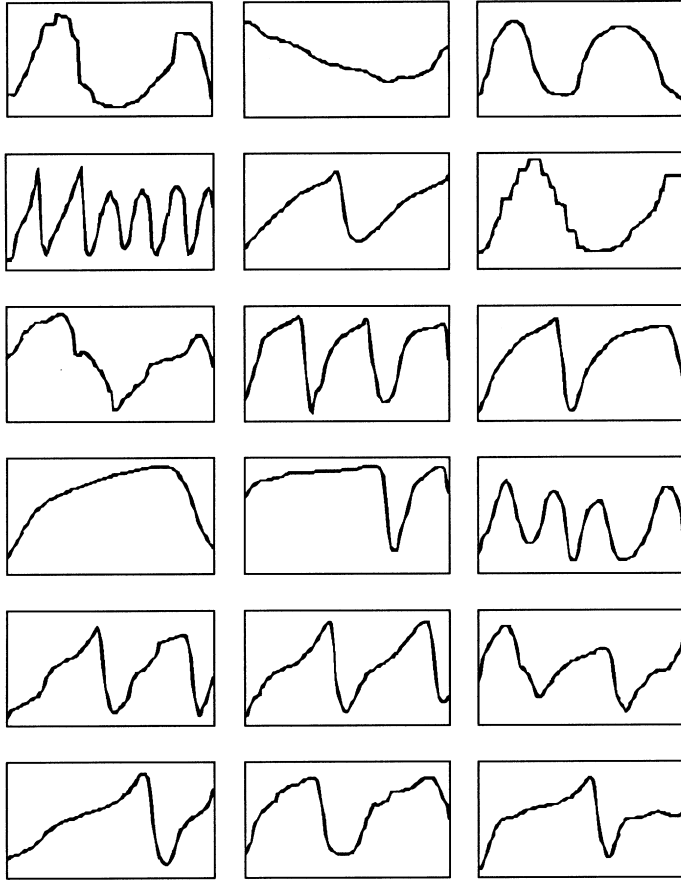


Fig. 3: Average contours for a random selection of 18 minor whistle types. Average contours are plotted using the mean value for each of the 100 frequency measures

all three males had two-hump whistles as their most frequent and second most frequent whistle types (Fig. 7).

Loss of Individual Distinctiveness

Despite the fact that each dolphin's whistles became more stereotyped, acoustic convergence between them made individuals less distinguishable over time. This trend is illustrated graphically by the increasing overlap between individual repertoires in MDS plots (Fig. 8).

To quantify this trend we examined changes over time in distinctiveness indices (see Methods). In 1985 both males we recorded were more acoustically similar to themselves than to the other male. Over the years, individual distinctiveness declined overall (albeit unsteadily), and by 1988 two of the three males were as

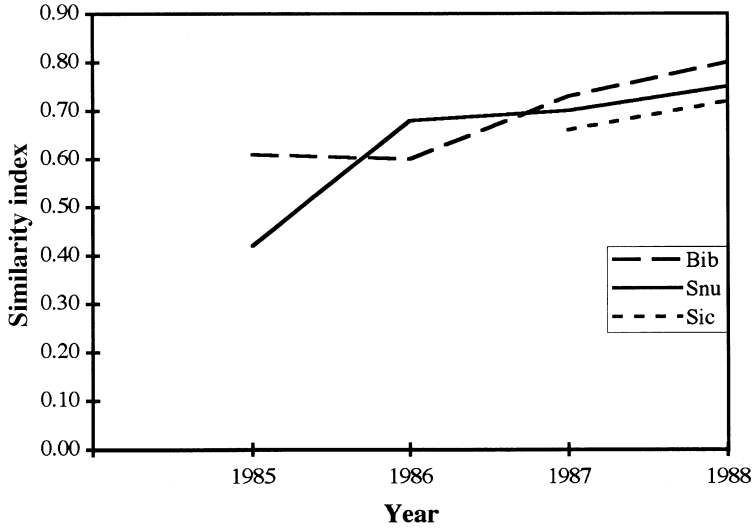


Fig. 4: Increasing similarity among whistles produced by the same individual. Each data point is the average of the similarity indices for all possible pairs of whistles produced by one dolphin in 1 yr (pooled $n = 187\,296$ whistle pairs)

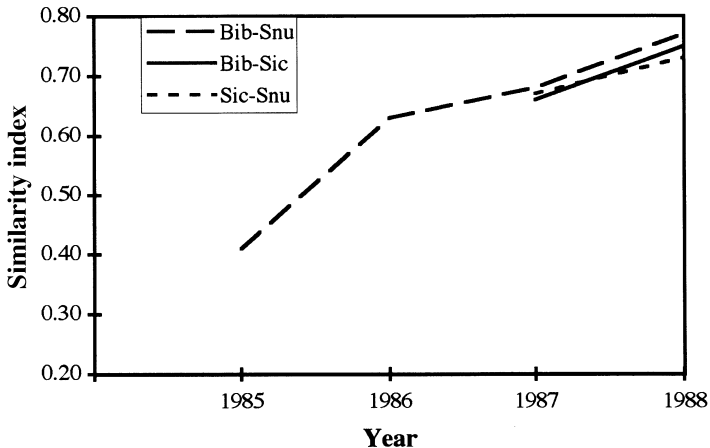


Fig. 5: Increasing similarity among whistles produced by different individuals. Each data point is the average of the similarity indices for all possible pairs of whistles produced by the two dolphins (pooled $n = 336\,102$ whistle pairs)

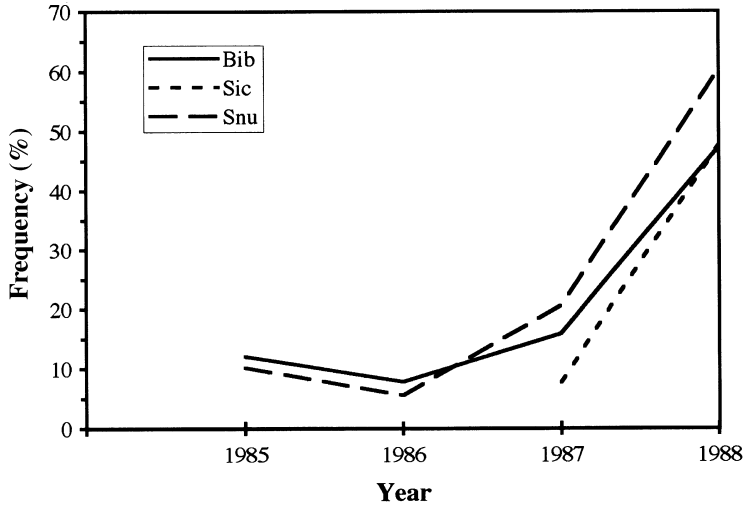


Fig. 6: The changing frequency of two-hump whistles across years (as a proportion of the total number of whistles recorded for each male). Two-hump whistle types include types 1, 2, 3 and 7

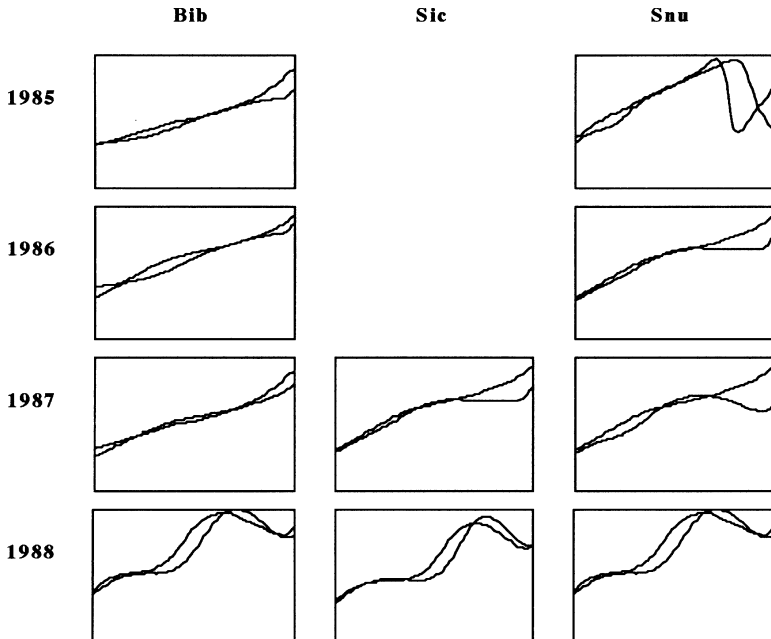


Fig. 7: Averaged contours for the most commonly and second most commonly produced whistle type for each male in each year. Contours are plotted using the mean value at each of the 100 frequency measurements for all whistles of that type

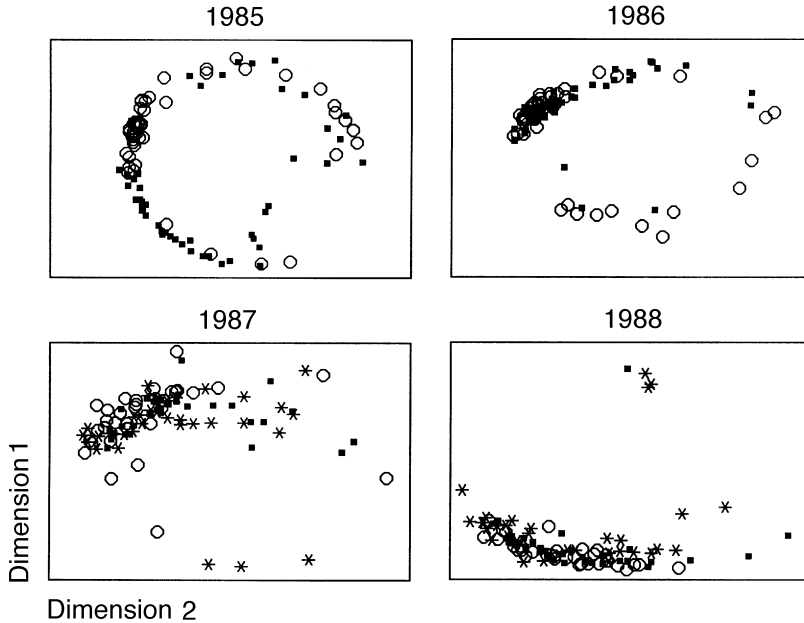


Fig. 8: Multidimensional scaling of whistles from each male, by year. Points include a random sample of 50 whistles from each of two males (Snu and Bib) in 1985 and 1986, and 33 whistles from each of three males (Snu, Bib and Sic) in 1987 and 1988

acoustically similar to their companions as they were to themselves (Fig. 9). This trend, however, was not statistically significant.

Discussion

Summary of Changes over Time

Over the 4 yr of the study, the three male subjects sharply increased the amount of time they spent together and began cooperatively herding females, behavior associated with adult male alliances in Shark Bay. Little is known about the development of alliances, but they are conspicuous by the time males approach adulthood. The three males in this study were known previous to this study, and this was apparently their first alliance.

Concurrent with their developing allegiance, the three males showed several parallel changes in vocal behavior. Each male's repertoire became less variable, and also more similar to those of the other males. The convergence was more pronounced between individuals than within individual repertoires, with the result that individual distinctiveness fell to near zero. All three males converged on a set of closely related whistle types ('two-hump' types) as their most commonly produced whistles. By the end of the study, all had either type 1 or type 2 (both 'two-hump' types) as their most and second most commonly produced whistle. Because changes

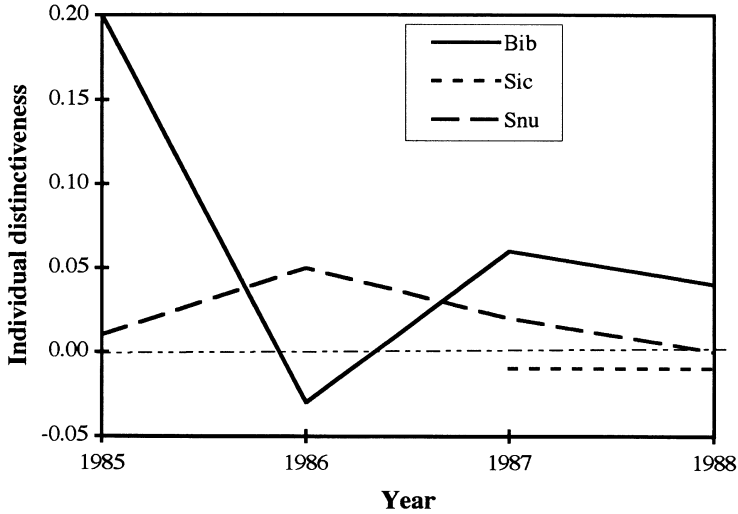


Fig. 9: Individual distinctiveness as a function of time. Individual distinctiveness was calculated as the average similarity of whistles produced by the same individual minus the average similarity of whistles produced by different individuals. $n = 10$ individual-years, $R_S = -0.46$, $p = 0.44$

in whistle production occurred concurrently with changes in alliance behavior, we hypothesize that whistle convergence functions in the context of alliance formation and herding of females.

The 'Signature Whistle' Hypothesis

Our results are relevant, first of all, to the traditional view that dolphins produce individual-specific 'signature' whistles, that most of the whistles an individual produces are its signature, and, therefore, that repertoires are limited (highly stereotyped). As in the study by McCowan & Reiss (1995a), we found that individual repertoires were much more variable than those reported in most other studies (see review in Caldwell et al. 1990 and Sayigh et al. 1990, 1995). In most years, our subjects did not have a single whistle type that predominated or accounted for even half of their whistle output. We found no whistle types that were specific to one individual (excluding types represented by only one example). Further, we found that each male's most common whistle type changed substantially between years (Fig. 7), in contrast to the long-term stability predicted by the standard model and reported previously (Sayigh et al. 1990, 1995).

We did find high degrees of stereotypy in a previous study of unrestrained wild dolphins in Shark Bay (Smolker et al. 1993), and our overall impression, from many years of recording dolphins in Shark Bay, is that individuals, including males within alliances, do possess signatures, and that these play a major role in their whistle repertoires, facilitating a complex, fission–fusion social system. The whistle

production of Snu, Bib, and Sic could prove to be anomalous with respect to other male alliances and dolphins in general in Shark Bay.

One possible explanation might be that these males, because they were at the provisioning area when we recorded them, were freed from the constant task of keeping in touch acoustically with their associates. Thus, they required use of their signatures less than dolphins roaming more widely in the bay. Janik & Slater (1998) demonstrated that, in one group of captive dolphins, signature use was largely restricted to times when animals were physically separated from one another (as was also true in our study of mother–infant separations and reunions; Smolker et al. 1993). Yet previous studies of captive dolphins revealed high degrees of whistle stereotypy even from animals housed together in small tanks where the task of keeping in touch must also be reduced.

Dolphins may be more likely to emit their signature whistle repetitively when stressed, a situation where contacting associates is of paramount importance. Dolphins produce their sounds internally, with no visible cues that can be used to attribute whistles to individuals (except occasional bubble emissions). In most previous studies where high levels of individual stereotypy were reported, captive (reviewed by Caldwell et al. 1990) or wild (Sayigh et al. 1990, 1995; Sayigh 1992) dolphins were captured and stranded out of water for recording in air. In one study with intermediate levels of stereotypy, dolphins were freely interacting, but fitted with a ‘vocalight’ device to indicate the whistle source (Tyack 1986). McCowan & Reiss (1995a) identified whistles to freely swimming individuals by means of bubble streams, sometimes emitted during whistle production, and attributed the lack of whistle stereotypy in their study to this less stressful recording context. If we assume that the provisioned dolphins at Monkey Mia experienced less stress than captive or wild dolphins held temporarily out of water, then decreased stress could, at least partly, account for the more variable whistle repertoires of our subjects. It does not fully explain these discrepant results, however. Even in those rare cases where it has been possible to record freely moving wild dolphins (Sayigh 1992; Smolker et al. 1993), high levels of individual stereotypy were found. In general, however, it appears that where recordings are made in situations where contacting associates may be critical (i.e. stress or visual separation), whistle stereotypy is high. Where stress is reduced and behavioral contexts are more diverse, whistle repertoires are more variable.

Vocal Convergence

We cannot yet determine whether the changes in whistle production we documented among the subjects of this study are typical of dolphins in Shark Bay (or dolphins in general). First, our data are ‘longitudinally’ rich (covering a span of 4 yr), but ‘latitudinally’ poor (from a single alliance). The highly unusual opportunity at Monkey Mia to record whistles from allied males consistently over a long period of time, ended unfortunately with the disappearance of all three males in 1988. Although we would prefer to have the same sort of data for multiple alliances, this is not currently feasible, and it remains to be shown whether vocal convergence is typical of other alliances.

Second, the circumstances at Monkey Mia were unusual. The dolphins, although wild, were provisioned and interacted with humans. We believe nonetheless that the context in which we recorded them more closely approximates a natural situation than has been achieved in other studies to date. In most respects these dolphins behaved like their nonprovisioned counterparts in the same population, had diverse social partners of their own 'choosing', and were free to come and go. The possibility remains that provisioning affected the whistle production of these males in ways that we cannot discern.

However, even if our results do not generalize to other male alliances, or are biased by the provisioning context, they are nonetheless of great interest because they reveal the potential of these dolphins to substantially modify whistle production as adults.

Possible Causes of Increasing Individual Stereotypy

In Shark Bay, as elsewhere, bottlenose dolphins usually develop a distinctive and stereotyped 'signature' whistle by the time they are 6 mo to 1 yr old (Caldwell & Caldwell 1979; Sayigh et al. 1990, 1995; Smolker et al. 1993; but see McCowan & Reiss 1995b). The increasing stereotypy we report here is thus part of a secondary shift in whistle production that accompanied alliance formation. Mitani & Brandt (1994) found that male chimpanzees giving long-distance calls together tend to match each other's acoustic structure. As a result, individuals with fewer different chorusing partners had less variable repertoires. If dolphins behave similarly (i.e. they 'chorus' with allies), then the more distinct and well defined their allegiances, the fewer 'chorusing' partners they will engage, and the more restricted their repertoire may become as a result.

Possible Mechanisms of Convergence between Individuals

Several different mechanisms could account for the increasing similarity of whistles from different males.

1. Adoption of a species-typical 'alliance whistle'. If the 'two-hump' whistle were a species-typical alliance whistle, all males who were members of alliances would produce that whistle. We have recorded whistles from several other well-documented male alliances away from the provisioning site, and visual inspection of their spectrograms did not reveal any two-hump whistles.

2. Response to a common eliciting stimulus. If the dolphins produced two-hump whistles in response to provisioning or some other specific eliciting stimulus, the apparent convergence could have arisen through increasing exposure to that stimulus. The provisioning context alone does not seem to explain our results. Although we only present data from the three provisioned males, we collected a similar set of recordings from three provisioned females in the same general contexts. Visual inspection of spectrograms of 720 female whistles from the same time period did not reveal any two-hump whistles.

Alternatively, herding of females could provide stimuli that only males experience, and herding did become more frequent during the study. However, the males

produced two-hump whistles both when they were herding females and when they were not. Moreover, other male alliances that we recorded offshore did not produce two-hump whistles while herding females.

3. Short-term matching. In short-term matching, one individual produces a similar sound in a direct response to hearing it from a second individual. For example, this occurs during counter-singing in some songbirds (Lemon 1968; Schroeder & Wiley 1983; Falls 1985). The case of chimpanzees matching pant hoot 'climax elements' during chorusing (Mitani & Brandt 1994) could be achieved in this manner. Analogously, one dolphin might produce a two-hump whistle in response to another individual doing so. This might result in whistle convergence as the individuals spend more and more time together. However, this explanation seems inadequate because all three males produced two-hump whistles when they were apart as well as together. It also fails to explain why only two-hump whistle types, which were initially very rare, increased dramatically in frequency.

4. Long-term adoption. Another possible mechanism is the long-term adoption of one male's signature whistle by the other two. Such long-term adoption of vocalizations occurs in some songbirds. For example, male indigo buntings that migrate to a new location learn new songs from a neighboring male (Payne 1982). Similarly, mated pairs in some finch species share the same flight call because one partner adopts the other's call type during pair formation (Mundinger 1970). This process does not fit our observations well, however. Each male was already producing two-hump whistles when first recorded, so that no single male is an obvious candidate for a model to copy. Moreover, there is no evidence that any of the males used a two-hump whistle type as a signature prior to 1988. Neither whistle types 1 and 2, which were the most common types in 1988, nor the other two-hump types (3 and 7) were among the most frequent for any individual in any earlier year (Table 1).

5. True convergence. Finally, different individuals may come to produce the same call type over time through a process in which all individuals alter their initial vocalizations in different ways. This kind of convergence has been demonstrated in winter flocks of chickadees (Mammen & Nowicki 1981; Nowicki 1989). A similar process occurs with contact calls in newly formed social groups of pygmy marmosets (Elowson & Snowdon 1994). This explanation fits our observations best, because the three males ultimately converged on a whistle structure that was previously rare. Although two-hump whistles were present in the repertoires of each individual from the earliest years they were recorded, it was only in 1987 that they began to increase in frequency, and only in 1988 that they included the most frequent whistle type of each male.

Possible Functions of Acoustic Convergence

From the idea of a 'signature' whistle that conveys the individual identity of the caller, it is only a short step to the hypothesis that the two-hump whistles observed are an 'alliance signature' that serves to identify the caller as a member of the alliance. Such an alliance signature could have several possible audiences, which are not mutually exclusive.

1. Alliance signatures could be directed towards fellow alliance members. It seems unlikely that close associates would be unable to recognize one another without a shared acoustic label, given dolphins' marked cognitive abilities (Herman 1980, 1986) and demonstrated capacity for individual recognition (Sayigh 1992). However, it is conceivable that sharing an alliance signature could play some role in initiating and maintaining social bonds within alliances.

2. Alliance signatures could be directed towards other males. Because male alliances compete against one another as units (Connor et al. 1992a,b), individual identity may at times be less salient than alliance membership. Sharing a common vocal label might make it easier for the members of an alliance to signal that they are allied and, therefore, represent a formidable competitive force.

3. Alliance signatures could be directed towards sexually receptive females. By signaling alliance solidarity, these whistles might indicate the males' ability to herd cooperatively and effectively, and thereby dissuade females from trying to escape. Alliance signatures could also play a role in female mate choice. If close cooperation among males is as critical to mating success as it appears, females may prefer to mate with males who demonstrate such abilities. Male cooperation may be sexually selected this way in other species. Male long-tailed manakins (*Chiroxiphia linearis*), a neotropical songbird, engage in highly cooperative sexual displays involving both vocal and 'dance' movements. The rate at which females visit a team of males is correlated with how closely the males' songs match each other (Trainer & McDonald 1993). Similarly, male alliances in Shark Bay engage in a variety of highly coordinated nonacoustic behavior patterns, including precise surfacing synchrony during travel and elaborate, synchronized displays (Connor et al. 1992a,b). Convergence on a common whistle type may represent an analogous coordinated display in the acoustic domain, and may function to attract or stimulate females.

Dolphins are unusual among mammals in that they clearly learn some of their vocalizations, apparently retaining this capacity into adulthood, and also are capable of accurate vocal imitation. Our results suggest that, in the wild, such capabilities may function in part during the development of alliances and herding of females.

Acknowledgements

Financial support for this project was granted by the National Geographic Society, the Dolphins of Shark Bay Research Foundation, The University of Michigan and NSF grant IBN 9408327 to R. Smolker. For help with logistics in the field we thank the Anatomy Department of the University of Western Australia, particularly Richard Holst, the West Australian Department of Conservation and Land Management, the West Australian Museum, and the rangers at Monkey Mia. We thank John C. Mitani for access to equipment for acoustic analysis. Gillian Haines, Bethany Mayer, and William Pepper helped to digitize whistle contours. Stephen Nowicki suggested the algorithm used to calculate moat indices. Bennett Fauber at the University of Michigan's Center for Statistical Consultation and Research helped with writing SPSS routines. Andrew F. Richards helped to collect party sighting and whistle data and made numerous helpful contributions to the analyses. Richard Connor and Janet Mann contributed party sighting data used to assess patterns of association. For comments on drafts

of this manuscript we thank Richard D. Alexander, John C. Mitani, Andrew F. Richards, Salvatore Cerchio and Barbara B. Smuts.

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Received: August 10, 1998

Initial acceptance: October 10, 1998

Final acceptance: December 22, 1998 (J. Brockmann)