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Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*

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Here we report that synchronous surfacing in male bottlenose dolphins is associated with alliance membership and that synchrony between members of cooperating alliances is more common during social behaviour than during nonsocial behaviour, especially during bouts of 'intense' social behaviour (e.g. mounting, displays, chasing) with female consorts. Alliances of three males varied in the degree to which all members participated in synchrony, possibly reflecting differences in alliance unity and the extent to which alliances consort with females. The lack of a discontinuity between the elaborate displays that males perform around females and the synchronous surfacing of alliance members reported here suggest that synchrony is an adaptive signal. If so, we have a remarkable convergence in the use of synchrony as an alliance signal in humans and bottlenose dolphins. However, whether an adaptive signal or a correlate of proximity, synchrony will be a useful tool in the study of delphinid social relationships.

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Synchronous behaviour occurs when two or more animals perform the same behaviour at the same time. Striking examples are found in a wide range of behavioural contexts, including synchronous flashing in fireflies (Buck 1938, 1988), movements of schooling fish (Pitcher & Parrish 1993), waving of the major claw by male fiddler crabs, *Uca annulipes* (Backwell et al. 1999), courtship displays of western grebes, *Aechmophorus occidentalis* (Nuechterlein & Storer 1982) and vocalizations of male long-tailed manakins, *Chiroxiphia linearis* (Trainer & McDonald 1993).

The term 'synchrony' has been used in odontocete studies to describe occasions when group members perform behaviours that show nonrandom temporal clustering (e.g. Würsig 1978; Whitehead 1996; Hastie et al. 2003) as well as those that are performed 'simultaneously' or 'in unison' (e.g. Mann & Smuts 1999). Here we are interested in the latter category. Odontocete behaviours performed 'in unison' have been described in a range of contexts.

For example, McBride & Hebb (1948) described swimming in unison by captive bottlenose dolphins, *Tursiops truncatus*, in response to the introduction of unfamiliar objects into their tank. Synchronous respiration in spinner dolphins, *Stenella longirostris*, and killer whales, *Orcinus orca*, has been used to characterize resting behaviour (Norris & Dohl 1980; Heimlich-Boran 1988). The synchronous movements of schooling spinner dolphins have been compared to fish schooling behaviour and may serve a similar antipredator function (Norris & Schilt 1988). Simila (1997) noted synchronous surfacing during cooperative feeding on herring by killer whales. Synchronous surfacing between mothers and infant bottlenose dolphins declines during the first 2 months of life as infants become more independent (Peddemors 1990; Mann & Smuts 1999).

Here we are interested in synchrony associated with alliance behaviour in male bottlenose dolphins that inhabit Shark Bay, Western Australia. The male dolphins in Shark Bay show two functionally defined levels of alliance formation (Connor et al. 1992a, b, 1999; Connor & Mann 2006). Males in stable pairs and trios cooperate to guard and herd individual females (Connor et al. 1992a, b) and teams of two or more alliances (4–14 individuals) cooperate in conflicts with other alliances over females (Connor et al. 1992a, b, 1999, 2001). Recent observations suggest a third level of alliance (Connor & Mann 2006).

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Connor et al. (1992a, 2000) described elaborate synchronous displays that allied males perform in the presence of female consorts that are probably directed towards females but may also serve a signalling role within or between male alliances (Connor et al. 1992a). These displays often include synchronous aerial leaps and underwater turns performed in a wide range of orientations (i.e. parallel movement, movement in opposite directions and turning in or away from each other). More often, two or three males will surface side by side synchronously as they travel, rest or socialize. Synchronous surfacing occurs commonly in all social contexts: when an alliance is alone, affiliating with another alliance, and when one or both alliances have female consorts. Here we examine synchronous surfacing in relation to alliance membership and behaviour.

MATERIAL AND METHODS

Data on synchrony and social behaviour were collected during focal follows on 20 male dolphins in Shark Bay during 1987−1989. Group membership was defined spatially using a 'chain rule'; any individual was included if it was within 10 m of an individual that was within 10 m of the focal individual, and so forth. Individuals were identified from their dorsal fin shape and scars. For details of individual identification and sex determination see Smolker et al. (1992), Connor et al. (2000) and Krützen et al. (2003).

We examined the relationship between alliance membership and synchrony using data from 74 focal individual follows (279 h) on eight adult males from alliances A, B, C and A′ that associated at high levels with each other and cooperated against other alliances (Connor et al. 1992a, b; Smolker et al. 1992; Connor & Mann 2006). In May 1989, two males of trio C disappeared and the third joined the pair A to form a new trio (that we will label here A′), which continued to associate at high levels with the other trio (alliance B).

To examine variation in synchrony within and between alliances, we included more than 300 h of focal data from several other trios (D, G, E and S). The S males, but none of the other alliances, were provisioned with dead fish in shallow water near a campground (Connor & Smolker 1985).

We also explored the relation between synchrony and social behaviour among alliance members. Many mammals use gentle contact behaviours to express affiliation and dolphins are no exception. Bottlenose dolphins, including male alliance partners, often 'pet' each other (i.e. touch and stroke each other with their pectoral fins; Tavolga & Essapian 1957; Connor et al. 2000). During follows, petting was scored when one individual was observed contacting another with its pectoral fin and both participants were identified. Petting was inferred if two individuals surfaced within touching distance (0.33 m) and one was tilting with respect to the other (tilting always occurs during petting). A new case of petting for two individuals was scored if at least 5 min had elapsed since the previous case or one of the participants was observed, in the interim, petting with a different dolphin. More intense social behaviour, often accompanied by splashing at the surface, may include body-to-body contact, sexual behaviour, displays and chasing.

Synchrony

A synchronous surfacing (synch surf) was recorded if two (pair synch), or less commonly three (triple synch), individuals in the group broke the surface simultaneously (see 'synchronous time differences' below). When following males, we attempted to maintain a position slightly behind and to the side to identify individuals as they surfaced. When in this broadside position, we recorded all occurrences of synchronous surfacing in the group. Our definition of synchrony has been consistent throughout our 20 years of study on male alliances.

Synchrony: distance and stagger

Two spatial components of synch surfs were recorded: distance and stagger. The distance between individuals surfacing synchronously (perpendicular to the axis of the body) was scored as 0, 1 or 2; 0 for ≤0.33 m (touching distance), 1 for ≤2 m (which is approximately one body length), and 2 for >2 m. The degree of stagger was recorded as 0, 1 or 2; 0 for two males that were side by side, 1 for cases in which one male led the other by half a body length and 2 for cases in which one male led the other by a full body length or more.

In 2004, during a study of alliance affiliations among more than 100 males, we examined in more detail the relation between synchrony and distance, estimating the intermale distance to the nearest 0.5 m for distances of 0.5 m or more and to the nearest 0.25 m for distances less than 0.5 m. Stagger was recorded as in the previous sample. The 2004 sample included all occurrences that involved two males even if each male was not identified (e.g. if a synch occurred in an all-male group).

Synchrony: time differences

We used videotaped follows from 5 days in 1994−1995 to measure time differences in surfacings that were called synchronous in real time versus those that were not (recorded with a Panasonic model AG-3P S-VHS camera fed to a JVC BR-S405U portable Video Deck; recording speed 60 frames/s). Three of the five videotaped males were from alliances A and C and the other two were males that became their alliance partners in the 1990s.

The dolphins always broke the surface first with their head or dorsal fin. For analysis we selected all surfacings that were recorded as 'synchronous' by the observer and for which we could conduct frame-by-frame measurements of each male's dorsal fin as it emerged and subsequently submerged. We also measured (where possible) the interval between heads emerging, the shortest interval between the emergence of the males' dorsal fins or heads, and the total surfacing duration for the first male of a pair to break the surface. Asynchronous surfacings were sampled from the same tapes and were restricted to all cases of surfacing by two males, identifiable on the videotape, surfacing side by side (<2 m) and overlapping at the surface, but that were not recorded as synchronous.

Synchrony and alliance membership

A synchronous surfacing was classified as intra-alliance if the two males were members of the same alliance; it was classified as interalliance if the two males were members of different alliances (e.g. A and B). Mantel's permutation tests (Mantel 1967; Schnell et al. 1985) were used to test whether alliance members performed more synchronous surfacing with members of their own alliance than with nonalliance members when two alliances were together. Mantel's tests assess the relation between two matrices by measuring the association between elements in the matrices using a suitable test statistic. The significance of the test statistic is assessed by comparing it to the distribution found by randomly permuting the order of elements, in this case 10 000 permutations, in one of the matrices. We constructed two matrices for each pair of alliances: a 0/1 matrix specifying whether individuals were from the same alliance and a corresponding matrix containing the proportion of the total number of synchs accounted for by each dyad, calculated across all follows when a particular pair of alliances were seen together.

Synchrony and social behaviour

All pair synchs from the 1987–1989 sample were later classified as occurring during nonsocial, social (=petting) or intense social behaviour. If no social event involving a male alliance member was observed within 2 min of a synch, the synch was classified as nonsocial; if petting occurred, the synch was classified as social. If any other social behaviour was observed (e.g. displays, chasing, social splashing, sex, etc.), the synch was included in the intense social category. We used sign tests (Sokal & Rohlf 1981) to test whether interalliance synchs occur more often during social than nonsocial behaviour and, if so, whether this result holds for the two major subcategories of social behaviour, petting and 'intense' social behaviour. Here, each follow, treated as independent, was the unit of analysis. For each follow, the proportion of synchs that were interalliance in each behaviour (i.e. social and nonsocial) were calculated and used in the sign test. Only follows with at least five synchs in each category were included. Matrices used to correlate petting with synchrony had the proportion of synchronous surfacing contributed by each pair of individuals in one-half and the proportion of petting observations contributed by each pair in the other.

Interalliance variation in measures of synchrony

Rates. To examine variation among alliances in the rates of synchrony, we counted pair and trio synchs from five trios when they were resting or travelling side by side with no other dolphins present. We calculated an alliance synchrony rate as the average of the rates for each follow on a member of that alliance. The rate for each follow was based on the time (minimum 15 min) that the alliance spent resting or travelling alone.

We examined two measures of the tendency for all three males in a trio to participate in synchrony as follows.

Proportion of triple synchs. We first measured the occurrence of triple synchs, when all three males surface synchronously side by side. We calculated the proportion of synchs that were triple synchs for each follow by dividing the number of triple synchs by the total number of pair and triple synchs. The triple synch score for an alliance was calculated as the average of the values for each follow. We only used follows with a combined total of at least 10 pair and triple synchs.

The odd-male out. Smolker et al. (1992) previously identified an odd-male out in a trio as the male that had the lowest coefficient of association with the other two. The odd-male out was consistent in each trio for the 2–5 years that the four trios were observed (Smolker et al. 1992). Here we explore whether the 'odd-male-out' phenomenon is also reflected in patterns of synchrony, when all three males in a trio are together. We defined the 'odd-male out' (OMO) as the male in a trio that, during a follow, engaged in the fewest paired synchs with members of his alliance. First we considered the proportion of pair synchs in a trio that involved the 'odd-male out'. We calculated the proportion of synchs that the OMO participated in, averaged across all follows with at least 10 pair synchs. Next, we examined the consistency of the OMO across follows. Here the identity of the OMO was tabulated for all the follows of an alliance to determine whether a particular male in each trio occupied the OMO role during more follows than the other two. Finally, we recorded which male was in the centre position of triple synchs to test the hypothesis that the OMO would be in the centre less often than the other males.

RESULTS

Synchrony: Distance and Stagger

Synchronous surfacings between males that were greater than one body length apart or staggered by more than half a body length were rare. Two males surfaced more than 2 m apart in only 1% of our samples (34 of 2807 in 1987–1989 and 1 of 110 in 2004). The more precise 2004 sample, which included 110 synchs between at least 64 known males, showed that the majority of pair synchs occurred when males were 0.5 m apart (Fig. 1). A minor proportion of the sample included synchs in which the males showed a stagger of 1 (1.5% in 1987–1989 and 3.6% in 2004), while synchs between males with a stagger of 2 (1 body length or more) were rare (0.3% in 1987–1989 and 0% in 2004). All remaining totals and analyses include only synchs with distance and stagger scores of 0 and 1.

Synchrony: Time Differences

The videotaped sample revealed that males recorded as surfacing synchronously with another male emerged for an average of 136 frames (range 97–173) or about 2.25 s. Measuring the interval between emergence of the two males' heads or fins or the shortest interval between emergence of the heads or fins yielded a similar result (mean: 7–9 frames, range 0–28 frames, or about 120–150 ms;
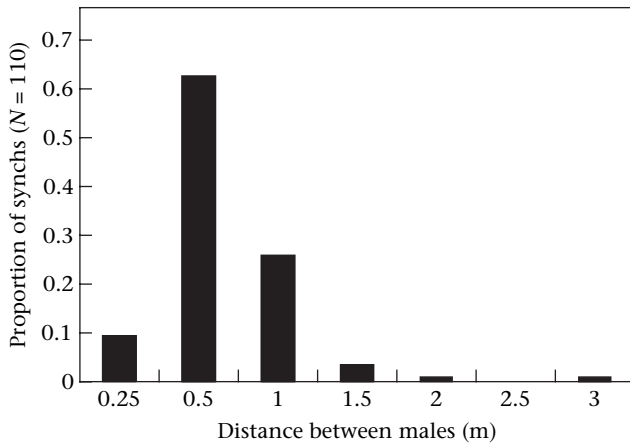
Figure 1. The estimated distance between males during paired synchronous surfacings.

Table 1). However, when we considered for each case the lowest of these scores ($N = 57$), the average difference fell to 4.6 frames (77 ms, range 0−18 frames). Average values for males surfacing side by side but not scored as synchronous were just under 1 s (Table 1).

Synchrony and Alliance Membership

We recorded 2773 synchs by two males during 47 follows of the eight ABC males when at least two alliances were together, including 409 interalliance synchs. Synchrony was strongly associated with alliance membership in all four pairs of alliances (Table 2). Given the constraints of the 0/1 matrices for these data sets, there were only 10 possible values for the matrix correlations, which means that the most extreme P value obtainable was 0.1.

Synchrony and Social Behaviour

A higher proportion of social synchs than nonsocial synchs were interalliance (sign test: $N = 23$ follows, $P = 0.017$). We also examined separately the two subcategories of social behaviour, petting and 'intense' social behaviour. The petting versus nonsocial synch comparison fell short of significance, probably because of the small sample size (sign test: $N = 13$ follows, $P = 0.092$).

A higher proportion of intense social synchs than nonsocial synchs were interalliance (sign test: $N = 15$ follows, $P = 0.035$). Most of the intense social behaviour included female consorts. In 75% (233 of 312) of synchs that

Table 1. Synchronous and asynchronous surfacings of male bottlenose dolphins measured in frames (60 frames/s)

		N	Range	Mean	SD	Median
Synch	Fin	79	0−28	8.65	6.38	8.00
Synch	Head	59	0−28	8.44	6.65	7.00
Synch	Fin or head	64	0−28	7.97	6.92	7.00
Asynch	Fin	76	1−136	49.84	31.48	42.00
Asynch	Head	70	3−144	52.01	33.43	44.50
Asynch	Fin or head	72	8−144	52.82	32.00	43.67

Table 2. Summary of Mantel permutation tests examining whether male bottlenose dolphins performed more synchronous surfacing with members of their own alliance than with nonalliance members

Alliances	N (synchs)	P (10 000 permutations)	Matrix correlation
A−B	1355	0.1034	0.85
A−C	962	0.1002	0.89
B−C	264	0.1028	0.92
A′−B	192	0.1024	0.91

Constraints of the 0/1 matrices for these data sets allowed only 10 possible values for the matrix correlations, and the most extreme P value obtainable was 0.1.

occurred during intense socializing with a female consort present, the social behaviour clearly involved the female consort or, occasionally, another female in the group. Of the remainder, 30 (10%) cases were clearly restricted to the males and in 49 cases it was not clear whether the female consort was involved.

Our data on petting were relatively sparse because much of it occurred underwater where it was more difficult to identify actors. During 22 follows we recorded 103 cases of petting when at least two of the ABC or A′B alliances were in the same group, including 89 when alliances AB or AC were together (Mantel permutation test: A−B: $N = 49$, $P = 0.1023$; A−C: $N = 40$, $P = 0.2027$). The strong association between petting and alliance membership for alliances A and B merited further analysis, revealing a strong correlation between petting and synchrony when they were together (Mantel permutation test: $P = 0.038$, matrix correlation = 0.63794).

Interalliance Variation in Measures of Synchrony

Rates

There was significant variation in the rate of synchronous surfacing for the five nonprovisioned trios during resting and travelling when they were not with other dolphins (Kruskal−Wallis test: $H_4 = 13.725$, $P = 0.008$; Table 3).

Proportion of triple synchs

Differences between trios in the proportion of within-alliance synchs that were triple synchs may reflect alliance

Table 3. Interalliance variation in rates of synchrony

Alliance	N	Time (min)	Rate	SD
B	6	539	0.32	0.146
C	4	848	0.45	0.259
G	4	282	0.28	0.204
E	8	712	0.15	0.095
D	4	511	0.52	0.105

For each trio, the mean ± SD rate of pair and trio synchs (per minute) during resting and travelling while the trio was alone (N = number follows, Rate = average of rates for each follow).

Table 4. Mean ± SD percentage of triple synchs for each alliance

Alliance	N	%Triple synchs	SD
B	35	15	0.1005
C	21	26	0.1428
G	13	5	0.0529
E	6	4	0.0489
D-1989	5	24	0.1831
D-1988	4	0	0
S	17	1	0.0273

%Triple synchs = number of triple synchs/(number of pair synchs + number of triple synchs), averaged across follows. Follows with at least 10 pair synchs and triple synchs combined were included. N = number of follows. Data for the D trio are separated by year because this trio's primary associates, the S trio, disappeared between the 1988 and 1989 seasons.

Table 5. Mean ± SD percentage of within-alliance pair synchs for each trio that included the odd-male out (%OMO)

Alliance	N	%OMO	SD
B	35	41.5	13.2
C	21	38.1	12.8
G	15	35.1	14.5
E	6	49.2	12.0
D-1989	5	44.0	9.7
D-1988	4	1.9	3.9
S	17	5.5	8.1

Calculated as the average of the %OMO for all follows on that alliance. Follows with at least 10 pair synchs were included. N = number of follows. Data for the D trio are separated by year because this trio's primary associates, the S trio, disappeared between the 1988 and 1989 seasons.

unity (Table 4). The average percentage of triple synchs for each alliance ranged from 0 to 26%. The two lowest values were for SSB and D in 1988 (0−1%). Provisioned by tourists in shallow water, the S alliance herded females at an unusually high frequency and showed unstable relationships (Connor et al. 1992a). Only two males from S consorted a given female, but the identity of the consorting pair changed often (Connor & Smolker 1995). The excluded male from S often consorted a female with a member of their second-order alliance partner, trio D, in 1988 but not in 1989 after S disappeared. The lack of unity within alliances S and D in 1988 is reflected modestly in association coefficients (Smolker et al. 1992), but strongly in synchrony (Table 4). Two other trios, G and E, also had very low values (4−5%). There was significant variation in the proportion of triple synchs among the five nonprovisioned trios (Kruskal−Wallis test: $H_4 = 28.168$, $P < 0.001$, using the 1989 value for alliance D).

Odd-male out

The percentage of pair synchs in each trio that included the OMO ranged from 35 to 49 for the five nonprovisioned trios, but much lower values (2−6) were obtained for S and D trios in 1988 but not in 1989 (Table 5). The variation in the proportion of pair synchs involving the OMO did not differ significantly between provisioned S and D trios in 1988 (Mann−Whitney U test: $U = 24.50$, $N_1 = 4$, $N_2 = 17$, $P = 0.368$) or between the five nonprovisioned trios, including D, in 1989 (Kruskal−Wallis test: $H_4 = 6.44$, $P = 0.169$). However, variation in the proportion of pair synchs involving the OMO was highly significant when data from S and D in 1988 were combined and included in a comparison with the five nonprovisioned trios (Kruskal−Wallis test: $H_5 = 49.41$, $P < 0.001$).

Three of the four trios from Smolker et al. (1992) yielded at least 15 follows with at least 10 pair synchs. In each trio the same male identified as the odd-male out based on association (i.e. he spent less time with the other two) was the odd-male out in synchrony (i.e. he participated less often in synchrony when all three were together; Table 6).

Data from two trios suggest that the OMO also occupied the centre position in triple synchs less often. In trio B, the odd-male out had the lowest score for occupancy of the

centre position in eight follows compared to one and zero follows for the other two males (chi-square test: $\chi_2^2 = 12.7$, $P < 0.01$) and in trio C, the comparable numbers were 9, 2 and 1 (excluding one tie, chi-square test: $\chi_2^2 = 9.5$, $P = 0.009$).

DISCUSSION

The degree to which synchrony is observed in the alliance behaviour of male dolphins appears unique among mammals, with the exception of our own species (McNeill 1995; Hagen & Bryant 2003). First we address the issue of whether synchronous surfacing is an adaptive alliance signal, adaptive for nonsignalling reasons, or an artefact of two dolphins swimming in close proximity. We then consider the potential for synchrony to yield important insights into delphinid social relationships.

Is Synchrony an Adaptive Signal?

Based on the results of the current study, we cannot say unequivocally that synchronous surfacing is an evolved signal in male dolphin alliance behaviour. A vocalization can be shown to have a signal function with a playback experiment. Conclusive tests of the hypothesis that motor synchrony is used as an alliance signal might require experiments using video playbacks with captive dolphins.

An indication that synchronous surfacing might be an alliance signal derives from variation in the phenomena. Interalliance synchrony varies with behavioural context,

Table 6. The number of follows in which each male was the 'odd-male out' (OMO) for each of four trios

Trio	Number of follows			χ_2^2	P
B	7	6	**21**	12.4	0.002
C	1	5	**14**	13.3	0.001
G	0	1	**14**	24.4	0.001
E	0	3	**3**		

The male identified as the OMO by association coefficients across years in Smolker et al. (1992) is in bold.

alliances vary in rates of synchrony when behavioural state and group size are held constant, alliances vary in the proportion of synchs that are triple synchs, and individuals vary in their participation in synchrony in ways that correspond to association coefficients. This variation might represent differences in alliance unity and age differences that pertain to participation in consortships. For example, the highest values for percentage of triple synchs in trios were shown by males that were mature and consorted females often (see Connor et al. 2000).

An alternative to the signal hypothesis is that the synchrony is simply an artefact of spatial proximity: individuals who are close together swimming side by side are more likely to surface synchronously. It is true that synchronous surfacing occurs more often when individuals are closer together (Fig. 1). Even our comparison of alliance rates is vulnerable to this hypothesis. Our analysis was restricted to groups that were resting or travelling, in which, by definition, individuals are in a 'tight group' (<2 m apart). Typically, individuals are within 0.5−1 m of each other in these groups, but our definition leaves room for spatial variation that could explain our results. If, for example, alliance E individuals were more often closer to 1 m apart and alliance B individuals were typically closer to 0.5 m apart during resting and travelling, then the differences in alliance synchrony rates could be explained as an artefact of proximity (we did not notice such a difference).

However, if synchrony is an artefact of spatial proximity in dolphins, why is motor synchrony not widespread in terrestrial alliances, especially primates, where alliances are common and individuals engage in closely spaced alliance behaviours? A reviewer of this paper offered the following seemingly reasonable hypothesis: 'the greater synchrony of dolphins relative to other nonhuman primates may be simply explained as a constraint associated with being an aquatic mammal. If a marine mammal is going to maintain close proximity in service of an alliance, it follows that the animals would need to synchronize their breathing or they would become separated as one was breathing at the surface and another submerged. One could further propose that synchronized breathing also synchronizes oxygen demand and permits allied dolphins to engage in allied under-water activities (i.e. foraging or mating) without one member of an alliance breaking ranks to get a breath'.

In fact, the Shark Bay dolphins remain in groups and coordinate their activities most of the time without surfacing and breathing synchronously. The dolphins live in a three-dimensional habitat and their groups have a three-dimensional structure. Like a monkey troop moving through the forest canopy, a dolphin group has depth. The dolphins typically maintain this three-dimensional structure as they move about in groups underwater, socializing, resting and travelling. This is why individuals in a group do not typically surface synchronously. Dolphins are therefore, less constrained than terrestrial primates who move about in two dimensions. If merely an artefact of spatial proximity, synchrony should be much more common in the alliance behaviour of terrestrial than aquatic mammals.

An alternative adaptive hypothesis is suggested by a factor that affects dolphins moving in close proximity much more than primates: drag. It may be that, as two dolphins swim closer together, synchrony reduces the overall drag on the pair and/or prevents one from having a drafting advantage (e.g. Weimerskirtch et al. 2001; Weihs 2004).

The strongest argument for the signal hypothesis derives from the extraordinary range of elaborate synchronous displays that males perform around females (Connor et al. 1992a, 2000). A proximity hypothesis is not plausible for male displays. These displays are highly variable and often include multiple underwater turns and aerial leaps, sometimes with animals going in opposite directions (Connor et al. 1992a, 2000). Importantly, there is no discontinuity between the regular synchronous surfacing reported here and the displays; in fact synchronous surfacings are often display components. A description of a simple display is illustrative: two males surface synchronously behind a female, swim forward on either side of the female, turn outward synchronously and swim parallel in the opposite direction to the female before turning in synchronously behind her and surfacing side by side synchronously again. The proximity 'artefact' hypothesis for synchronous surfacing demands that while male displays have an adaptive signalling function, synchronous surfacing does not; the side-by-side synchronous surfacing either provides no information or individuals do not use it. The lack of a discontinuity between the displays and side-by-side synchronous surfacing weakens considerably the 'proximity artefact' hypothesis.

Importantly, even if the synchronous surfacing reported here is an artefact of proximity or a drag-related adaptation for dolphins swimming in close proximity, its utility as a potential measure of social interactions and bonds is undiminished. For example, consider the question of why interalliance synchs occur more often during excited socializing when males have female consorts. Tension within and between associating alliances may be expected because of the indivisible nature of the resource (fertilizations) that males compete for (van Hooff & van Schaik 1994). A possible interpretation is that synchrony serves as a signal to reduce tension and/or signal cooperation, as in some forms of primate affiliative behaviour (Aureli et al. 1999). Alternatively, swimming closer together may be the tension-reducing signal, which we measure from the occurrence of incidental synchronous surfacing.

Synchrony and Social Relationships

The variation in synchrony yields predictions of variation in reproductive success. Differences between alliances in the participation of the 'odd-male out' in synchrony suggests that synchrony may be a useful measure of alliance 'unity.' If unity is advantageous, then more unified alliances should enjoy greater mating success. Similarly, the proportion of triple synchs might also be correlated with mating success. Within-alliance paternity distributions could be used to test the hypothesis that the 'odd-male out' reproduces less than do other alliance members. The proportion of triple synchs may be

associated with participation in consortships, which is most common in mature but not old males (Connor et al. 2000). Again, these predictions hold regardless of whether synchrony or proximity is the adaptive signal.

Humans are thought to be unique in the extent to which they use synchrony to mediate alliance bonds and behaviour (McNeill 1995; Hagen & Bryant 2003). We have explored previously the interesting convergence between humans and Indian Ocean bottlenose dolphins in the formation of nested within-group male alliances (Connor et al. 1992). Our results raise the possibility that humans and dolphins may have converged in the use of synchrony as a signal in those alliances as well (Connor, in press).

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