

Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals

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Bottlenose dolphins in Shark Bay, Australia, live in a large, unbounded society with a fission–fusion grouping pattern. Potential cognitive demands include the need to develop social strategies involving the recognition of a large number of individuals and their relationships with others. Patterns of alliance affiliation among males may be more complex than are currently known for any non-human, with individuals participating in 2–3 levels of shifting alliances. Males mediate alliance relationships with gentle contact behaviours such as petting, but synchrony also plays an important role in affiliative interactions. In general, selection for social intelligence in the context of shifting alliances will depend on the extent to which there are strategic options and risk. Extreme brain size evolution may have occurred more than once in the toothed whales, reaching peaks in the dolphin family and the sperm whale. All three ‘peaks’ of large brain size evolution in mammals (odontocetes, humans and elephants) shared a common selective environment: extreme mutual dependence based on external threats from predators or conspecific groups. In this context, social competition, and consequently selection for greater cognitive abilities and large brain size, was intense.

Keywords: dolphins; brain size; alliances; social complexity

The open sea is an environment where technical knowledge can bring little benefit and thus complex societies—and high intelligence—are contraindicated (dolphins and whales provide, maybe, a remarkable and unexplained exception).

(Humphrey 1976)

1. INTRODUCTION

In his famous essay on ‘The social function of intellect’, Humphrey linked social complexity to environments where improvements in ‘technical knowledge’ paid large dividends. Dolphins were left as an unexplained puzzle. Many would agree now that Humphrey’s essay deserves praise for getting it right as to *what* we use our big brains for (social competition) but not necessarily *why* the environment humans lived in was one where social success paid big dividends (although technical knowledge may have played two very important roles in human brain evolution, as I describe below).

The most complex social relationships described so far in cetaceans are found in bottlenose dolphins (*Tursiops aduncus*, family Delphinidae) that live in Shark Bay, Australia. Males affiliate in nested alliances that vary in stability, size and relatedness. Synchrony may play an important role in mediating alliance relationships, suggesting an interesting convergence with humans based on imitative abilities, motion

perception or relationship *uncertainty*. A consideration of the ecology of alliance formation reveals that the interaction between ecology, alliance relationships and degree of social competition is a complex arena in dolphins just as it is in primates.

The evolution of a large brain probably played a key role in the impressive delphinid radiation. One of the reasons the delphinids have large brains is that they can afford them. A high quality diet supports a high metabolic rate that renders large brains less costly. The small-brained dolphins also consume a high quality diet, but it remains unclear whether they have a high metabolic rate. I offer a novel cost-saving hypothesis for delphinid brain evolution, based on the evolution of a high energy budget for group-feeding on schooling fish.

Increasingly, it seems that the social competition hypothesis may be the best explanation for all three ‘peaks’ in mammalian brain size: humans (and apes), elephants and odontocetes (primarily delphinids and sperm whales). It seems a good time, therefore, to revisit the question of environment to see if we can find common selective pressures that favoured extreme brain size evolution in these groups. This presents an interesting challenge, as one would be hard pressed to find three more different types of mammals in appearance and lifestyle.

In §17, I argue that extreme brain size evolution in elephants, toothed whales and humans was driven by a shared feature of their environment: a threat from conspecifics and/or predators leading to an extreme degree of mutual dependence. The relative importance

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of inter-group conflict seems secure for humans, and protection from predators is clearly important for odontocetes and elephants. An important role for inter-group competition is indicated by the nested alliance structure in dolphins and can be plausibly suggested for elephants and sperm whales, given their pattern of affiliation between stable groups.

2. THE SHARK BAY DOLPHINS: GENERAL FEATURES

(a) *Relationship uncertainty*

The social cognition hypothesis for primates was captured succinctly by Seyfarth & Cheney (2002), 'Primates...live in large groups where an individual's survival and reproductive success depends on its ability to manipulate others within a complex web of kinship and dominance relations'. Knowledge of the kin and dominance relationships between others has been touted by some as a characteristic that distinguishes primates from other mammals (Harcourt 1988, 1992), but this claim is undermined by the recent finding that hyenas recognize third party relationships (Engh *et al.* 2005). I suspect that recognition of third party relations does not represent a pinnacle of social intelligence but instead provides a necessary foundation that allows individuals to 'manipulate others'.

Recognition of third party relations has not been demonstrated in dolphins. However, our research in Shark Bay implies that if dolphins have this ability, their knowledge of third party relations must be incomplete and this *uncertainty* presents special perceptual and cognitive challenges. Relationship uncertainty is imposed by the sheer size and 'open' nature of the Shark Bay society as well as their fission–fusion grouping pattern.

(b) *Size*

The Shark Bay dolphin society is large and apparently unbounded. We have currently identified over 600 dolphins in our approximately 200 km² study area. The dolphins inhabit a mosaic of overlapping ranges where A might know B and B might know C but A and C do not know each other because their ranges do not overlap (figure 1; Connor & Mann 2006). Estimating the number of associates is not an easy matter for a large open society with a fission–fusion grouping pattern. Combining 4 years of survey data, we found that individuals typically had around 60–70 associates (Connor *et al.* in preparation), similar to the largest primate societies (Dunbar 1992; Barton 1996). Given the small percentage of time we actually observe the dolphins, this number is likely an underestimate. In addition to knowing some individuals and not others, the dolphins' distribution suggests that they might know some individuals well and some not at all well. Whereas in closed primate societies, individuals might be able to develop a fairly complete picture of third party relations (kin and rank), even if dolphins have such an ability, considerable uncertainty in their knowledge of third party relations may be unavoidable.

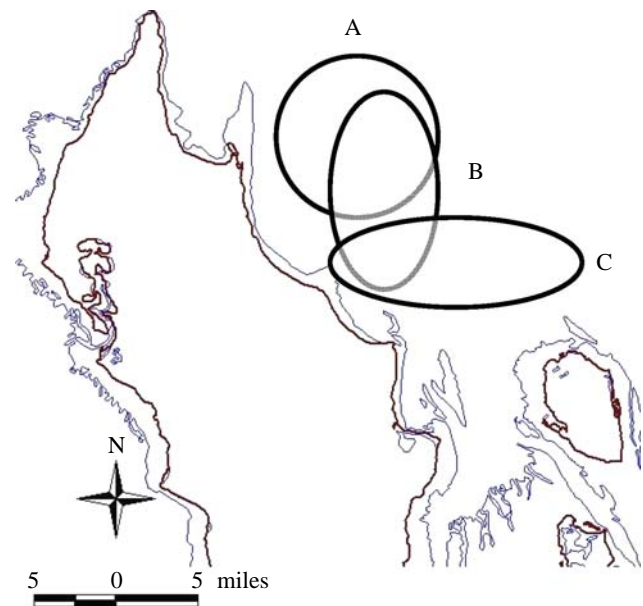


Figure 1. *Relationship uncertainty* in Shark Bay occurs because of the fission–fusion grouping pattern and is exacerbated by the mosaic of overlapping ranges. Individual B might know A and C well, but minimal range overlap will prevent A and C from knowing each other well.

(c) *Fission–fusion*

The Shark Bay dolphins live in a classic fission–fusion society where individuals associate in small groups that change composition frequently (Smolker *et al.* 1992; Connor *et al.* 2000). A fission–fusion grouping pattern presents two types of cognitive challenge. First, social relationships occur in a constantly changing social milieu 'placing a premium on the evolution of cognitive abilities' (Smolker *et al.* 1992; see also Barrett *et al.* 2003). This is especially true when the fission–fusion is of the 'atomistic' type (Rodseth *et al.* 1991). Second, fission–fusion also introduces uncertainty into an individual's knowledge of third party relations. Changes in relationships between others, even well-known individuals, may occur in other groups or 'off camera', posing significant cognitive challenges (Connor & Mann 2006).

3. THE DURATION OF RELATIONSHIPS: LIFE HISTORY AND PHILOPATRY

(a) *Philopatry*

Natal philopatry by both sexes may be common in cetaceans (Connor *et al.* 2000). At the two longest running bottlenose dolphin field sites, Sarasota and Shark Bay, it is clear that at least some individuals of both sexes continue to use their natal range as adults (Wells 1991, 2003; Connor *et al.* 2000; Connor & Mann 2006). This may allow individuals to begin very early in life to shape relationships strategically that will have reproductive consequences when they mature. Möller & Beheregaray (2004) maintain that genetic evidence from Port Stephens, Australia, contradicts the 'bisexual philopatry' hypothesis (Connor *et al.* 2000) in favour of 'females being the more philopatric and males being the more dispersing sex'. It is worth avoiding a sterile debate by pointing out here that both Wells (1991, 2003) and Connor *et al.* (2000) have stated that (i) males may have

larger ranges than females and (ii) philopatry by some males does not preclude complete dispersal by others (some males and females disappear). We are not surprised to see this produce differences in local relatedness, as it has in Shark Bay (Krützen *et al.* 2004). That some male and female offspring continue to use their natal ranges as adults in both locations is not a hypothesis but a fact, and one that raises interesting possibilities in the arena of social cognition.

4. THE STRUCTURE OF MALE DOLPHIN ALLIANCES IN SHARK BAY

Males in Shark Bay form two, and possibly three, distinct levels of alliance *within* their social network (Connor *et al.* 1992a,b; Connor & Mann 2006). The first level of alliance is associated with the formation and maintenance of consortships with females that may last for minutes to weeks (Connor *et al.* 1992a,b, 1996). These associations almost invariably involve two or three males consorting a single female.

The second level of alliance is associated with cooperation between first-order alliances to take females from other alliances or to defend against such theft attempts (Connor *et al.* 1992a,b). In spite of thefts being relatively uncommon (we are lucky if we observe 2–3 in a field season lasting several months and including several hundred hours of observation) males in second-order alliances exhibit high levels of association (Smolker *et al.* 1992; Connor *et al.* 1992a, 1999; Connor & Mann 2006). This likely reflects the importance of defence in these formations: during the peak of the mating season it is not unusual to find most or all members of a second-order alliance together or near each other, even though the group is ‘saturated’, or nearly so, with female consorts.

The size of second-order alliances varies considerably, from 4 to 14 or more males. A possible correlate of the second-order alliance size is first-order alliance stability (Connor & Krützen 2003). At one extreme, we find bonds between particular males that are highly stable for up to 20 years (Connor *et al.* 2000; Connor & Krützen 2003; Connor & Mann 2006). Such stable pairs or trios are usually found alone or in small second-order alliances. At the other extreme, members of one large 14 member second-order alliance (the ‘super-alliance’) shifted partners often between consortships but with distinct partner preferences and avoidances (Connor *et al.* 2001). Another possible correlate of alliance size and stability is relatedness. Krützen *et al.* (2003) found that males in stable first-order alliances that formed small second-order alliances were more related to their allies than expected by chance. However, relatedness in the super-alliance, even among preferred partners, was not above chance expectations (Krützen *et al.* 2003).

In recent years (2001–2005), as we expanded our study area to monitor alliance affiliations of over 100 adult males, it became evident that some second-order alliances associated regularly and amicably with other groups, suggesting a third level of alliance formation (Connor & Mann 2006). Our discovery in 1987 of two levels of alliance formation was preceded by similar observations of consistent associations between

particular first-order alliances. The alternative to three levels of alliance is two levels with varying degrees of association between first-order alliances (Connor & Mann 2006). Association and network analysis will resolve this issue. In 2001, we observed two conflicts involving the same three second-order alliances (Connor & Mann 2006). In each case, one second-order alliance attacked another, but the engagements were, unfortunately, too chaotic for either us or our video-cameras to discern if the third second-order alliance present supported one of the other two groups.

5. MAINTAINING ALLIANCE RELATIONSHIPS: AFFILIATIVE INTERACTIONS

The obvious dolphin equivalent to primate grooming is petting or ‘gentle rubbing’ where dolphins touch and stroke each other with their pectoral fins (Tavolga & Essapian 1957; Connor *et al.* 2000). Adult males pet with first- and second-order alliance partners and occasionally other males. Although commonly observed, petting typically occurs underwater where it is visible but individual identification is spotty. A behaviour that is more easily quantified and potentially interesting from the ‘social cognition’ perspective is synchrony. Commonly two, and sometimes three, dolphins will surface side-by-side synchronously, usually less than a metre apart (Connor *et al.* 2006). Frame-by-frame video analysis reveals that in cases judged to be synchronous by observers in real time, the males broke the surface within 80–120 ms of each other (Connor *et al.* 2006). The synchronous surfacing of male dolphins may be a by-product of proximity, for example, if synchrony reduces the overall drag on the pair or at least prevents one from having a drafting advantage (e.g. Weihs 2004). However, Connor *et al.* (2006) argued that synchrony is most likely an adaptive signal because normal synchronous surfacing is a common component of the astonishingly variable synchronous displays males perform around females (Connor *et al.* 1992b, 2000). These displays, which may include a variety of underwater and aerial leaps and turns, are not explicable as by-products of proximity.

Connor *et al.* (2006) examined patterns of synchrony among males that formed stable first-order alliances and small second-order alliances. Unsurprisingly, we found that when two first-order alliances were together, synchrony was more common between first-order alliance partners. Of more interest were the patterns that emerged when synchrony was examined in relation to activity. Inter-alliance synchrony, when a male from one first-order alliance surfaces side-by-side synchronously with a male from another first-order alliance, was much more common when the males were socializing, especially when they were engaging in excited socializing (chasing, mounting and splashing) with a female consort. Connor *et al.* (2006) suggested that inter-alliance synchrony in such a potentially competitive context might reduce tension between the males.

A comparison of several male trios revealed significant variation in several measures of synchrony including rates of synchrony and the proportion of synchronous surfacing that included all three males (measured as the ratio of pair/triple synchs for the

alliance). These measures may reflect alliance ‘unity’ more accurately than coefficients of association, and synchrony may be more common in males that are mature and engage in frequent consortships (Connor *et al.* 2006).

6. SYNCHRONY AND DOLPHIN COGNITION

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). If synchronous movement is prominent in human and dolphin alliance behaviour, why is synchrony not found more often in non-human primates that form alliances? Descriptions of synchrony are rare in non-human primates and we are not aware of any quantitative studies linking synchrony to social bonds. The fact that allied baboon males, *Papio anubis*, do employ synchronous manoeuvres on occasion (e.g. Ransom 1981) simply begs the question of why such visually oriented mammals do not employ such a powerful signal consistently. Here, we consider several adaptive hypotheses to explain this apparent dolphin–human convergence.

(a) Motion perception

Several authors have suggested that the dolphins’ visual system may be well adapted for motion detection (Dawson 1980; Madsen & Herman 1980). These suggestions are based mostly on peripheral anatomy: a horizontally elliptical eye that should cause images to sweep rapidly across the retina and a class of giant cells in the ganglion layer that subserve large regions of the visual field (Walls 1942; Dawson 1980; Madsen & Herman 1980). An enhanced ability to perceive motion could select for motion-based signals. At any rate, it seems likely that the social cues (e.g. spacing, posture and glance) that effectively signal alliance behaviour in primates might be less effective in lower light levels underwater and in animals where selection for streamlined form disfavours the ability to exhibit subtle facial contortions.

Intriguingly, recent magnetic resonance imaging studies indicate that humans have a region of the brain, the intraparietal sulcus, where motion detection is much more prominent than in the macaque homologue (Orban *et al.* 2003). Thus, humans and bottlenose dolphins may have converged on the use of synchrony as a social signal owing to a convergent enhancement of motion perception. In other words, the puzzle of why non-human primates do not use synchrony is one of our own (perceptual) making—it is not a powerful visual stimulus to them.

However, the likely functional reasons for a convergence between humans and dolphins in motion perception are different. Orban *et al.* (2003) suggest that the use of tools and hunting with primitive weapons may have favoured a greater investment in motion detection in humans. Of course, conflict between humans using hand-held or distance weapons may have been an even stronger selective factor. In contrast, a dolphin motion adaptation would likely be associated with the detection, pursuit and avoidance of prey and predators. Further research is needed on

motion perception in other non-human primates such as chimpanzees. Unless humans have a motion perception adaptation that is unique among alliance forming primates, this hypothesis fails.

(b) Imitation

A provocative possibility is that the convergent use of synchrony in alliance behaviour by humans and dolphins reflects a broader convergence related to having large brains and impressive cognitive abilities. Motor synchrony is under sophisticated cognitive control in bottlenose dolphins. Herman (2002, 2006) trained bottlenose dolphins to perform novel synchronous behaviours on command. Specifically, when dolphins were given two commands, ‘tandem’ (perform a behaviour together) and ‘create’ (perform any behaviour), the dolphins would self-select a behaviour and perform it synchronously. Of 79 different behaviours elicited with the ‘tandem+create’ commands, 23 were novel in the sense that they were not under the control of established gestures (Herman 2002, 2006). Imitation of one dolphin by the other is the most likely explanation for this ability (Herman 2002). In contrast, considerable research effort has failed to produce comparable skills in most non-human primates (Call & Carpenter 2002; Visalberghi & Fragaszy 2002), but the debate on whether apes are far from over (e.g. Whiten *et al.* 2004). The relative lack of imitation in non-human primates is puzzling, given the discovery of mirror neurons in monkeys and the finding that macaques recognize when they are being imitated by humans (Paukner *et al.* 2004). Byrne (2005) suggests that monkeys fail to learn by imitation because imitation is actually two different processes, ‘social mirroring’ or the more complex ‘learning by copying’, which involves ‘hierarchical construction of a behavioural program’ (Byrne & Russon 1998). Byrne (2005) suggests that monkeys are limited to social mirroring. Unfortunately, this distinction does not help us understand why allied monkeys fail to employ motor synchrony as an alliance signal. Dolphin synchrony may be parsimoniously interpreted as social mirroring and monkeys do not do it, at least not systematically.

While Herman’s work shows that synchrony in dolphins is under cognitive control of some kind, it is no more necessary to invoke complex cognitive processes for the simple repetitive movements of dolphins surfacing synchronously than for synchronous claw waving by fiddler crabs (Backwell *et al.* 1999). Indeed, dolphins may have been pre-disposed to incorporate synchrony into their social signals if motor synchrony was already an important part of their behavioural repertoire. Synchronous movements in schooling dolphins may have been favoured originally because they induced confusion in predators, much like the schooling behaviour of fish (Norris & Schilt 1988). An obvious objection to this line of argument is the same as given for the ‘proximity by-product’ hypothesis for synchronous surfacing. If synchronous displays are under cognitive control and synchronous surfacing is a common component of such displays, then it follows that synchronous surfacing must be under cognitive control as well. I am not particularly concerned with the outcome of this

argument, however, because I think that a more inviting ‘cognitive constraints’ hypothesis can be developed if we focus on the *social* context of synchrony. While imitation may not be necessary to explain synchronous surfacing in dolphins, their ability to imitate may have rendered synchrony more useful as a signal in the richly varying social contexts of within-group hierarchical alliances. For example, the relationship between inter-alliance synchrony and behaviour reveals that dolphin synchrony depends on context and not merely the strength or duration of an association. Facility with imitation may make it easier for a dolphin to surface synchronously with the right individual at the right time.

(c) Signalling benefits

Another possibility is that humans and dolphins are distinguished from non-human primates by the benefits they accrue from having a clear alliance signal such as synchrony. Lack of knowledge about alliance relationships could be very costly to individuals attempting to take resources from others (as well as to those they attack). Thus, factors that increase uncertainty about who is allied with whom should favour a strong alliance signal like synchrony. A male dolphin may learn who is allied by observing synchrony in others and may use synchrony to ‘test the bond’ (Zahavi 1977) with his putative allies. We identify three factors, shared by humans and Shark Bay bottlenose dolphins, which increase uncertainty about alliance relationships relative to most non-human primates. As noted earlier, changes in alliance affiliation may be unobserved in a fission–fusion society (Connor & Mann 2006); second, unobserved changes are more likely to occur in larger, open social networks; and third, unobserved changes are also more likely (other factors being equal) with additional alliance levels. Most primates, living in smaller bounded social groups, may simply not need such a signal.

7. ALLIANCE RELATIONSHIPS AND SOCIAL COMPLEXITY

Alliances and coalitions are, at a minimum, an important category of relationship, usefully illustrative of how social interactions can become complex, and at most, may be the kind of relationship that drove large brain evolution generally (Alexander 1989; Cords 1997; Harcourt 1992; Connor 1992b).

8. LEVELS OF ALLIANCE

As pointed out by Kummer (1967), within-group alliances are complex because they involve *triadic* interactions. Consider the trio of individuals labelled A, B and C (figure 2a). Any of these three individuals might try, using a variety of affiliative interactions, to form an alliance with another against the third; possibly giving rise to competition for alliance partners (see also Harcourt 1988, 1992). In contrast, interactions between non-human primate groups are not complex because they are not triadic (Connor *et al.* 1992a, figure 2b), but they may complicate within-group interactions by increasing mutual dependence within groups (see §15).

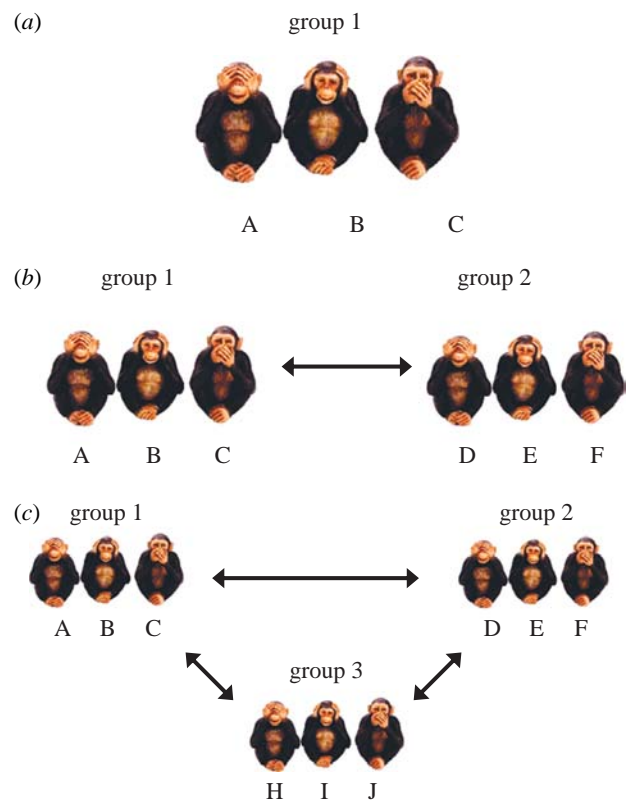


Figure 2. (a) Within group alliances may be complex when individuals compete for allies, e.g. if A and B compete for C. (b) Alliances against other groups are not usually complex because they are exclusively hostile. They may impact within group alliances by increasing mutual dependence within groups. (c) Humans and dolphins are exceptional to the degree to which they form ‘alliances of alliances’. Here alliance ABC could side with DEF or GHI against the other. Triadic interactions complicate within and between group interactions.

Having nested alliances *within* their social network allows dolphins to engage in triadic interactions between individuals *and* alliances (Connor *et al.* 1992b; Connor & Krützen 2003; Connor & Mann 2006, figure 2c). Such nested alliances are a hallmark of human social structure but are rare in other primates. The best primate examples come from female cercopithecines where matrilineal may cooperate to overthrow higher ranking matrilines (see discussion in Connor & Krützen 2003; Connor & Mann 2006). The decisions individuals make at one level of triadic interaction may be further complicated by possible impacts at the other level(s). Consider the trio ABC (figure 2c). A decision by individual A to recruit B against C could injure C and render ABC less attractive as an ally to DEF who might instead ally with GHI (Connor *et al.* 2006). It is not difficult to imagine the potential for this sort of problem to intensify demands on social intelligence. At this point, the word *potential* must be emphasized, for two factors must be in play for selection to put a premium on strategic alliance formation requiring enhanced social cognition: *options* and *risk*

(a) Options

Imagine that alliances are formed only between close relatives, and members of alliance ABC are related to DEF but not GHI. In this case, a sibling spat between

A and C will not impact the choice of alliance DEF because the simple 'kinship rule' eliminates strategic options. Thus, even though they have multilevel within-group alliances, the social world of cercopithecine females may be simplified significantly by the kinship rule (Connor & Mann 2006).

Options that might increase selection for greater social intelligence range from which potential ally to choose or compete for, to how much reproduction to yield to a partner, to how much to groom or stroke an ally. The number of potential partners will impact the difficulty of the decisions of how to behave towards a partner. This follows because there will often be a correlation between the number of options for an individual and that individual's potential partners: if A can choose B and C for alliance partners then B may choose A or C and so on. Asymmetries in resource holding power may render A the obvious ally for the other two (e.g. Noë 1990) but that does not make A's decisions necessarily simpler. B might have to be clever to win A's allegiance, but A might need to be clever about extracting the maximum benefit from B and C.

Connor & Mann (2006) reviewed the evidence for options at both levels of male alliance in Shark Bay. The greatest restriction on options appears to be among males that form stable pairs and trios, sometimes with close relatives (Krützen *et al.* 2003). However, strategic alliance shifts do occur among these males, who are not always close relatives (see Connor & Mann 2006). We have also documented males moving between second-order alliances.

(b) *Risk*

If alliance partners are interchangeable, so that the choice of B or C makes no difference to the fitness of A, or the choice of ABC or GHI makes no difference to the success of DEF, then decisions will be unimportant and alliance relations will not pose great demands on social cognition. In this case, individuals might employ a simple equivalence rule (Schusterman *et al.* 2003). The frequent partner changes in the 14 member super-alliance invite such an interpretation, but permutation tests revealed strong preferences and avoidances within the group (Connor *et al.* 2001).

A high risk decision is one where the difference between a good and bad decision has a high probability of a significant fitness gain or loss (the sum of many 'smaller' decisions could have the same impact). Note that decisions could be the difference between maintaining a fitness 'status quo' versus toppling off a fitness cliff (if you are ostracized or killed) or enjoying a huge fitness bonanza (choosing the right ally that allows you to assume top rank). In two cases where we observed Shark Bay males discontinue their second-order alliance affiliations (in one case the male appeared to have been ostracized; Connor & Mann 2006), they began associating with juveniles and ceased participating in consortships. In both cases, they began participating in consortships again several years later when those juveniles matured.

My studies have focused on adult males that are already members of alliances. Studies of what happens

prior to maturation will be essential to answering the question of how and how many potential alliance partners are evaluated during the juvenile period.

9. THE ECOLOGY OF ALLIANCE FORMATION

(a) *First-order alliance size*

Given that most consortships involve three males, but a minority two, it was commonly speculated among our research group that the optimal size of first-order alliances was a bit less than three males. For example, of the 58 consortships by non-provisioned males documented by Connor *et al.* (1992a,b), 26 were by pairs and 32 by trios for an average of 2.6 males. Of 100 consortships by males in the 14 member super-alliance, 95 were performed by trios and five by pairs, for an average of 2.95 males per consortship. During 2001–2002, we observed 103 males participate in 135 consortships with an average of 2.9 males. This latter sample affirms that the average across the whole study area is likely closer to 3.0 than 2.5.

Whitehead & Connor (2005) examined the question of alliance size using individual-based models in which alliances of greater net competitive ability out-compete those with less, and where males could switch alliances based on expected success. The most critical variable was the average number of males (m) competing for each receptive female. For example, the average alliance size ranged from 2.6 to 2.8 when $m=4-5$, with a clumped alliance distribution (versus Poisson) and assuming that males can leave alliances in pairs with no cost but suffer a cost when leaving alone. These assumptions are reasonable. Males probably do not move randomly among receptive females, likely avoiding those strongly defended by large second-order alliances. Further, a pair of males can leave as an alliance capable of consorting females, but we do not see consortships by single males. Thus, leaving alone would be more costly than leaving an alliance with another male. The value of m may well be less than five in Shark Bay. The adult sex ratio is not highly biased (Mann & Sargeant 2003, report that 46% of sexed non-calves are males). The operational sex ratio will be male-biased, given the typical 3.5 year interval between cycling periods for females that become pregnant and successfully wean calves (Connor *et al.* 1996). The average interval will likely be less than this, given the 44% calf mortality, two-thirds of which occurs in the first year (Mann *et al.* 2000).

In Sarasota Bay, Florida, adult males form stable pairs, but trios and second-order alliances are not in evidence (Wells *et al.* 1987; Connor *et al.* 2000; Wells 2003). Greater sexual size dimorphism, a less male-biased operational sex ratio or fewer sharks could explain the lack of trios (Connor *et al.* 2000), but the population density and thus overall encounter rates between males may be much higher in Shark Bay, favouring larger and more levels of alliances (Connor *et al.* 2000; Connor & Whitehead 2005).

(b) *Second-order alliance size and stability*

While first order alliance size is constrained within a narrow range of 2–3 males, the size of second-order alliances is much more labile, ranging from 4 to 14 or

more males. In primates, larger groups suffer more feeding competition as revealed by higher daily travel costs (Janson & Goldsmith 1995). Two factors might mitigate this problem for dolphins. First, dolphin travel costs are very low compared with terrestrial mammals (Williams 1999), so the costs of grouping should be substantially less (Connor *et al.* 1998; Connor 2000). More subtly, slight increases in grouping costs might be offset by a slight increase in some benefit of grouping, producing a benefit/cost ratio that is similar across a range of group sizes (Connor & Krützen 2003). Second, individual differences in foraging strategies are common in Shark Bay and these may impose different grouping costs on individuals. The ‘sponge-carriers’ (Smolker *et al.* 1997) are suggested to be relatively solitary owing to higher grouping costs, specifically the time it takes to forage successfully in this manner and the distribution and size of prey patches (Connor *et al.* 2000). If males differ in the average patch size they exploit (e.g. solitary benthic prey versus schooling fish) then they will experience different costs of grouping that might be reflected in the size of second-order alliances.

10. ECOLOGICAL INFLUENCES ON SOCIAL COGNITION

The differences we find between the Sarasota and Shark Bay bottlenose dolphin populations are likely ecological (but possibly owe to morphology or even phylogeny; see Connor *et al.* 2000). Perhaps, owing to their habitat and/or size, Sarasota males may have a less challenging social environment than males in Shark Bay. Sarasota males do not appear to have to negotiate second-order alliances, they do not experience the complications of trios, and once they choose their alliance partner the association may last a lifetime (Wells 2003). Further, the large size range of second-order alliances in Shark Bay may effectively create an ‘imbalance of power’ problem, putting smaller groups at risk (Manson & Wrangham 1991).

Should we expect the Sarasota dolphins to have relatively smaller brains and less advanced cognitive skills? Perhaps, but primatologists will recognize the ‘orangutan problem’ here, where one of the great apes appears to live in a less challenging social environment than the other two, especially the chimpanzee, but nonetheless has a large brain and in captivity seems quite clever. In the orangutan case, detailed observations in a new habitat revealed a more complex society than was known previously, as well as more complex, learned foraging cultures (van Schaik *et al.* 2003; van Schaik 2004). Compared with the great apes, the radiation of large-brained delphinids is huge and likely includes a range of social systems. Until a wider range of species are studied, we cannot begin to speculate as to what sort of ancestral society or pattern of alliance relationships was involved with the expansion of the delphinid brain. The bottlenose dolphins studied in Sarasota Bay and Shark Bay are in many ways ecological outliers of the family, as most genera live farther offshore in more open and deeper water habitats. What we can say is that the Shark Bay population reveals the level of social complexity that

Table 1. Three brain size comparisons for small odontocetes of approximately the same body size. (*Sotalia*, *Delphinus* and *Tursiops* belong to the family Delphinidae. Each of the others belongs to a different family with only 1–2 species in each (Adapted from Connor *et al.* 1992b; Connor & Mann 2006).)

species	N	body length (cm)	body mass (kg)	brain mass (g) or volume (cm ³)	brain size ratio
<i>Pontoporia</i>	9	153	39	227	
<i>Sotalia</i>	1	158	42	688	3.0
<i>Platanista</i>	4	197	60	295	
<i>Delphinus</i>	10	193	68	836	2.8
<i>Lipotes</i>	2	252	167	570	
<i>Tursiops</i>	19	246	231	1588	2.8

becomes possible in dolphins under the right ecological conditions. And we should not imagine that we have stumbled, so early in the game, on the most complex society in the entire family.

11. EXTREME BRAIN SIZE EVOLUTION IN PRIMATES, PROBOSCIDIANS AND ODONTOCETES

There are three ‘peaks’ in brain size evolution in mammals: in the primates, elephants and odontocetes. Outside of humans, the highest degrees of encephalization are found in the delphinid odontocetes (Jerison 1978; Connor *et al.* 1992b; Marino 1998).

Comparisons of species similar in body size demonstrate clearly extreme differences in brain size among odontocetes (Connor *et al.* 1992b; Connor & Mann 2006). The large-brained delphinids, ranging from 1.5 to 2.5 m in length, have brains in the 650–1600 g range. The smallest brained (non-monophyletic) group includes four single species families (*Pontoporia*, *Platanista*, *Lipotes*, *Inia*) that live in rivers, with the exception of *Pontoporia* which is marine. These animals range in size from 1.5 to 2.5 m and have brains in the 225–625 g range. Table 1 shows three size-specific comparisons revealing 2.8–3.0 fold differences in brain size, a figure similar to the difference between apes and humans. Members of the porpoise family Phocoenidae, appear to have brains of intermediate size (Marino 1998; Connor *et al.* 1992b; Connor & Mann 2006). Recent phylogenies confirm that the sperm whale is an ancient sister group to other odontocetes (Cassens *et al.* 2000; Nikaido *et al.* 2001; Hamilton *et al.* 2001; Arnason *et al.* 2004). Thus, the large sperm whale brain was most likely derived independently and will be considered separately. This distinction is also interesting given the remarkable convergence between sperm whales and elephants (Weilgart *et al.* 1996).

The ‘encephalization quotient’ or EQ is a popular way to compare species of different body sizes. The EQ is the ratio of actual brain size to the brain size ‘expected’ for a similar sized mammal, usually calculated from the slope for all or a large sample of mammals (Jerison 1973). Given that brain–body slopes change with taxonomic level (Martin & Harvey 1985; Pagel & Harvey 1989), the interpretation of EQs of different sized animals is problematic. Brain–body

slopes differ between orders and, in some orders, with taxonomic level. Thus, evaluating the encephalization of cetaceans with the overall mammalian slope (usually close to 0.75) might disguise what Martin (1980) called 'grade' differences. A grade difference is implied when regression lines for two groups at a given taxonomic level are found to have similar slopes but differ in their vertical displacement. The vertical displacement is taken to represent an adaptive shift in relative brain size (Martin 1980). For example, Manger (2006) argues that large brain evolution in odontocetes was driven by selection for increased thermogenesis in cold water, a feat he contends is accomplished by increasing the number of glial cells. Manger considers the encephalization of the bottlenose dolphin (*Tursiops truncatus*) to be similar to the much smaller harbour porpoise (*Phocoena phocoena*) based on similar EQs calculated from the general slope for mammals (note that Marino 1998, calculated lower EQs for *Phocoena phocoena*). However, comparison of similar sized delphinids and phocoenids removes the scaling problem and suggests that the delphinids may be more encephalized (tables in Connor *et al.* 1992a; Connor & Mann 2006), a conclusion that is problematic for Manger's 'thermogenesis' hypothesis as porpoises are generally distributed in cooler water than similar sized delphinids. More generally, if the odontocete brain size increase was driven by thermogenesis, we would expect a tight correlation between water temperature and brain size given that the 'ratchet effect' often postulated for the brain size evolution (see Humphrey 1976) holds only for information processing capacity. Selection should, for example, strongly favour a smaller brain in delphinids that live in warm water habitats. The warm water riverine but highly encephalized delphinid, *Sotalia* shows this not to be a necessary outcome.

12. PAYING THE COSTS

(a) *Brains, food and metabolic rates in dolphins*

Some hypotheses to explain primate brain size differences focused exclusively on costs (e.g. Martin 1981, 1982, 1983; Armstrong 1982, 1983) and were rejected convincingly (McNab & Eisenberg 1988). However, relative brain size differences among mammals must be determined *partly* by differences in available energy. Delphinids are fortunate, in this regard, to enjoy a high-energy diet that can be characterized as 'fish, squid and the occasional invertebrate'.

It is worth noting that the metabolic costs of a large brain for dolphins may be even less than indicated by their basal metabolic rate (BMR). What really matters, of course, is the proportion of the total energy budget used by the brain. The BMR was established as a standard by which different species could be compared. BMR comparisons will reflect relative brain costs only if BMR correlates closely with the total energy budget. Many terrestrial mammals, ourselves included, spend a large proportion of a 24 h day in a state that closely approximates standard metabolic conditions (e.g. during sleep). Evidence suggests, however, that many dolphins do not remain at rest for such extended periods and may continue to travel for nearly the entire day (see Connor 2000). The Ganges River platanistid,

the susu, swims continuously in captivity, a habit Pilleri *et al.* (1976) attributed to the ever-present currents in the susu's river habitat. Therefore, to the extent that the total energy budget/BMR ratio of dolphins is relatively greater than that for terrestrial mammals, their brains will be relatively cheaper to maintain than is indicated by their BMR alone.

In primates, brain size differences are sometimes associated with categorical differences in the energy yield of the diet, e.g. folivores versus frugivores (Clutton-Brock & Harvey 1980; but see Oftedal 1991; Dunbar 1992). This is not the case in odontocetes as the 'fish, squid and occasional invertebrate' characterization fits both the small- and large-brained dolphins. *Pontoporia* is an especially interesting case because, unlike the slower swimming river dolphins, they live in the marine habitat and have a scapular morphology indicating that they are stronger, more manoeuvrable swimmers than the small-brained riverine species (Strickler 1978). An extensive recent study of diet in this species could have been taken from the delphinid playbook, revealing *Pontoporia* to be an opportunistic feeder eating a variety of schooling and solitary fish and squid (Basso 2005). One has to look outside of the cetaceans, to the herbivorous sirenians, to find categorical differences in diet quality (see Connor & Mann 2006).

A measure of energetic requirements, the amount of food required to maintain body weight, indicates that *Inia* may have a lower metabolic rate than delphinids (Best & da Silva 1989) but data from a single captive *Lipotes* were in the same range as delphinids (Peixun 1989). A phocoenid, *Phocoenoides dalli*, whose brain size falls between the delphinids and 'river' dolphins, consumed much more fish than two delphinid species, likely owing to the importance of maintaining a high BMR for thermoregulation in this cold water deep-diving species (Ridgway & Johnston 1966).

(b) *Brain size differences in small odontocetes: the schooling fish hypothesis*

At this juncture, the data do not suggest a strong correlation between brain size and available energy in odontocetes. The data on metabolic rate in *Phocoenoides* clearly contradict the energy availability hypothesis, but they cannot be refuted for the smallest brained dolphins, *Inia*, *Platanista*, *Lipotes* and *Pontoporia*. To encourage further work in this area, I construct a diet-related hypothesis that takes into account the lack of obvious categorical differences in food type among small- and large-brained dolphins. Schooling fish offer a possibility. Fish schools represent a large patch of high quality but also highly mobile food. Dolphins digest quickly and with a high efficiency of assimilation (Shapunov 1973) using a longer than expected small intestine (Williams *et al.* 2001). Williams *et al.* argue that the additional investment in metabolically expensive gastrointestinal tissue is required to maintain the dolphins' high BMR. The metabolic rate/intestine relationship described by Williams *et al.* (2001) is just the sort of adaptation that would allow dolphins to take maximal advantage of feeding on fish schools. It allows dolphins to eat a lot quickly and move rapidly over long distances between schools. Operating on a higher

energy budget would render a larger brain more affordable. An obvious weakness of this hypothesis is that even the small-brained *Pontoporia* feeds on schooling fish (Basso 2005). However, if the early delphinids specialized more on schooling fish than other groups, and this specialization was associated with coordinated group feeding to corral or trap fish schools (as occurs in a wide variety of delphinids, e.g. spinner dolphins, *Stenella longirostris*, Benoit-Bird & Au 2003; killer whales, *Orcinus orca*, Simila & Ugarte 1993; the dusky dolphin, *Lagenorhynchus obscurus*, Wursig 1980; bottlenose dolphins, Gazda *et al.* 2005), then the hypothesis is feasible. I also note that a prominent function of the delphinid whistle is to maintain contact over distances (Smolker *et al.* 1993; Janik & Slater 1998), an important ability for coordinated group hunting (Herman & Tavolga 1980). Delphinid whistles are so different from those of other species that Podos *et al.* (2002) argued that they were a derived character for the group. The delphinid whistle may be adapted to provide information to others about orientation as well as distance. Lammers & Au (2003) suggest that the relatively high frequency of spinner dolphin whistles may provide useful information on whistler orientation to school members.

While delphinids are racing around digesting all those schooling fish, they are generating a lot of metabolic heat. Thus, the same adaptations that might have allowed dolphins to take full advantage of this rich resource generated additional body heat that allowed them to inhabit colder water. Can we distinguish these ideas conceptually? Consider an ancestral, sluggish, warm water dolphin. Selection acted to increase the energy budget, allowing investment in the musculature and digestive tissue needed to travel further and faster to capture and digest, quickly and efficiently, schooling fish. The benefit of this investment had to be greater reproductive success. Assume that the reproductive returns were associated with additional energy intake (as opposed to, for example, reduced predation risk) so the dolphins were essentially paying 5 to get 10. If the benefit of consuming additional energy was entirely heat production then the reproductive advantages might be associated with being able to live in new habitats and exploit new prey (or, yes, avoid predators). The schooling fish hypothesis is independent of the thermoregulation hypothesis only to the extent that the additional energy from feeding on schooling fish was associated with increasing fat stores and the ability to invest in offspring. Investment in brain tissue would have increased adult and offspring fitness in a challenging 'k'-selected environment. Most likely, given that heat production from increased digestion was inevitable, the two selective factors often operated in tandem. Differences in encephalization between delphinids and phocoenids suggest that the distinction may be useful.

It should be possible to test the 'schooling fish' hypothesis with comparative tests of small odontocetes' habitat and feeding modes to estimate the 'ancestral feeding type' and comparative studies of larger and smaller brained dolphins' feeding efficiency, basal

and field metabolic rates, heat balance, gut anatomy and feeding behaviour.

(c) *The sperm whale and the elephant*

A major early increase in odontocetes' brain size took place roughly 35 Myr ago (Marino *et al.* 2004). The more recent expansion of the brain in delphinids occurred about 15 Myr ago (Marino *et al.* 2004), long after sperm whales split from other toothed whales (Heyning 1997). The large sperm whale brain may have evolved independently, eased as well by a squid and fish diet, and additionally, a *large body size*. As noted by Whitehead (2003), the fraction of metabolism devoted to the brain depends on relative brain size which declines with increasing body size. Simply, other things being equal, big brains are cheaper for larger animals such as elephants and sperm whales. Elephants do not consume the high quality food of sperm whales, but may compensate by processing a lot of food at a high rate (Clauss *et al.* 2003).

(d) *Humans*

One possible role 'technical abilities' played during human evolution (Humphrey 1976) was in the realm of food processing. Several authors (Milton & Demmet 1988; Wrangham *et al.* 1999) have argued that early humans used tools (including fire) to make foods more digestible. This improved food quality could have paved the way for a reduced gut size and large energetic savings that could be redirected to the brain (Aiello & Wheeler 1995).

13. REAPING THE BENEFITS

(a) *The non-social cognitive challenges: food*

Although the focus here is on social cognition, I would be remiss not to discuss, at least briefly, how resource acquisition may have favoured enhanced cognitive abilities in dolphins and sperm whales. Cetaceans have enormous day and home ranges relative to terrestrial mammals and often feed on food that is distributed in patches (Connor 2000). I emphasize that the 'patchiness' of cetacean resources varies to an extreme degree across spatial and temporal scales (see Whitehead 2003). A bottlenose dolphin in Shark Bay may seek mobile patches of schooling prey or feed on benthic prey that occur only on patchily distributed shallow water banks. A sperm whale may move between patches separated by hundreds of kilometres and given areas may change productivity over periods of months or longer (Whitehead 1996, 2003). Greater memory and spatial knowledge may be favoured to the extent to which patch availability fluctuates predictably in space and time. To some extent, the mobility of dolphin prey will render 'mapping' difficult (Whitehead 2003). Ridgway (1990, 2000), has argued that the large delphinid brain was driven by the demand for more neural tissue to map acoustically the dolphins' environment in real time. However, it is not clear why delphinids would need to map a larger area in real time than, for example, the wide ranging, pelagic and deep diving but smaller brained beaked whales of the family Ziphiidae.

As Nicholas Humphrey was writing his 1976 essay, he would have been pleasantly surprised to learn what

we know today: the sea is indeed a place where 'technical knowledge' may bring benefits and innovation is highly rewarded (see Rendell & Whitehead 2001; Reader & Laland 2002). Bottlenose dolphins exhibit a remarkable range of feeding behaviours that they employ throughout the water column and even into the air, onto the beach and into the substrate (reviewed in Connor *et al.* 2000) which likely require considerable learning (e.g. Mann & Sargeant 2003). Moreover, compared with terrestrial environments, the marine habitat also seems to be the one that favours learned individual foraging specializations. Connor (2001) suggested that any or all of the following four factors might explain why individual foraging specializations are more prominent in the marine environment: a greater density of high quality foods; a greater variety of high quality foods; reduced seasonality; and greater improvements in feeding efficiency with practice. Whitehead (1999, 2003) suggests that significant differences in reproductive success between groups of matrilineal whales may result from innovations developed in one group and transmitted vertically.

14. THE SOCIAL COMPETITION HYPOTHESIS

In many primates, individuals compete for high-ranking alliance partners and solicit help in contests from those that outrank themselves and their opponent (see Harcourt 1992). This behaviour implies that individuals know the rank relations of others in the group, a challenging task when group size is large.

The claims of Harcourt and others for the uniqueness of primate strategic alliances were challenged with the finding that hyenas can also recognize third party relations in the context of coalition formation (Engh *et al.* 2005). In hindsight, as usual, the findings of Engh *et al.* are not surprising. After all, the brains of hyenas and the mid-sized old world monkeys that exhibit an understanding of third party relations are not vastly different, and the hyenas live in large complex societies (Drea & Frank 2003; Engh & Holekamp 2003; Wahaj & Holekamp 2003).

Further, most of the 'complex web of kinship and dominance relations' perhaps is not so complex if the monkeys follow a few simple rules, such as ally with close kin (female cercopithecines) and compete for the highest ranking ally available (Connor & Krützen 2003; Connor & Mann 2006). Greater social cognition would be required if individual rank or kinship were less of a deciding factor so that other strategies, such as cultivating friends based on more than simple rank, were employed to maximize reproductive success (see Cords 1997; Silk 2003).

What of the very largest mammalian brains? Among mammals that usually includes humans, with brains three times larger than similar sized apes, many delphinids, who place second behind humans in relative brain size and which boast brains 2–3 times larger than similar sized non-delphinid odontocetes (table 1, Jerison 1978; Connor *et al.* 1992a; Marino 1998; Connor & Mann 2006), and perhaps elephants and sperm whales, animals so large they are hard to compare with anything else and whose social lives and

life history have converged to a remarkable degree (Weilgart *et al.* 1996).

Alexander (1979, 1989, reviewed in Flynn *et al.* 2005) emphasized the importance of mental simulations of social situations or 'scenario building'—a much more cognitively challenging skill than simply recognizing the relations between any two other individuals. This is the social equivalent of Jerison's original (1973) argument that brains provided a model of the external world. Mental simulations might permit an individual to preview alternative future social outcomes based on choosing different options (e.g. A or B as an ally). A socially skilled brain must not only model the complexities of the current world but mentally play out the longer-term consequences of alternative scenarios (smack this individual, embrace that one). Recognizing third party relationships might be the basic foundation upon which increasingly sophisticated abilities to model social scenarios are based. And as I suggested earlier, it may not be the ability to learn third party relations that matters for big-brained mammals, but trying to keep track of many third party relations when the size of the social network and pattern of grouping constantly introduce varying degrees of uncertainty in that knowledge.

Why did humans get shunted down this path? Alexander (1989) argues that it was not predators but other human groups that drove the extraordinary evolution of the human brain. Ecologically removed from the risk of predation, inter-group conflict became the greatest threat to humans. As mutual dependence increased exponentially, so did the importance of *coalition cognition*. This is the second area where 'technical benefits' played an important role in humans; improvements of weapons would have given some groups a great advantage over others (see also Flynn *et al.* 2005).

15. CONVERGENT BRAIN AND LIFE HISTORY EVOLUTION IN HUMANS, TOOTHED WHALES AND ELEPHANTS

van Schaik & Deaner (2003) and Deaner *et al.* (2003) revisit the correlation between slow life history and large brain size (see Sacher 1959; Sacher & Staffeldt 1974; Pagel & Harvey 1988, 1989). Their new analysis, based on mammalian orders, revealed a weak relationship between EQs (observed brain size/expected based on body size) and longevity quotients (observed maximum lifespan/expected maximum lifespan based on body size) that became highly significant once the outlier Chiroptera were removed.

Low mortality is essential for slow life history to be favoured (Sterns 1992); this may derive from larger body size (Read & Harvey 1989) or an escape from terrestrial predators by flying or climbing (van Schaik & Deaner 2003). In primates, there is a weak relationship between arboreality and life history but not arboreality and brain size.

Although, as van Schaik & Deaner (2003) suggest, arboreality may have induced the initial evolution of slow life history favouring larger brains in early primates, it seems clear that the three peaks in brain evolution (or four if you count sperm whales as an

independent case) occurred in open, exposed habitat on the ground or in the sea. Humans, dolphins, sperm whales and elephants all depend on group living, and in some cases large size, to reduce mortality risk necessary for the evolution of long lives and large brains. The key is the vulnerability of offspring for animals that invest a lot in each one (Connor & Norris 1982). Alexander (1979, 1989) made a persuasive case for extreme mutual dependence based on inter-group conflict during human evolution. In elephants, sperm whales and dolphins, offspring vulnerability is extreme; elephant infants can neither run nor hide effectively and infant dolphins and sperm whales live in an open three-dimensional habitat without refuge (Connor & Norris 1982; Whitehead 2003 Connor & Mann 2006). A positive feedback loop may develop between sociality, group defence, reduced adult mortality and slow life-history processes for those species with a high investment in vulnerable offspring (see Whitehead 2003).

The extraordinary mutual dependence among individuals in these groups creates exactly the situation that leads to high risk social strategies. Individuals are in social competition with the same individuals their lives depend on: 'individual reproductive success would depend increasingly on making the right decisions in complex social interactions involving selves, relatives, friends and enemies' (Alexander 1979, p. 214). The key is that as group living, and in some cases large size, reduced adult mortality, smaller infants remained extremely vulnerable.

As longer-lived adults invest proportionally more in fewer offspring, mutual dependence increases in two ways. First, each offspring represents a higher proportion of lifetime reproduction. Second, as the period of parental dependency increases, so does the total number of predation attempts that have to be prevented (or, more exactly, the larger dependent offspring of larger, longer-lived mothers will be less vulnerable to the smaller, more abundant, predators and so will be attacked less often. However, this decrease in attack rate should not be in proportion to the increased duration of parental dependency, i.e. an infant dependent on its mother for 4 years will experience more threats than one weaned after 4 months).

The importance of group living and mutual dependence can explain why bats are an outlier in the relationship between longevity and brain size (see van Schaik & Deaner 2003) and why the relationship between life history and arboreality in primates is not matched by a similar relationship between arboreality and brain size.

We can consider also whether the source of the mutual dependence experienced by humans, toothed whales and elephants have elements in common. We have assigned the extreme mutual dependence in humans to other human groups and the elephants and toothed whales to predators. However, the nested alliances of male dolphins in Shark Bay and patterns of affiliation between female elephant and sperm whale groups hint at a role for inter-alliance conflict (see also Connor & Krützen 2003).

16. LIFE HISTORY AND SOCIAL COGNITION: ADDITIONAL CONSIDERATIONS

van Schaik & Deaner (2003) also argue that the longer inter-birth intervals associated with slow life histories will bias the operational sex ratio more towards males because fewer females will be receptive at any point in time. This greater potential for inter-sexual conflict, including infanticide, may favour more complex social strategies by both males and females (van Schaik & Deaner 2003). A male-biased operational sex ratio may impact directly the formation of alliances. Whitehead & Connor (2005) found that the expected size of roving male alliances was impacted primarily by the number of males competing for a female.

Another impact of slow life histories is less direct but no less important. By investing more in fewer offspring, long-lived animals reduce the options for forming same-sex alliances with close kin. If kin are favoured, and females produce litters with several males, then ready-made alliances of kin may be the preferred option. This eliminates the need for choosing partnerships strategically with the development of friendships and constant testing of bonds (Zahavi 1977). Longer inter-birth intervals also reduce the chance that a single born male will have close male relatives available as potential allies. Dolphins are at one extreme, where a female gives birth to one calf at a time several years apart. Consistent adherence to a simple rule such as ally with close kin will be less viable compared with offspring that are part of litters, or even better, synchronized litters of related females, e.g. lions (Packer & Pusey 1987). As it is clear that some male dolphins form alliances with close kin, but many and probably most do not, it is likely that kinship is the only one factor influencing their partner choice (although it may be a highly preferred characteristic when similar age relatives are available).

17. COMMUNICATION

It is appropriate to end this discussion of peaks in mammalian brain evolution with communication, because humans have the largest brain relative to body size and only humans have the facility of language. Language opened possibilities for social manoeuvring and manipulation that were not possible before. It is easy to imagine how just one of the abilities bestowed by language, communication about others in their absence, might have been put to advantage by those skilled in using and dispensing such information (and misinformation) to enhance their social position (e.g. Dunbar 2003). It follows that language may have become more than a tool necessary to maintain a large number of relationships (Dunbar 2003); by opening new frontiers in social manoeuvring, language itself may have generated selection for greater social intelligence.

It is easy to argue that our language facility is what really separates humans from other large-brained mammals such as elephants and dolphins, but if history teaches us anything, it would be to proceed cautiously with this conjecture. A lack of language does not preclude *a priori* complex communication about relationships, even relationships of those not present. It will be useful to illustrate how such a system might work, given what we know of dolphin vocalizations.

Consider our current understanding of social communication in dolphins (which means the bottlenose dolphin, *Tursiops*). Dolphins produce a bewildering range of vocalizations that are easily divided into two types: whistles, which are relatively long duration (mean duration 0.1–2.3 s; Matthews *et al.* 1999) often frequency-modulated tonal sounds; and pulsed sounds, which have a short duration and are relatively broad band. The communication functions of pulsed sounds have been studied hardly at all, primarily because they are difficult; they often *appear* to be graded and they are certainly difficult to quantify. Whistles come in discrete research-friendly packages which can be recorded and played back to dolphins with relative ease. In short, we have learned that a prominent type of whistle produced by bottlenose dolphins is their ‘signature’ whistle (Caldwell & Caldwell 1965; Caldwell *et al.* 1990), a learned vocalization (Tyack 1997; Miksis *et al.* 2002) that yields information about identity (Sayigh *et al.* 1999) based not on voicing but frequency contour (Janik *et al.* 2006), and that whistles are used as a contact call when animals are out of visual range (Smolker *et al.* 1993, Janik & Slater 1998).

The possibilities get very interesting when the dolphins’ imitative abilities are juxtaposed with the recent finding that it is the contour of the signature whistle that conveys identity (Janik *et al.* 2006). These two ingredients could form the basis of a system that allows dolphins to communicate about others in their absence, especially when combined with other whistle attributes or pulsed sounds that communicate affect (that pulsed sounds play an important role in communicating affect seems clear; beyond that our understanding of this rich vocal output is minimal, but see Connor & Smolker 1996; Herman & Tavolga 1980, pp. 164–166).

What is the current evidence for signature whistle imitation by dolphins—that dolphins can address each other ‘by name’? Dolphins certainly can imitate whistles, and a variety of other artificial sounds, with astonishing speed (Richards *et al.* 1984). Reiss & McCowan (1993) linked four distinct artificial whistles to the presentation of four different objects given to captive dolphins that later produced imitations of these sounds when interacting with the objects.

There are several reports of ‘sharing’ or ‘matching’ of signature whistles. Tyack (1986) recorded two captive dolphins producing whistles of two types in roughly inverse proportions (78 and 22% versus 31 and 69%). Obviously, similar data from a larger number of individuals would be more convincing. Janik & Slater (1998) and Burdin *et al.* (1975) found a few examples of whistle matching in captivity. Smolker & Pepper (1999) demonstrated convergence in the use of one whistle type by three male Indian Ocean bottlenose dolphins as their alliance developed. Similar whistle sharing was reported for allied males in Sarasota Bay, Florida (Watwood *et al.* 2004). The existence of such a learned alliance ‘badge’ has very interesting implications for communication about alliance status, but may result from a slower learning process and does not imply context-dependent imitation of others’ whistles.

Using a hydrophone array to localize underwater sounds, Janik (2000) reported whistle matching by unidentified individuals in the Moray Firth, Scotland. He recorded 176 whistle ‘interactions’ where whistles occurred in close temporal proximity but too far apart spatially for one individual to have swum rapidly between locations to produce both. Of these, 39 (22%) were matching interactions, where the same whistle type was produced. In one case three individuals produced the same whistle. The distance between individuals producing matching whistles was significantly less than for non-matching whistle interactions.

While Janik’s (2000) results might be explained by imitation of signature whistles where individuals are specifically ‘addressed’ by others, there is a more mundane possibility. Sayigh *et al.* (1995) report that in Sarasota Bay, Florida 9 of 21 (43%) male calves and 2 of 21 (10%) female calves developed signature whistles that were ‘very similar’ to their mothers. Given the long duration of parental care and the continued use of their natal range by males and females, the matching exchanges in the Moray Firth might be between mothers and offspring that have very similar signature whistles or allied males that have converged on a whistle type. In sum, the evidence for context-dependent signature whistle imitation in bottlenose dolphins, i.e. calling others ‘by name’, is suggestive but remains inconclusive. Evidence confirming spontaneous and context-specific whistle matching should not surprise us; rather, it would be surprising if the complexity of social relationships we find in Shark Bay is *not* matched by complexity in social communication.

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