Chapter 16
Social Cognition in the Wild: Machiavellian Dolphins?
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Abstract: Bottlenose dolphins have large brains and exhibit impressive cognitive abilities in captive studies. Observations of wild dolphins in Shark Bay, Western Australia suggest that these abilities are important for solving problems dolphins face in the social and foraging domains. Dolphins must keep track of a large number of social relationships while associating in groups that vary often in composition, be able to navigate nested within-group alliances and learn how, where and when to forage on a wide range of prey. The social problems dolphins encounter appear especially daunting, suggesting that the Machiavellian Intelligence hypothesis might apply to dolphins as well as to large-brained terrestrial mammals. With cetaceans, we are presented with a group of large, long-lived mammals that live in a habitat strikingly different from the terrestrial sphere and that exhibit striking diversity in brain size among species of comparable body size. We here review field studies of wild dolphin behavior that is potentially relevant to the Machiavellian intelligence hypothesis, describing general features of dolphin society, multi-level male alliances, female relationships, and affiliative interactions. We then explain why it is more plausible that brain evolution in dolphins was driven social demands than by foraging demands.

16. 1. Introduction: General features of dolphin society.
        For three days in 1976, 30 false killer whales[1], including 17 females and 13 males, remained in the shallows along the shore of the Dry Tortugas off the Florida coast. Oceanographer James Porter described this unusual but fascinating mass-stranding where, because there was little tidal movement, the whales were not actually stranded but floating in the shallows (Porter 1977). The whales flanked a large male that lay on his side, blood seeping from his right ear. When well-meaning people attempted to push them seaward, separating them from the group, the whales became agitated. Otherwise, they did not react when people rubbed sunscreen on their backs, but a female did bare her formidable teeth when a person ventured too close to her calf. Strangely, when Porter entered the water with a mask and snorkel, a flanking whale broke rank, approached him and pushed him shoreward. He tried this 3-4 times on each side with the same result. Nothing happened when he swam without the snorkel. After the male died (he had a severe nematode infestation in his ear) people were able to push the whales offshore, indeed, a few had already left the night before.
        On the face of it, such behavior seems anything but rational—especially in an adaptationist sense (as in Kacelnik's 'biological rationality, this volume). Certainly an extreme degree of mutual dependence is indicated—not surprising perhaps for mammals that live in a predator-rich but refuge-poor habitat. But why would these animals take such a risk to remain in the company of a dying male? He might be a relative or an alliance partner to the other males, but why would the females remain? Indeed, it would be difficult to generate a sensible adaptationist hypothesis if all we had to go on were studies of terrestrial mammals. One hypothesis is suggested by results from studies of killer whales (*Orcinus orca*), another large delphinid. In the 'resident' population of killer whales off south-western Canada, neither males nor females leave their mothers (reviewed in Baird 2000). This degree of not only geographic but also social philopatry[2] has no match on land. It suggests the reasonable

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[1]   *Pseudorca crassidens*, a large member of the dolphin family *delphinidae*, which also includes the bottlenose dolphin.
[2]   Philopatry, 'love of home,' describes the tendency of animals to remain in the place they were born (or more exactly, natal philopatry). In almost all mammals, members of one sex, usually males, disperse further than individuals of the other sex. Social philopatry

and testable hypothesis that both the male and female false killer whales may have been taking risks to help a relative. Of course, even if he were a relative, we would still like to know why his relatives valued him to that degree. Do adult males help defend offspring from predators or infanticide? Are old individuals reservoirs of social and foraging knowledge? Unfortunately we cannot begin to address these questions with what little we know of the social lives of false-killer whales.

While the social systems of killer whales and false killer whales may be highly unusual, for present purposes we are more interested in whether the individuals navigating those social systems face unusually severe cognitive challenges. The social system has a number of components, including social structure (pattern of social interaction, dispersal, nepotism, tolerance), social organization (size, sex ratio, spatio-temporal organization), and mating system (social and genetic components involved in reproduction, Kappeler & van Schaik 2002).   The Machiavellian Intelligence hypothesis about the evolution of large brains posits that analysis of social systems is critical for understanding selective pressures favouring greater cognitive capacity. Such an analysis requires examination of dyadic interactions and how these relationships are influenced by further relationships with others—i.e. how dyadic interactions fit into the broader social system.

Only four species of cetaceans have been studied well enough that we understand the basics of their social system (Mann et al. 2000a). Even among these few species, our knowledge of individual social relationships is reasonably advanced in only one, the bottlenose dolphin. And of the numerous locales where bottlenose dolphins have been studied, we have learned the most about their social relationships in a population in Shark Bay in Western Australia.

As we observe wild bottlenose dolphins in Shark Bay we can see what they do and, with the logic of natural selection, sometimes infer why. That inference can then be used to generate hypotheses and predictions suitable for testing. But at present we have no knowledge of what sort of mental or cognitive processes guide their decisions or whether they are conscious of their decisions, goals or beliefs or the beliefs of others[1]. Our studies in Shark Bay are thus relevant to what Kacelnik (this volume) calls 'biological rationality', but not yet to psychological rationality in a sense that requires actions to result from reasoning or from other specific cognitive processes. Whether the behaviors we observe can be interpreted in terms of an intermediate 'economic' sense of rationality is an interesting further question that we do not try to answer here. However, our observations *can* help us understand how the cognitive abilities demonstrated in captivity (see Herman and Tschudin, this volume) might be put to use in the wild, not only in the pursuit of social advantage but in resource acquisition as well. As was the case with primates, our studies of the complex behavior of wild dolphins will in due course lead to better understanding of the functions of dolphins' cognitive capacities and to further development and assessment of the Machiavellian intelligence hypothesis (see Byrne & Whiten 1988).

After providing some general background, we will review evidence of the social bonds among dolphins in Shark Bay, focussing on male alliances, both first-order and second-order, on female relationships, and on affiliative interactions. We have no data on the role that social rank and reconciliation play in the dolphins' lives, but we infer that they may be important on the basis of captive studies (Samuels & Gifford 1997, Weaver 2003, Samuels and Flaherty 2000). Other Machiavellian favourites, including tactical deception and knowledge of third party relationships, have not been explored systematically in captive or wild dolphins.[3]

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describes the tendency to remain with the group you are born in, irrespective of place.

[3] Metarepresentation--the ability to 'know what one knows' and to attribute belief or 'know what another individual knows' (for discussions, see Call, Shettleworth and Sutton, Proust, Currie, Tschudin, this volume)--is often thought to result from selection for social or 'Machiavellian' intelligence. Deceit and its use and detection are also thought to be important signs of social intelligence (Whiten & Byrne 1988). Some authors, notably

Some features of Shark Bay dolphin behavior, such as a fission-fusion grouping pattern, within-group alliances and parental care lasting several years, invite comparisons with primates (e.g. Connor et al. 1992, Connor et al. 2000, Whitehead & Mann, 2000). By contrast with the case of non-human primates, the social, cognitive and developmental features of bottlenose dolphins cannot be attributed to a common phylogenetic history with human beings. Dolphins thus provide a window into the underlying social and ecological conditions that might favor convergent evolution of complex forms of behavior and learning. Like the resident killer whales, the Shark Bay dolphins exhibit features, such individual foraging specializations, that are not common in terrestrial mammals (Connor 2001, Mann & Sargeant 2003). These areas of apparent behavioral convergence and divergence among species should be reflected in the differential cognitive demands on dolphins in the wild.

In the final section, we will return to the Machiavellian hypothesis in light of our review of the social cognition and behavior of wild dolphins. We will argue that cetaceans present an extraordinary opportunity to examine the relationship between advanced cognitive skills, complex behavior and the evolution of large brains. Compared to any group of terrestrial mammals, cetaceans have a greater number of large brained species and, more importantly, more size-matched species that exhibit extreme differences in brain size.

Before we provide details of dolphin relationships in Shark Bay, it will be helpful to have some general background on dolphin life history and reproduction and on Shark Bay dolphin society.

16.1.1. Life history and reproduction. Like primates, delphinids such as the bottlenose dolphin, have 'slow' life histories and delayed maturity in comparison with most other mammals. Females in Shark Bay have their first calf no earlier than 11 or 12 years of age (Mann et al. 2000b) and may live for several decades (Connor et al. 2000). Males may be capable of sexual reproduction at a younger age but do not appear to solidify alliances until their mid-to-late teens (Connor et al. 2000). A mature male that has not achieved whatever size, rank, or experience is required for alliance membership is likely to employ a different, perhaps more opportunistic, tactic (Connor et al. 2000). Indeed, recent paternity analyses suggest that subadult or 'juvenile' males may sometimes sire calves (Krützen et al. 2004).

After a 12-month gestation period, a female gives birth to a single calf she will nurse for an average of four years (range 3-8 years, Mann et al. 2000b). Variation in weaning age may be related to sex-specific strategies. Daughters are weaned, on average 11 months later than sons, with most males weaned at age 3, and most females weaned after age 4 (Mann et al. 2003). The respective advantages of early weaning for sons and late weaning for daughters may reflect differences in social advantages to males (developing strong male-male bonds and potential alliance partners) and to females

Trivers (1985) and Alexander (1979), have taken the social intelligence hypothesis to its logical conclusion and suggested that self deception is the result of an arms race between skills at deception and at detecting deception. To put it simply, if you are not conscious of your deceit then others will not be able to detect subtle signs that you are lying. Alexander (1979,1987) has argued that we may not have conscious access to considerable social information, including (some of) our intentions and motives. If self-deception is a hallmark of human social intelligence, then other large brained animals (or at least some hominid in our past) might have greater conscious access to their social knowledge than humans; they would 'know more about what they know' than do modern humans. Moreover, it would be interesting to ask if human beings self-deceive not only about their intentions and beliefs, but also about what they know or believe about others. In many social interactions it would pay to conceal subtle clues about what you are able to read in the minds of others.

(integration into her mother's network and the development of foraging strategies like the mother [Mann & Sargeant 2003]).

During the third year of her calf's life (but ranging from 1.5 to older) a female will be followed and consorted by males that cooperate in alliances to consort females. We have often used the term 'herding' to describe consort associations because many, and possibly all, are initiated and maintained by threats and aggression. Reproduction is 'diffusely seasonal' in Shark Bay with a peak in the Austral spring/early summer (September to January) but births can occur during any month (Connor et al. 1996, Mann et al. 2000). Given the 12-month gestation period, this means that there is a peak mating season as well, but that conceptions, like births, may occur during any month. One of the more interesting puzzles in Shark Bay is the fact that females that conceive in the primary spring/summer breeding season will often become attractive to males during the preceding Austral winter (July to August). Consortships during the winter months are typically shorter than during the breeding season and may play a role in allowing females to mate with many males, confusing paternity and reducing the risk of infanticide (Connor et al. 1996). We suggest two possible explanations of why males initiate consortships with non-attractive females. First, as we will describe below, some consorting may have more to do with male-male bonds than female attractiveness. Second, some consortships might be anticipatory. Consortships sometimes last longer than the estimated cycle duration of bottlenose dolphins (30 days, Yoshioka et al. 1986) and especially the 5-7 day period of rising estrogen levels reported by Schroeder (1990, see Connor et al. 1996). Goodall (1986) suggested that chimpanzees may consort 'flat' females (with non-tumescent sex skins) to avoid being pre-empted by other males; likewise, dolphins may consort a female that they anticipate will become attractive (Connor et al. 1996). Such pre-season consorting might also allow males to assess the female's response to capture, aggression and other behaviours associated with consorting or to impress females with their vigor.

16.1.2. General features of Shark Bay dolphin society. The Shark Bay dolphins live in an open 'fission-fusion society', i.e., individual dolphins associate in small groups that change in composition, often many times a day (Connor et al. 2000). The fission-fusion characteristic is one found in a number of other social mammals with complex social relationships. Among primates, the chimpanzees and spider monkeys have fission-fusion systems similar to that found in bottlenose dolphins (Wursig 1978, Goodall 1986, Symington 1990, Smolker et al. 1992). Smolker et al. (1992) argued that the constantly changing social milieu of a fission-fusion society can select for social intelligence:

> In some species an individual is almost always in association with the same set of conspecifics, while in others, an individual may rarely associate with the same conspecifics from day to day. Bottlenose dolphins exhibit an intermediate pattern, associating very consistently with a few others, but within the context of a wide range of different party types, containing individuals of varying degrees of familiarity drawn from an extremely large social network. Thus, each dolphin's social relationships are maintained within a constantly changing social environment, perhaps placing a premium on the evolution of cognitive abilities. (pp. 65-66).

This hypothesis has been further developed by Barrett et al. (2003) to explain differences in the cognitive abilities of monkeys and apes.

The 'open society' Shark Bay dolphins inhabit is dissimilar to primate societies in that primates almost invariably live in groups with strong social boundaries. In our current 200 km^2 study area off the east side of Peron Peninsula in Shark Bay, there are no boundaries demarcating closed or semi-closed groups such as one would find between two baboon troops or chimpanzee communities. Rather, we find a pattern of variably overlapping home ranges extending from one end of the study area to the other and offshore. Of course, we do not know what occurs beyond our study area.

A large number of individuals live in our study area; we have over 600 individuals in our

current identification catalogue. It is unlikely that all of these individuals know each other, as the home ranges of many do not overlap. What must happen often in such a society is that dolphin A knows dolphin B who knows dolphin C who does not know A because A and C's ranges do not overlap or overlap only slightly. This again is very different from the case of primates, who are likely to know all of the members of their semi-closed groups. Primates might be able to develop a reasonably complete knowledge of relationships between group members and use this information in strategically advantageous ways (e.g. Seyfarth & Cheney 2001). From a given dolphin's point of view, living in an open society can exacerbate a problem facing individuals living in fission-fusion societies: uncertainty about changes in third party relationships may occur out of sight and sound or 'off-camera'. Imagine, for example, that during occasional forays to the edge of their range a male dolphin alliance occasionally encounters a potential rival, but has no knowledge as to whether the rival is supported by two or twelve alliance partners.

        The number of individuals an individual knows has been used as an indirect measure of social complexity in order to test the Machiavellian Intelligence hypothesis (Dunbar 1992, 1998, but see van Schaik & Deaner 2003). Counting the number of relationships in non-primates is as easy as counting the number of group members; but how do you count associates in an open society? Without following individuals constantly, you can't. However, Connor et al. (in prep) took a four-year 'snapshot' of the number of associates an individual has in resting, travelling and socializing groups combined. This number is likely to underestimate even an 'instantaneous' measure of associations, since we observe such a tiny fraction of the dolphins' dynamic social lives. Two interesting results emerged; the number of associations (typically 60 to 70) were similar to those found in the largest large primate societies (Dunbar 1992, Barton 1996), and the largest (and smallest) numbers of associations were found in females (a few were over 100).   The variation in group size for females may be related to foraging strategies, thus raising the possibility of trade-offs between costs and benefits of foraging and social strategies in females.

        The Shark Bay dolphin society also differs dramatically from primate societies in exhibiting natal philopatry by both sexes, a phenomenon that may be ubiquitous in cetaceans (or nearly so; Connor 2000). Males may have larger ranges than females, and while we cannot exclude emigration by some individuals, it is clear that normally members of both sexes continue to maintain their natal range in their adult range (Connor et al. 2000, Krützen et al. 2004). From a cognitive perspective, this means that individuals of both sexes can potentially begin negotiating relationships from infancy that may be important when they are reproductive adults.

        Shark Bay dolphins maintain their strongest social affiliations with members of the same sex (Smolker et al. 1992). We begin our discussion of social relationships by exploring the cognitive challenges facing a male dolphin trying to negotiate the Shark Bay network of alliances.

16.2. Male alliances in Shark Bay: structure and complexity
        Male dolphins in Shark Bay exhibit multi-level alliances within their social group. Groups of two to three males (first-order alliances) cooperate to sequester and consort females for periods of minutes to over a month (Connor et al. 1992a,b, 1996). Teams of first-order alliances make up second-order alliances, which cooperate to take females from other alliances and to defend against such attacks. Males bonds within some first-order alliances show extraordinary short and long-term stability.   In a given year, certain males will be observed together in most or all sightings, yielding half-weight coefficients of association (COAs) [4] of 80-100 (Smolker et al. 1992, Connor et al. 1992a).

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[4]   COA = coefficient of association, a measure of how often two individuals are found together. We employ the 'half-weight' method (Cairns & Schwager 1987), defined as 100 x

Bonds between males in stable alliances have endured for as long as 18 years.   Stable first-order alliances typically form second-order alliances with one or two other stable first-order alliances. Occasional transient relationships among male dolphins cut across alliance levels (Connor et al. 1992).

     Males in a fourteen- member second-order alliance called the 'super-alliance' (Connor et al. 1999) formed first-order alliances that were labile, but variably so. Males in this group participated in 17 to 57 percent of their consortships of females with their most common first-order alliance (all trios). This result suggests a general correlation between first-order alliance stability and second-order alliance size.   In 2001 we began a study of over 100 adult males in the community, including several other large groups, and current trends suggest that, in general, the predicted correlation will be found. Why might such a relationship exist? A simple explanation is that in larger groups more males are available (not already in a consortship) at any given time to form a trio and consort a female. A more complex and interesting explanation would be that forming first-order alliances with more males helps to maintain second-order alliance bonds (Connor et al. 2001). However, while there may be elements of truth to both of these explanations, neither is sufficient to explain the complexities revealed by more detailed analysis of first-order alliance formation in the super-alliance (Connor et al. 2001, below). The males exhibited striking preferences (and avoidances!) in whom they formed first-order alliances with, and males in more stable first-order alliances spent more time in consortships with females (Connor et al. 2001).   Consistent choice of alliance partner however, did not yield the same advantage (i.e. a male forms first-order alliances with the same partner but the third member of the trio varies, Connor et. al. 2001).   These results suggest a complex social structure, perhaps including important dominance relationships, within the super-alliance.

     16.2.1. Alliance levels. Alliances within social groups, common in primates and some large social carnivores, but infrequent elsewhere, are a canvas for complex social relations (Harcourt 1992, Cords 1997, de Villiers et al. 2003, Engh et al. in press). Why is this so? Firstly, within-group relations are triadic (Kummer 1967) so individual A might form an alliance with B against C. Second, relationships are mediated by affiliative interactions, so individual B might recruit A as an alliance partner against C by grooming her. But imagine that C is also trying to recruit A (perhaps A is high ranking) and that there is competition for allies (e.g. Seyfarth 1976). This combination of characteristics, triadic interactions mediated by affiliative behavior, so prevalent in within-group interactions, is not found in interactions between groups in non-human primates. While two groups of monkeys might simultaneously threaten or chase a third (for example, members of two bands of hamadryas baboons on a sleeping cliff might threaten a third band), there is no evidence that such interactions reflect a higher level allegiance between groups that is maintained by grooming between members of different bands. While threats from other groups might temper aggression within groups (e.g., if you kill a member of your group you may be more vulnerable to attacks from other groups), imagine how much more complex decisions would become if relations between groups were triadic and mediated by affiliative interactions. Suppose that members of one social group use affiliative interactions to recruit allies in contests against other groups. Now when individual B considers recruiting A against C, B might also have to consider potential consequences at the next level of alliance, when her second-order alliance ABC tries to recruit alliance DEF against alliance GHI. For example, it is possible that conflict within their group—if C is injured—might make their group a less attractive ally for alliance DEF who would then be more likely to ally with GHI against ABC.   If this has a ring of familiarity, it is because the one primate to which such nested or 'hierarchical' alliances

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$2Nt/(N_A + N_B)$ where Nt is the number of groups containing both individuals A and B, and N_A and N_B are the total number of groups for each individual, respectively. COA's range from 100 for two individuals that are always in the same group, to 0 for two individuals that are never together.

are extremely important is *Homo sapiens* (Boehm 1992). Human beings routinely navigate a landscape of nested alliances that range from kin factions to nation states (see discussions in Connor 1992a; Connor & Krützen 2003).

The potential of nested alliances to exacerbate demands on cognition in the social realm has long been under-appreciated.   Among non-human primates, we find the best example of nested within-group alliances in female-bonded old-world monkeys.   Matrilineal relatives form first-order alliances and members of matrilines share adjacent ranks.   Most of the monkeys' alliance behavior can be explained by two simple rules, ally with members of your matriline against non-members and with high-ranking non-relatives against low-ranking non-relatives. Additional complexity is suggested by the occasional reversal of the second rule, in which lower ranking matrilines unite to overthrow a higher ranking matriline (Samuels et al. 1987, Chapais 1992, Gygax et al. 1997) and the existence of more transient social relationships among females from different matrilines (Seyfarth & Cheney 2001). Nonetheless, if an individual's relationships at the first alliance level (e.g. matrilines) are entirely predictable (or nearly so), then a second alliance level might not introduce a significant burden on social calculations---compared, say, with the burden for a species that negotiates only one level but of relatively unpredictable alliances (Connor & Krützen 2003).

An alliance landscape can be considered complex to the extent that it entails strategic options and risk. This will be true if individuals can benefit by developing or changing alliances strategically and if the bonds they form are always at risk because of the strategic options available to others. If a female monkey has no real options other than to ally with her matrilineal kin, then her alliance landscape is simplified. On the other hand, increasing the number of options (e.g. choosing allies from among a large number of non-relatives) may not, by itself, increase complexity unless there is also significant risk involved in decision making. In general, a high-risk alliance is one where alternative choices can result in a significant increase or decrease in reproductive success. The latter might result from injury, a loss of rank or expulsion from the social group.   High-risk alliances, such as those that might occur among non-relatives and/or where the consequences of losing are severe, would place a premium on social intelligence. Choosing the wrong ally or the wrong time to form an alliance could be very costly. Our female monkey who has limited options as to her choice of first-order allies—the matriline she is born into—may engage in high risk alliance behavior with other matrilines when they join forces to overthrow the top-ranking matriline. In addition to the second order alliances between female old world monkeys, other examples of high-risk alliances in primates are first order alliances between individual male chimpanzees and New World cebus monkeys (de Waal 1982, Nishida 1983, Perry 2003).

Sometimes hierarchical association patterns are interpreted too generously as hierarchical alliances. Kitchen and Packer (1999) claim that 'discrete social groups' of
African savannah elephants and Hamadryas baboons ' show second-, third-, and fourth-level alliances'. There is no evidence, however, of repeated agonistic interactions between groups at each level of association for either of these species (see Connor et al. 1992a for a discussion of male alliances in Hamadryas baboon). While further study might reveal hierarchical alliances in some cases, hierarchical social structure can clearly exist for other reasons. For example, Mitani and Amsler (2003) report male sub-groups, but not alliances, among male chimpanzees in an unusually large community of 140 individuals in Uganda. They suggest that the subgroups, distinguished by the age and rank of their members, are an outcome of peer relations in a large community where integration into the adult social network is difficult. By contrast, both first- and second-order dolphin alliances operate within the social network and are mediated by affiliative interactions (Connor et al. 1992a,b, 2000, submitted., below).

To assess how complex the dolphin alliances are, we need to consider each level of alliance.

Pairs and trios that are highly stable and include relatives might be the most predictable and risk free. However, some stable alliances are not composed of relatives; it is not clear that even a majority are. Moreover, over a period of years we have seen shifts that suggest a significant risk even in stable alliance relations.

16.2.2. Shifting alliance relationships. The following sort of interaction has been reported in chimpanzees: a beta male attempts to overthrow the alpha male by forming an alliance with the third ranking male, only to have the alpha and third ranking male join forces against him, leading to a drop in rank. Here the beta male took a significant risk and lost. We might expect relationships to be less risky if they are at either extreme of stability. A perfectly stable alliance relationship likely entails less risk for its members, and highly fluid alliance relations suggest that members are inter-changeable, so interactions should pose little risk or cognitive challenge for that matter--if you fail to acquire one alliance partner you simply switch to another. Some male dolphins' alliance relationships are highly stable and some are quite fluid. In the rest of section 16.2 we examine patterns of shifts in alliance membership closely for evidence of strategic options and risk.

16.2.3. Shifting relations in 'stable alliances': a 17 year history. The potential for strategic behavior among males in stable alliances is shown by alliance shifts over time. In Box 1 we illustrate this with a 17 year history (1985-2001) of two males whose alliance affiliations intersected during this period but who have very different histories; Real Notch (Rea) and Lucky (Luc, who apparently isn't very lucky!). Three salient points emerge from the review of Luc and Rea's social histories. First, stable alliances aren't really very stable; rather, they are at the stable end of a continuum. Although infrequent, the changes that occur (such as Luc's apparent expulsion from the alliance), suggest that stable alliance bonds carry a significant risk. Second, when observing these interactions between dolphin *alliances*, it is difficult not to see parallels with interactions between *individual* primate males. We can speak of social relationships between alliances, not simply between individuals. Third, the history suggests how changes at one level of alliance might impact another. When the trio of Rea & Hii & Poi quit associating with Luc in 2000, they were left without a second-order alliance partner. While they increased their association with some members of two large second- order alliances (achieving COAs of 20-30 with several of these males in 2001), as of 2003 they still did not associate consistently with any other alliance.

16.2.4. Shifting relations in the super-alliance. Whereas partner shifts in stable alliances were usually associated with disappearances (or the lingering presence of Luc in the mid-1990s), shifts were the norm in the 14 member super-alliance. Based on 100 consortships of females observed during the 3-year study (1995-1997), we documented 39 different first-order alliances in the group. Male trios were involved in ninety-five of the consortships and only five consortships were by pairs of males (we have never conclusively documented a consortship by more than three males). No consortships involved males from outside the 14-member group. Each male was observed in 10-30 consortships with 5-11 different alliances and 5-11 alliance partners.

As with stable alliances, partner shifts in the super-alliance occurred between, not during, consortships. The frequency of the shifts in this group might suggest that for the purposes of consorting females, males in the super-alliance have no preferences about male partners. Cognitively, the males could be following a simple 'equivalence' rule (Shusterman et al. 2000), consorting with any available male in the group. Connor et al. (2001) tested and rejected this hypothesis; super-alliance males exhibited strong and significant partner preferences and avoidances within the group. Alliance relationships within the super-alliance are thus individually differentiated (a more complex hierarchical equivalence model might do it justice, Schusterman & Kastak 2002, but see Seyfarth & Cheney, 2003). The sheer size of the super-alliance is also of interest in light of the correlation in primates between neocortex size and the number of primary social associates an individual maintains

(Kudo and Dunbar 2001). Whether one uses the total group size (14) or the number of first-order alliance associates in the super-alliance (5 to 11), the number is larger than that found in most primates.

16.2.5. Shifting relations among the provisioned males and their allies Frequent alliance partner shifts also characterized relations among three provisioned males that made daily visits to a beach where they accepted dead fish from humans (Connor & Smolker 1985, Connor et al. 1992a). This trio of provisioned males were second-order allies of a pair in 1987, which itself became a trio in 1988. Two of the three provisioned males were paired for any given consortship, and the excluded male sometimes paired with a male from their 'buddy' alliance. We suspect that the free food played a relatively indirect role in the extraordinary rate that the provisioned males consorted females (over 250 cases in 1987-1988!). A substantial reduction in fish fed had no apparent affect on the frequency of consorting. Feeding may have exacerbated conflict between the males, who had to pay attention to fish buckets arriving from the shore as well as to the female, who was often trying to escape in the opposite direction.

We suspect that much of the consorting by the provisioned males had more to do with maintaining fragile male-male bonds than the proximity to female ovulation.[5] Observations suggest that some of the females they consorted may have not been receptive. For example, only the provisioned males were observed to consort females with newborn calves and 53% of the females they consorted in 1987 were back with them in 1988 (having not produced a surviving calf), compared to 11% for the non-provisioned alliances during the same period (Connor et al. 1996).

For two consecutive years before the provisioned males died in 1989, the frequency of partner changes among them was high from May through August (3 to 11 changes per month), before dropping significantly during the breeding season months of September through December (1 to –2 changes per month; see Connor et al. 1992, Connor & Smolker 1995). Again, although consortships lasted longer during the breeding season, reduced availability of male partners during the breeding season could not explain this result (Connor & Smolker 1995). Rather, we suggest that frequent shifts prior to the breeding season may function in testing or competing for potential alliance partners and forming alliances (Connor & Smolker 1995).

16.2.6. Shifting Relations among second-order alliances. Interactions between males that belong to different second-order alliances may be hostile or amicable and such relationships can change over time. This is illustrated by relationships between three large second-order alliances that have extensively overlapping home ranges, the original super-alliance (the WC group), and the PD and KS groups. During the original super-alliance study, the WC group had 14 members that shared COA's of 29 to 96 (81% were in the 40 to 70 range). PD group members were juveniles in the mid-late 1980s and formed their second order alliance during the mid-1990s; COA's in the group ranged from 26 to 73 during 1994-95, 56-96 during 1996 and 75 to 91 during 1997; i.e. the lowest COA during 1997 was greater than the highest in 1994-1995. The large (at least 11 members) KS group was more of a mixed bag during this time with mostly older juvenile/maturing males, but at least one was clearly an adult that had been apparently excommunicated from his original group (but unlike Luc, he found a new home).

Interactions between the WC group and the KS and PD groups during the three years of the WC study were infrequent and hostile. By 2001 the WC group was down to 10 males; three of the original 14 had disappeared and one joined a different second-order alliance. The KS group (now a coherent second-order alliance with 14 members) and the PD group were intact and, importantly,

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[5]   As in the month in 1994 when the pair Bot & Poi were consorting a different female during each sighting; see Box 1.

several years older. In 2001 the PD group was observed associating (sometimes with affiliative interactions) several times each with the KS group, with the WC group and even with the trio Rea & Hii & Poi; however, the WC and KS groups did not associate with each other.

Two observed interactions between the second-order alliances WC, KS and PD suggest a third level of alliance formation. The more interesting of these interactions involved all seven members of the PD group, five members of the KS group and all ten members of the WC group. We first encountered the PD and KS groups together. Two trios in the PD group were consorting females and four KS members had a female. It was not clear which KS males were consorting the female, which may have been a source of conflict in the group as two KS males chased and fought. Then a trio of WC males blasted into the group and the aggression level escalated, with much chasing and aggressive vocalizing. One of the KS members involved in the fight was surrounded and attacked by at least six to eight males. Later the WC trio left briefly to meet seven other WC males that were leaping in from hundreds of meters away, so all ten WC males surged past our boat into what was now a very tight group of KS and PD males. This entrance resulted in a group of 22 males engaging in an especially intense and chaotic period of chasing, fighting and splashing, with a cacophony of aggressive vocalizing that at one point, incredibly, stopped abruptly. Finally the five members of the KS group left, minus their female, which was now with the first WC trio that joined. After the altercation, the PD group still had their two females. Neither of the two later arriving WC trios had a female when they entered and they evidently did not try to take the females from the PD group. Critically, in neither this nor the other observed interaction were we able to determine if the PD group 'took sides' or remained neutral.

Second-order alliances occur when two first order alliances cooperate against another first-order alliance. Similarly, cooperation between two second-order alliances against another second-order alliance would constitute a remarkable third level of within-group alliance in the Shark Bay society. If, in all the chaos of the fight, we had been able to determine that the PD group sided with the WC group against the KS group, this criterion would be met. Our observations fell short of that, but the affiliative associations we see between second-order alliances and the presence of three second-order alliances in a fight is certainly suggestive. Thus, at this stage we cannot claim that males form third-order alliances, but we can say that there are generally affiliative relationships between some second-order alliances, as indicated by associations between members and even complete groups that sometimes include petting between males from the different groups.

16. 3. Female relationships in Shark Bay

Female relationships display greater flexibility and lability than male relationships. While members of a male alliance are frequent associates, females are likely to spend less that 30% of their time with their closest female associate (Smolker et al. 1992). The average group size for adult females is four to five animals, but they range from being highly solitary to highly social (Smolker et al. 1992, Mann et al. 2000b, Connor et al. 2000).   While the competitive nature of male relationships is obvious from the striking agonistic interactions among males, observations of female – female agonistic interactions are rare.[6] Of the few cases that were observed, nearly all occurred in the provisioning area in Monkey Mia, Shark Bay where three-to-four adult females have been hand-fed fish by tourists standing in knee-deep water over the last thirty years (Mann & Smuts 1999; Mann & Kemps 2003). Thus females can be characterized as tolerant in their social relationships.

Access to food is likely to be the limiting factor in female reproductive success (Mann et al. 2000; Mann & Watson in press). Thus, one might expect females to compete over food. However the

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[6]   Having been observed only a few times in fifteen years and 1960 hours of observation on focal adult females (Scott et al. submitted).

nature of dolphins' food source--single, mobile, difficult-to-capture prey--may limit competition. Each dolphin catches and typically quickly swallows her prey whole. Shark Bay dolphins, whether female or male, almost never steal each other's fish. This 'ownership' rule extends even to fish tossed several meters (Connor et al. 2000). Such respect for ownership is notable. Moreover, unlike many carnivores, females do not share prey, even very large fish catches, with their offspring (Mann & Sargeant 2003). Thus dolphins are both 'polite' and 'selfish'; they neither steal nor share food. This characteristic pattern may further support tolerance amongst female dolphins. They stay close when resting, socializing or travelling, but can disperse easily for foraging, which is more of a scramble than a competition. Nevertheless, it remains possible that dolphins may be excluded by others from particular foraging areas, or from active-feeding groups (see Wilson et al. 1997). We have seen dolphins leap toward a group actively feeding on a fish school, only to stop short and simply watch without joining.

Each female has a distinctive foraging profile with a limited range of foraging techniques (Mann & Sargeant 2003). These may well dictate the patterning of her social relationships, since some of those techniques (such as sponge-carrying, a form of tool-use) seem to require a high proportion of her activity budget (Smolker et al. 1997, Mann & Sargeant 2003). Some females use techniques rarely used by other members of the population and/or they may become specialists, using predominantly one foraging tactic. For example, four females regularly beach themselves to catch prey in a specific area of Shark Bay, despite the apparent risk of stranding (Berggren 1995, Sargeant & Mann 2003; Mann & Sargeant 2003). Although dozens of dolphins regularly associate with the beaching dolphins and can clearly view this behaviour, they have never been observed beaching (Sargeant & Mann 2003). Thus, these females engage in a highly specialized foraging tactic that may require years of practice. The two calves born to these beaching females have been observed engaging in intermediate stages of the behaviour (Sargeant & Mann 2003). At least two of the beaching females have been using this foraging method for over ten years. Females who engage in similar foraging tactics may be more likely to associate if only because of extensively overlapping home ranges; the beaching females commonly associated even when away from the beach (Sargeant & Mann 2003).

Female associations may be related to reproductive state (Connor et al. 2000), but evidence on this is currently lacking. Females in the same reproductive condition are likely to experience similar energetic constraints and needs. During lactation, association with other lactating females may reduce predation risk and provide social opportunities for the calf. Pregnant females are typically still nursing their previous calf until mid-way through the 12-month gestation period (Mann et al. 2000), and the presence of a large dependent calf may have a greater influence on her activity budget than pregnancy per se. Cycling females may cooperate to reduce the costs of harassment by juvenile males (Connor et al. 1992, Connor et al. 2000). However, since cycling females are relatively rare (dolphins operate with a skewed operational sex ratio, given 4 to 5 year inter-birth intervals), most of the available female associates for cycling females would be lactating.

Females have been observed jointly mobbing sharks (Mann and Watson in press; Mann and Barnett 1999), but not attacking males. However, there is some anecdotal evidence illustrating the potential of female tactics even against adult males. For example, while Puck was being consorted by three males (Rea & Hii & Bot), Puck suddenly sped up to join an all female group. As soon as the males joined the group of females, the females began petting and rubbing with all three adult males. Puck was flanked by two females and slowly escorted away from the group. When Puck was about 50 meters outside of the group, she bolted and the two escorts slowly returned to the group. Moments later, the males apparently noticed Puck's absence and suddenly broke from petting and rubbing with the females. They bolted in three different directions, but failed to find Puck until the next day.

It is tempting to interpret these events as evidence for tactical deception rather than as a confluence of coincidences, since all the behaviours exhibited are infrequent. It is not common for three males to be involved in petting females at the same time or for a single female to be flanked by

two other females. By flanking Puck, the females essentially concealed her, both visually and acoustically, from the males. The slow movement away from the group prior to the rapid bolt appeared "intentionally" deceptive; but in any case, the males were clearly fooled.

Most of a female's life is consumed with calf care and balancing the trade-offs between maternal care and foraging. During foraging, females accelerate to chase fish and cannot easily maintain contact with their calves. Calves begin to learn to hunt as early as 4 months of age; their hunting increases steadily throughout dependency (Mann & Sargeant 2003). Mothers may reduce the costs of lactation by facilitating foraging skill in their calves. Although some foraging tactics are probably learned individually without social exposure, most of the techniques likely involve social learning, primarily from the mother (Mann & Sargeant 2003). Social learning (broadly defined as learning that is influenced by conspecifics through mechanisms such as imitation, social facilitation, local or stimulus enhancement) is clearly implicated in dolphin foraging, although the precise mechanisms are not well understood. There is ample field evidence for social learning in the acoustic domain for cetaceans (e.g., see Janik and Slater 1997; Noad et al. 2000; Deecke et al. 2000), but evidence for social learning of gestures and motor movements has been limited to captive studies of bottlenose dolphins (Janik 1999) and one field study (Mann & Sargeant 2003).

Foraging presents an appropriate avenue for investigating social learning in bottlenose dolphins because they exhibit diverse foraging techniques both within and between populations (Shane 1990; Connor et al. 2000; Mann & Sargeant 2003). In Shark Bay we are examining the matrilineal patterns of foraging, the ontogeny of foraging among calves, and foraging patterns of the larger population. Foraging might represent the best examples of socially learned motor (as opposed to vocal) activity and the development of calf foraging might be a critical factor in determining the length of nursing or nutritional dependency on the mother (ranging from 3 to 8 years in Shark Bay, Mann et al. 2000). An understanding of skill development during infancy informs theoretical models about life history schedules. Our current work demonstrates that at least four foraging strategies qualify as "traditions," socially-mediated learning that is transmitted across generations. For example, sponge-carrying, the only form of tool-use in any wild bottlenose dolphin or whale, emerges between 2 and 4 years of age, and only among calves born to sponge-carrying mothers (Mann & Sargeant 2003). This specialization is exclusive to approximately 33 (mostly female) dolphins, less than 10% of the female study population. It involves finding and tearing off conical marine sponges from the substrate, placing the sponge on the rostrum (beak) and using the sponge to ferret fish from the sea floor. Sponge-carrying is used in the search process and ceases prior to the final chase and prey capture. Genetic data also suggest matrilineal transmission (Krützen et al. submitted). Sponge-carrying and other foraging techniques likely involve both social and individual learning, and are relevant to ecological models of learning which predict, for example, that intergenerational transmission of learned techniques is favored when environmental variability is moderate (see Laland & Kendal 2003).

16. 4. Affiliative interactions

One of the key features of intragroup bonds in primates is that they are established, negotiated, maintained and repaired by affiliative interactions. Affiliative interactions, such as grooming in primates, may have beneficial effects, such as removal of parasites or stress reduction; but close physical contact may also act as a potential stressor. In an intriguing but under-appreciated paper, Zahavi, (1977) argued that the function of affiliative contact is to 'test the bond' between the individuals. Since physical contact of some kinds, such as kissing or embracing in human beings, would be stressful or otherwise unacceptable between two individuals that do not enjoy a particular bond, it can be used by one party to test the strength of their bond with the other.

16.4.1. Petting. Dolphins don't have hands with which to groom each other, but they do 'pet'

each other with their flippers and can rub other parts of their body against each other (Connor et al. 2000). Petting may reduce stress but may also allow for testing of bonds. A category of petting that occurs often enough to rate special mention in our ethogram is 'mutual face-genital' petting where one dolphin is being petted on the genitals while the other receives petting around the face. Dolphins will also pet each other on the flukes and fins and it is not uncommon to see one dolphin stroke another directly on the blowhole. That touching in these areas is a potential stressor is obvious from watching humans interact with the provisioned dolphins. The dolphins are quite particular about where they will allow people to touch them—basically limiting contact to a stroke down the side. Petting the dolphin on top of the head (where the blowhole is), anywhere around the face or on the dorsal fin or flukes usually results in a warning (head jerk) followed by a bite or hit if the offending party persists.

A key distinction between inter- and intra-group relationships in primates is that only in the latter are bonds formed and mediated by affiliative interactions, allowing triadic interactions (Kummer 1967). Here and elsewhere (Connor et al. 1992, Connor & Krützen 2003) we have argued that having both alliance levels within a social network distinguishes male dolphins from non-human primate males that form two levels of alliance, but only one within a social group. We should expect to find affiliative interactions not just between males in the same first-order alliance but also between males in the same second-order alliance but different first-order alliances. And this is indeed the case; petting occurs both within and between alliances that are members of the same second-order alliance, and even between different but affiliating second-order alliances. However, since a male's primary affiliation is with his first-order alliance we should expect to see males pet preferentially with members of their first-order alliance when two alliances are together.

The most intensively studied males were the three stable alliances that formed the social triangle in the 1980s: the pair Rea & Hii and their relationships with the trio Cho & Bot & Lam and with the trio Tri & Bit & Cet in 1987-1988, and then the relationships of the trio Rea & Hii & Bot with the trio Tri & Bit & Cet in 1989. We examined affiliative interactions when all members of two alliances were together. Although petting was frequently detected, telling who is stroking whom is difficult when the principles remain underwater. Thus sample sizes are unfortunately small and the results equivocal. Petting interactions between the pair Rea & Hii and the trio Tri & Bit & Cet (n=49) were strongly correlated with alliance membership, but interactions between Rea & Hii and the different trio Cho & Bot & Lam were not (n=40) (Connor et al. submitted). While petting between alliances is observed, especially during excited interactions with females, and is probably very important for maintaining cooperation between alliances, we suspect that with a larger sample size it will be shown that males pet more with their first-order alliance partners.

16.4.2. Synchrony. In addition to the elaborate synchronous displays males perform around females (Connor et al. 2000), male dolphins often "synch" (surface side-by-side synchronously; see also Herman's discussion, this volume, of synchrony in captive dolphins). Since this behavior occurs at the surface, individual participants are easier to identify than in petting. We found a strong relationship between first-order alliance membership and synchrony (Connor et al. submitted). Further, synchrony and petting were highly correlated in the relationship between the two alliances for which we had the largest sample size of both petting and synchs, (Connor et al. submitted).

Synchs recorded between males of different alliances were more common when the males were socializing than when they were travelling or resting. This interesting result also holds when we remove petting from the analyses and focus specifically on 'excited socializing' that includes splashing, displays, chasing, and sexual behavior. Tension between alliances should be greatest during these conditions and approximately 75% of inter-alliance synchs occurred during excited socializing with the female consort or, occasionally, another female in the group. Thus, the relationship between inter-alliance synchrony and social behavior may indicate that synchrony serves

to reduce tension and/or to signal cooperation, as in some forms of primate affiliative behavior (Aureli et al. 1999). Synchronous surfacings begin at birth and newborn calves have very high rates of synchronous surfacing with their mothers (Mann and Smuts 1999). This may be where calves learn the relationship between movement and bond formation that is so important also in adulthood.

     16.4.3. Contact swimming: A female specific affiliative behaviour Because females do not form the strong alliances found in males, are rarely observed behaving aggressively, and have a much 'looser' network of same-sex associates, one might be tempted to conclude that social bonds are not that important to females. However, not only do females pet each other, but a striking category of pectoral fin contact behavior is almost exclusively conducted between females (Richards 1996, Connor et al. submitted). In *contact swimming*,

> …one dolphin (actor) rests its pectoral fin against the flank of another dolphin, behind the other dolphin's pectoral fin and below or just posterior to the dorsal fin. Two individuals swimming in this close staggered fashion are highly visible. (Connor et al. submitted)

A common context for contact swimming is mixed sex groups with males consorting or harassing females.   These observations indicate that contact swimming may function to signal cooperation between females and/or reduce stress (Connor et al. submitted).   Additionally, the staggered position of contact swimming suggests that the trailing female may enjoy a brief 'free ride', but we suspect the real importance of this slight altruism is its value as an honest signal from the ride-giver.

     16.4.4. Sociosexual behaviour. Sexual behavior in bottlenose dolphins is observed in a wide range of contexts, from aggression to affiliation (Connor et al. 2000). In addition to male-female sexual behavior, observations among males range from one alliance member mounting another in a very relaxed manner, to one alliance herding another alliance. In the only clearly observed case of its kind, the pair Rea & Hii herded the second-order alliance partners of their rivals, the provisioned males, for 65 minutes (Connor & Smolker 1996). The sexual and aggressive behaviors directed at the male pair included charging, biting, chasing, mounting and other contact with erections and the 'pop' vocalization that is associated with female consortships (Connor & Smolker 1996).

     Studies of dependent infants reveal that male-male relationships are preferential from an early age. This is particularly evident in sociosexual behaviour: male calves prefer to interact with other male calves, when the availability of partners for each age-sex class is controlled for (Mann in press). Male calves were typically the actors, rather than recipients of sociosexual behaviour and were commonly involved in triadic interactions involving three males (Mann in press). Synchronous sociosexual behaviours (simultaneous mounts or beak-to-genital pokes or pushes) were conducted by males almost exclusively, although the recipients could be male or female. Homosexual behavior is likely to be important in mediating the development of these male bonds, possibly by establishing reciprocity, "trust,"(cf. Zahavi 1977) and assessing the manoeuvrability and social skills of potential alliance partners. For example, male partnerships in socio-sexual activities could mediate the development of long-term bonds through taking turns as actor and recipient (symmetrical relationships) and practicing synchronous movement in chasing, mounting, displaying and goosing (where one dolphin pokes its rostrum into the genital area of another) other males or females. The recipient of socio-sexual behaviour is vulnerable by exposing the belly and genital area to one or more males in the advantaged rear position. Role exchanges may be important for establishing trusted allies.

16.4.5. Rational or emotional dolphins? The affiliative and aggressive interactions we observe make it seem obvious to us that emotions play an important role in dolphin social relationships (whether they are conscious of them or not). What role *should* emotions play in a rational dolphin? If a dolphin is interacting with another and assessing their relationship in an economically or adaptively rational way, it should recall all of its interactions with the other individual, whether they were positive or negative, and weight each interaction by its value (for example, whether, as a result of the interaction, the dolphin gained a fish or lost an estrus female). This history should be integrated in some fashion and the output of that integration, in combination with the value of the present interaction, should be used to make a decision about how to behave toward the other dolphin (e.g. pet it, smack it, or ignore it). Aureli and Schaffer (2002) suggest that emotions provide just such a bookkeeping and integration system. Emotions, in their view, function to provide a timely assessment that can guide social decisions. This is very similar to Damasio's view (1994) about the role of emotions in human decision making in social and other arenas. Ironically, as he describes, if affect is removed (say, by a stroke) human beings become incapable of making rational choices (assuming that these must take efficiency and the value of outcomes into account).

16.5. Discussion: Brains, Cognition and Behavior

Most readers of this volume will be aware that bottlenose dolphins and other delphinids have large brains--larger than great apes of similar body size (Connor et al. 1992a). Herman (this volume) describes an impressive range of cognitive abilities that likely relate to the complex social lives and foraging tasks described in this chapter. We would like to understand why these attributes evolved in a group of aquatic mammals and if the same selective pressures were at work in the evolution of large brains on land. While these are not easy questions to answer, we nevertheless think that cetaceans have a great deal to bring to the table of comparative studies.   This view is based on something that readers of this volume are probably *not* familiar with: the huge variation in brain size among cetaceans.

Delphinids have brains that are two to three times the size of some of the other small toothed whales of similar body size—a ratio similar to that distinguishing humans from the great apes (Connor et al. 1992a). Table 2 displays some interesting comparisons. For example, the first listed member of the Delphinidae (*Sotalia*), the Phocoenidae (*Neophoenaena*) and the Pontiporidae (*Pontoporia*) are quite similar in body size but vary markedly in brain size. Or one can compare species of similar brain size but vastly different body size, such as the 5.5 m killer whale (*Orcinus*) and the 12m Humpback whale (*Megaptera*).[7]

We cannot do justice to the myriad hypotheses that have been forwarded to explain large brain evolution in dolphins, so we will limit ourselves to a few issues pertinent to perception, cognition and brain evolution in animals.

16.5.1. Food and brains: energetics, resource distribution and echolocation. Several hypotheses emerge from a consideration of dolphin prey acquisition. First, it is important to note that the energy-rich foods consumed by dolphins support an overall energy budget that renders a large brain much more affordable. A useful contrast is the relatively small-brained herbivorous manatee (from the only other mammalian order, Sirenia, to evolve a fully marine existence), which has a low metabolic rate

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[7] See Whitehead 2003 for an interesting discussion of the controversy about absolute versus relative brain size in relation to our interpretation of brain size in sperm whales. Note that the data in Table 2 probably underestimate relative sperm whale brain size, given that the brain data are all from males and that there is the striking sexual size dimorphism in this species.

and whose low-quality forage spends six days passing through its digestive tract (Lomolino & Ewel 1984). Five male and eight female manatees from Florida that ranged in length from 281-376cm and mass from 449-1620 kg, had an average brain size of only 364 gm (range 309-455, Pirlot and Kamiya 1985; O'Shea and Reep 1990). By comparison, at a length of only 2.5 m, the 'small' brained Chinese river dolphin (*Lipotes vexellifer*) has a brain 50% larger than the manatee. A bottlenose dolphin (*Tursiops truncatus*), at a length of 245 cm has a brain over 1550 grams. Larger delphinids similar in length (320-340; but smaller in weight) to manatees have brains in the 2000-2500 gm range (Table 2). At 7.5 m, the recently extinct Stellar sea cow was as long as a large killer whale, but had a brain 1/5 as large.[8]

The significant costs of large brains must be exceeded by the benefits they provide. Large brains might be useful for animals facing the potentially difficult problem of predicting where food will be found in space and time and extracting it (e.g. Milton 1988). The spatial distribution of dolphin prey species that live on or near the seafloor, the temporal and spatial distribution of schooling prey and, especially, we are finding, the particular methods used to procure prey, may require a considerable amount of learning.

Dolphins employ an extremely sophisticated echolocation system to find food and navigate in their habitat (Au 1993, Thomas et al. 2004). Perhaps selection for sophisticated echolocation abilities led to the enlargement of the delphinid cortex. Herman (this volume) rejects this common but 'specious' argument, based partly on the echolocation abilities of much smaller-brained bats. Comparative data on neural structures associated with acoustic processing in similar-sized dolphins also fail to support the echolocation hypothesis (Table 3). Differences in the size of cranial nerves and the colliculus that readily distinguish dolphins with different visual capabilities do not appear in acoustic comparisons. Thus, Morgane & Jacobs (1972) obtained an optic nerve fiber count of 15,500 for *Inia* (n=1) compared to 147,118 for *Tursiops* (n=8) but only 19,500 for the delphinid *Sotalia* (n=1) which inhabits the same murky river waters as *Inia*. In contrast, Morgane and Jacobs (1972) report fiber counts in the VIIIth nerve for *Tursiops* of 116,414 (+4014) and for *Inia* of 120,000. Even with a much smaller brain, *Pontoporia* has an acoustic nerve and inferior colliculus as large as the common dolphin, *Delphinus delphis* (Table 3). Behavioral studies of the perceptual abilities of smaller-brained odontocetes are required to test the hypothesis that greater acoustic discrimination accounts for the larger cortex in delphinids (Worthy & Hickie 1986). Worthy & Hickie's hypothesis also predicts that there is no correlation between the volume of acoustic tracts and primary auditory cortex in dolphins, unlike, for example the correlation between the optic tract and primate primary visual cortex (Dunbar 2003).

16.5.2. Machiavellian Intelligence in Dolphins. Herman (1980) was the first person to suggest that the key to understanding large brain evolution in dolphins might be found in their social lives. The complexity of the social lives of dolphins in Shark Bay does nothing to undermine this perspective. Perhaps what makes the Machiavellian Intelligence hypothesis heuristically more attractive than the hypothesis that foraging demands have driven brain evolution is a fundamental difference between food and foes: individuals in your social group try to outwit you, but your food does not.

Why did dolphins evolve complex social lives? In his deservedly famous essay on the social function of intellect, Humphrey (1976) linked social complexity to technical knowledge; "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)." But if not technical knowledge, then what? Given that the social complexity hypothesis assumes a strong dependence on group living, we can ask what there is about living in the ocean that may have

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[8]   Cranial capacity of 1,100-1225 ml, compared to a brain weight of over 6000 gm for the killer whale; O'Shea and Reep 1990.

fostered a strong mutual dependency in some cetaceans. There are two obvious candidates: predators and each other.

Prior to the recent focus on intragroup alliance formation in primates, a leading theory of the evolution of human brain size and intelligence focused on inter-group alliances, i.e. warfare (Alexander 1979, 1989; Alexander and Tinkle 1968, Bigelow 1969). Inter-group conflict places a premium on social cognition because individuals in a group are in reproductive competition with the same individuals with whom they must cooperate against a most formidable adversary, other humans (Alexander 1979). In other words, as the danger of inter-group conflict escalates, so does the mutual dependence of group members (Alexander 1979; Connor and Norris 1982), and consequently, 'individual reproductive success would depend increasingly on making the right decisions in complex social interactions involving self, relatives, friends and enemies" (Alexander 1979, p. 214).

The theories of intra-group alliances in non-human primates and inter-group alliances in humans have rarely crossed paths; most papers on the evolution of social complexity in non-human primates neither discuss nor cite the theory that inter-group conflict promoted social complexity in human evolution (e.g. Harcourt 1988, 1992, but see Rodseth and Wrangham 1991, Manson and Wrangham 1991). The multiple levels of alliance formation in dolphins provide a conceptual link between theories of intra-group conflict in non-human primates and theories of inter-group conflict in humans. The key issue is whether individuals must base decisions at one level of interaction at least partly on the impact that those decisions will have at other levels.

Even for species with only one level of alliance formation within the group, the interaction between within-alliance conflicts and between-alliance conflicts can be very important. Levels of aggression within alliances will likely be influenced by the magnitude of threat from neighbouring alliances (see Vehrencamp 1983). In humans and chimpanzees, for example, this threat can be substantial (Goodall 1986, Manson and Wrangham 1991, Alexander 1979) and it is exacerbated by a fission-fusion social system that can produce encounters with an imbalance of numbers on opposing sides. This can reduce the cost of escalated aggression for those 'with the numbers' thereby increasing the risk and dependency for all involved (see Manson and Wrangham 1991). Dolphins often separate widely from their alliance partners during foraging bouts where they might find themselves at risk, as might a lone pair or trio in the range of a large second-order alliance. While no lethal aggression has been observed among males in Shark Bay, cases where several males line up head-to-head against one in an almost ritualistic fashion (in one case the fifth dolphin came from behind the target to do so), suggests the possibility.

Predators may have (at least) started dolphins on the road to more complex social lives. Sharks prey on dolphins and can threaten the calves of larger odontocetes and baleen whales (Wood et al 1970, Chapter 3). Cetaceans at sea inhabit a three-dimensional environment in which they cannot climb up a tree, crawl down a burrow or hide behind a rock; they have nothing to hide behind except each other. Connor and Norris (1982) pinpointed birth and early nurture of offspring at sea as the critical factor increasing mutual dependence in dolphin societies. Vulnerable offspring that require significant investment would have favored selection for those life history characteristics (long periods of dependency, late maturation and longevity) associated with large brain size in mammals (see van Schaik & Deaner 2003). A focus on vulnerable offspring explains why mutual dependence may be high in mammals that are relatively invulnerable to predators as adults, such as sperm whales (Best 1984, Whitehead 2003) and elephants (Douglas-Hamilton 1975, Lee and Moss 1986); and it offers a partial explanation for their convergent social systems and large brains. The typical ungulate strategies of 'hiding' and 'following' are not available to elephant calves, which are slow and hard to conceal. Likewise, sperm whale calves have nowhere to hide and may not be able to follow their mothers to great depths. Sperm whale calves approach other older sperm whales at the surface while their mothers dive; thus they are not left unprotected at the surface when their mothers are feeding (Whitehead 1996).

16.5.3. Concluding remarks. Our observations in Shark Bay have revealed a society of great size with complex social relationships including nested alliances, affiliative behaviours that range from the expected (gentle touching) to the surprising (synchrony and the sex-specific 'contact swimming'), and individual foraging specializations and tool use. After over twenty years of observation at this 'Dolphin Gombe', we are still learning how the cognitive skills discussed by Herman (this volume) are employed in the wild. The studies of synchrony reported in Herman's chapter and ours illustrate the potential exchange that may occur between captive and wild studies. It is unfortunate that there are not more institutions with captive dolphins supporting long-term research on cognition and behaviour (apart from the heavily funded but narrowly focused studies on echolocation).

Combined with results from captive studies and the remarkable variation in brain size among species of similar body size, our Shark Bay discoveries suggest strongly that, apart from primates, no animal group offers more potential for productive exploration of the relationship between brain size, cognitive skills and behaviour than cetaceans. The difficulties of studying many wild cetaceans that once appeared insurmountable have been mitigated to a significant degree by advances in technology (such as acoustic localization techniques and dive 'tags' that record everything from vocalizations to swimming speed; see Whitehead & Tyack 2000).

Here we have compared the Shark Bay dolphins to terrestrial species, especially primates. However, it is also essential that we should be able to compare the Shark Bay society to other species of cetaceans such as the Baiji, the Susu and Pontopora that have much smaller brains--- if those poorly known species can be saved from their current race to extinction (Whitehead et al. 2000). Only then will we be able to understand the selective forces that produced such remarkable brains, societies and cognitive skills in a habitat so strikingly different from the terrestrial habitats in which primate brains evolved.

Box1: Real Notch and Lucky: A 17 year history

During 1985-89 Lucky (Luc), who appeared to be a small adult, maintained a mutually strong association with Poi, a juvenile. Each also associated with another juvenile, Lod (Table 2). During 1985-87, Luc & Poi maintained modest associations with members of a second-order alliance composed of the trio Snu & Sic & Bib and the pair Wav & Sha. Luc & Poi & Lod did not consort females in the 1980s.

Meanwhile, by at least 1986 Rea and his associates, all adults, were consorting females on a regular basis. In 1985 Rea was in a pair with Hac and Hii was in a pair with Pat; these two pairs associated closely (Smolker et al. 1992). These four males associated only occasionally with two stable trios, Tri & Bit & Cet and Cho & Bot & Lam (Table 2).

An important shift occurred in 1986 with the disappearance of Hac and Pat. Before disappearing, Pat received aggression from his own alliance partners, including a coordinated attack with Cho & Bot & Lam. In the ensuing attack, Pat was bitten and chased away. With Hac and Pat gone, Rea & Hii formed a very strong bond (COA =100) and from early 1987 through April 1989, they split their time between the trio Tri & Bit & Cet and the trio Cho & Bot & Lam. This shift was associated with a sharp decline in the association between the latter two trios (whose between-alliance COAs dropped from 55-71 in 1985-1986 to 7-16 in 1987-88).

On rare occasions when all three alliances were together, aggression and avoidance revealed conflict. To illustrate, in one sequence Rea & Hii dropped behind the group, surfaced side-by-side synchronously, then charged into the group and, with Cho & Bot & Lam, proceeded to chase off Tri & Bit & Cet. About half an hour later, Cho & Bot & Lam separated from Rea & Hii and a few minutes later captured the female Yog. In another two minutes, Rea & Hii bolted into the trio controlling Yog and there was aggression between Rea and Cho. This was followed by an intense petting session among the males, including a bout between males from the different alliances. The two alliances later separated, and shortly afterwards Cho & Bot & Lam released Yog. Then the other trio, Tri & Bit & Cet, while petting each other, approached and joined Cho & Bot & Lam for about fifteen minutes, before departing again. Five minutes after their departure, Rea & Hii approached and joined Cho & Bot & Lam. Again, there was an inter-alliance petting bout.

1989 was another transition year, as Cho and Lam vanished and Bot joined Rea & Hii to form a new trio. Rea & Hii & Bot continued to associate with Tri & Bit & Cet through 1989, after which the latter trio disappeared.

It is at this point, in early 1990, the alliance histories of Rea and Luc intersect. From 1990-1994, the trio Rea & Hii & Bot enjoyed a second-order alliance relationship with Luc & Poi, who also began consorting females during this period.

The first indication of Poi switching allegiance from Luc to Bot occurred during a month long period in 1994. Rea & Hii consorted a female for 35 days from 21 Jul- 24 Aug. Bot, excluded from this consortship, paired with Poi for the period at the apparent expense of Luc. On each of the eight days they were observed during this span, Bot & Poi consorted a different female. We suspect that some of the consorting by Bot & Poi had more to do with their new and likely fragile first-order alliance bond than with the reproductive state of the consorted female (one of the females they consorted had a 1.5 year old calf and was unlikely to be receptive). During this period Lucky was observed 'shadowing' the other males at a distance and leaving female groups before they joined. After the 35-day consortship, Bot reformed the trio with Rea & Hii, who associated often with the pair, Luc & Poi.

In 1995 Luc associated infrequently with Poi and the other males. Luc spent more time with Poi et al in 1996; three times Luc formed a trio with Bot & Poi to consort a female. An interesting and unusual sequence later that year suggests how some pair switches may simply be expedient. One day

the female Squ was being consorted by Rea & Hii & Bot, who were also in the company of Luc & Poi. The next day on they were observed, Luc was gone and the pair Rea & Bot were consorting Squ, while the novel pair Hii & Poi consorted the female Try. A few days later Hii & Poi were consorting the female Puc, who they consorted for nearly a month. When Rea & Bot ceased consorting Squ after three weeks, Hii & Poi still had Puc. Given that pair changes rarely, if ever, occur during a consortship (Connor et al. 1996, Connor & Smolker 1995), it not surprising that Rea & Bot proceeded to consort more females. This sort of observation suggests that availability can play an important role in explaining alliance shifts. On the other hand, availability does not explain why Hii left the trio to ally with Poi instead of Poi's usual partner Bot. Luc rejoined Poi for the last two months of observation (October through December), occasionally consorting females and associating with the trio Rea & Hii & Bot.

From 1997 to 1999 Luc associated infrequently with the others, who associated as two pairs, Rea & Hii and Bot & Poi. Luc's association coefficient was slightly higher in 1997 (see Tables 1-2) because of an increase in his association for two months late in the breeding season (November and December). However, Luc failed to pull off a similar 'late season rally' in 1998. As Luc's association with Poi and the others declined during 1997 to 1999, he was increasingly found with older (9 to 11 year old) juvenile males (Coo & Smo & Jes & Urc).

Bot was gone by 2000, which coincided with a return to the 1990-1994 pattern: Luc & Poi, associating with Rea & Hii. Concomitantly, Luc's association with the older juveniles fell sharply (Table 2). Unfortunately for Luc, in 2001 Poi abandoned him to join Rea & Hii and form a new trio. Luc did not return to associating with the older juveniles, who were now 11 to 13 years old. Instead, Luc has since been found almost exclusively in female groups.

Dates	1985	1986	1987	1988	1989	1990	1991-1993	1994	1995	1996	1997	1998	1999	2000	2001
Real Notch															
Hii	**81**	**100**	**100**	**100**	**100**	**100**	**95**	**100**	**100**	**92**	**98**	**96**	**98**	**95**	**95**
Hac	**79**	**64**	**64**												
Pat	**100**	**85**	**85**												
Cho	10	16	**35**	**46**	**33**										
Bot	10	19	**38**	**43**	**79**	**81**	**94**	**96**	**90**	**94**	**91**	**76**	**68**		
Lam	10	15	**34**	**46**	**33**										
Tri	14	**26**	**42**	**39**	**56**										
Bit	14	**27**	**39**	**37**	**51**										
Cet	15	16	**31**	**31**	**51**										
Luc	0	0	6	0	0	**52**	**50**	**50**	0	**36**	19	10	4	**52**	0
Poi	0	6	5	0	0	**48**	**59**	**76**	**79**	**90**	**89**	**74**	**68**	**69**	**95**
Lucky															
Poi	**79**	**64**	**73**	**76**	**82**	**86**	**77**	**76**	0	**48**	22	10	15	**73**	0
Lod	**39**	**34**	**66**	**50**	**76**										
Rea	0	0	6	0	0	**52**	**50**	**50**	0	**36**	19	10	4	**52**	0
Hii	0	0	6	0	0	**52**	**47**	**50**	0	**41**	19	10	4	**52**	0
Bot	8	3	12	13	5	**38**	**41**	**44**	0	**43**	19	9	4		
Snu	**37**	**38**	**27**	0											
Sic	24	**35**	**32**	0											
Bib	**29**	**25**	**27**	0											
Wav	**36**	**40**	**31**	0	10	0	0	0							
Sha	**29**	**39**	**37**	0	10										
Jes								0	**40**	5	20	**32**	**50**	10	11
Urc								0	13	0	**39**	**29**	**47**	6	17
Coo								10	**38**	0	18	**28**	**54**	9	16
Smo								**38**	**40**	0	18	19	**46**	13	11

Table 16.1. Alliance affiliations of Luc & Rea from 1985-2001. Numbers in cells are halfweight association coefficents (COAs). A blank cell indicates that a male has died or disappeared. Following Smolker et al. 1992, all coefficients over 24 are in bold.

Taxon	N	Body length (cm)	Body weight (kg)	Brain weight (gm) or Volume (cm^3	Coefficient of variation for brain weight
Suborder odontoceti (toothed whales)					

Superfamily Delphinoidea

F. Delphinidae

Sotalia (c)	1	158	42.2	688.0	
Stenella l. (e)	9	178		643.6	
Delphinus (g)	10	193	67.6	835.6	0.10
Lagenorhynchus (g)	2	208	99.5	1256.5	
Steno (i)	1	215		1369.0	
Stenella c. (j)	18	226	137.8	937.2	
Tursiops (g)	19	246	167.4	1587.5	
Grampus (g)	1	320	400.0	2551.0	
Globicephala (l)	2	545		2711.0	
Globicephala (i)	1		1200.0	3050.0	
Pseudorca (l)	1	550		3650.0	
Orcinus (m)	3	564	2262.0	6143.3	0.01

F. Phocoenidae

Neophocaena (a)	4	151	37.3	471.3	0.08
Phocaeana (d)	3	162	59.7	500.7	0.02
Phocaenoides (f)	10	187	86.4	871.1	0.12

F. Monodontidae

Dephinapterus (g)	1	340	636.0	2083.0	

Superfamily Platanistoidea

F. Pontoporiidae

Pontoporia (b)	9	153	39.0	227.0	

F. Platanistidae

Platanista (h)	4	197	59.6	295.3	

F. Iniidae

Inia (h)	2	212	62.4	617.5	

F. Lipotidae

Lipotes (k)	2	252	230.5	570.0	

Superfamily Physeteroidea

F. Kogiidae

Kogia (g)	1	320	248.0	999.0	

F. Physeteridae

Physeter (n)	15	1530		7913.0	0.09

Superfamily Ziphioidea

F. Ziphiidae					
Ziphius (g)	1	549	2273.0	2044.0	
Suborder Mysticeti (baleen whales)					
F. Balaenidae					
Balaena (o)	5	953		2774.2	
Eubalaena (p)	4	1568		2850.0	
F. Balaenopteridae					
Megaptera (q)	6	1268		6100.3	
Balaenoptera b. (c)	1	1585		4900.0	
Balaenoptera p. (r)	11	1869		6746.4	
Balaenoptera m. (q)	1	2552		6500.0	

Table 2. Cetacean brain size comparisons. Sources: (a) Pilleri & Chen 1982, Pilleri & Gihr 1972; (b) Pilleri & Gihr 1971, Kamiya & Yamasaki 1974; (c) Morgane & Jacobs 1972; (d) Weber 1897, Warncke 1908, Pilleri & Gihr 1970; (e) Ridgway & Brownson 1979; (f) Ridgway & Johnston 1966, Pilleri & Gihr 1970; (g) Ridgway & Brownson 1984; (h) Pilleri & Gihr 1970; (h) Greunberger 1970 [(h) is repeated; please correct]; (i) Pettit 1905; (j) Miyazaki et al 1981; (k) Gihr et al 1979; (l) Elias & Schwartz 1969; (m) Morgane & Jacobs 1972, Ridgway unpublished data; (n) Kojima 1951; (o) Ridgway 1981; (p) Quiring 1945, Morgane & Jacobs 1972, Omura et al. 1969; (q) Pilleri & Gihr1972, (r) Jansen 1952, Quiring 1945, Morgane & Jacobs 1972.

Genus	number	Brain Weight (gm)	Superior Colliculus		Inferior Colliculus		Cranial nerve II: optic nerve (mm)	Cranial Nerve VIII: 'auditory' nerve (mm)
			length (mm)	width (mm)	length (mm)	width (mm)		
Pontoporia (a)	3	229.3	3.0	6.0 (1)	8.0	12.0	2.7	6.0
Platanista (a)	4	295.3	3.5	2.2	15.8	13.8	0.5-0.8	6.8
Lipotes (b)	1	550.0	5.5	5.0	10.0	13.0	2.0	7.0
Inia (c)	2	617.5	5.0	7.0	17.5	15.5	2.0	6.0
Delphinus (d)	3		9.6	10.0	14.6	14.3	5.0 (16)	6.3 (16)
Tursiops (d)	8						4.6	6.0
Stenella (d)	2						7.0	8.0
Grampus (d)	1						5.0	6.0

Table 3. Subcortical visual and acoustic structures in the odontocete brain. Sources: (a) Pilleri 1972; (b) Chen 1979; Gruenberger 1970; (c) [please add]; (d) Pilleri & Gihr 1970. Numbers in parentheses indicate where sample sizes vary from those given under 'number'. Pilleri & Gihr (1970) did not state the size of the delphinid from which the data were taken. However, the range of brain sizes in Pilleri's data were: 635-875g (Delphinus); 785-980g (Stenella); 1930-2240g (Tursiops).

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