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Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study

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Bottlenose dolphins, *Tursiops cf. aduncus*, in Shark Bay, Western Australia exhibit the most complex alliances known outside of humans. Advances in our understanding of these alliances have occurred with expansions of our study area each decade. In the 1980s, we discovered that males cooperated in stable trios and pairs (first-order alliances) to herd individual oestrous females, and that two such alliances of four to six, sometimes related, individuals (second-order alliances) cooperated against other males in contests over females. The 1990s saw the discovery of a large 14-member second-order alliance whose members exhibited labile first-order alliance formation among nonrelatives. Partner preferences as well as a relationship between first-order alliance stability and consortship rate in this 'super-alliance' indicated differentiated relationships. The contrast between the super-alliance and the 1980s alliances suggested two alliance tactics. An expansion of the study area in the 2000s revealed a continuum of second-order alliance sizes in an open social network and no simple relationship between second-order alliance size and alliance stability, but generalized the relationship between first-order alliance stability and consortship rate within second-order alliances. Association preferences and contests involving three second-order alliances indicated the presence of third-order alliances. Second-order alliances may persist for 20 years with stability thwarted by gradual attrition, but underlying flexibility is indicated by observations of individuals joining other alliances, including old males joining young or old second-order alliances. The dolphin research has informed us on the evolution of complex social relationships and large brain evolution in mammals and the ecology of alliance formation. Variation in odontocete brain size and the large radiation of delphinids into a range of habitats holds great promise that further effort to describe their societies will be rewarded with similar advances in our understanding of these important issues.

The 'social brain' hypothesis posits that the cognitive demands of negotiating social relationships that are numerous and complex drove the evolution of large brain size and intelligence (Alexander, 1979; Dunbar, 2003; Humphrey, 1976). Alliances may be an especially important category of social relationship in this regard, as noted by Chapais (1995, page 39): 'Alliance behavior lies at the heart of social bonding and cognition. The ability to form alliances generates the most complex social structures in the animal world'. Humans form the most complex alliances and coalitions known, including nested alliances that range from kin factions within villages to, in modern society, alliances among nation states (Boehm, 1992; Falger, 1992). Outside of humans, the most complex alliances known are found in a population of bottlenose dolphins, *Tursiops cf. aduncus*, in Shark Bay, Western Australia.

Shark Bay is a 13 000 km^2 embayment bisected by the Peron Peninsula. The extensive shallows along the eastern shore of the peninsula are violated by deeper water at only one location, at the south end of Red Cliff Bay about half-way down from Cape Peron (Fig. 1). The access to deeper water and fish drew people to the camp called 'Monkey Mia' and, since at least the 1940s, people offering fish drew dolphins to the narrow shallows by the camp (see Supplementary Material). In the 1970s, the presence of habituated bottlenose dolphins attracted the dolphin enthusiast Elizabeth Gawain (Gawain, 1981), who then visited University of California in 1981 to alert students of Professor Kenneth S. Norris to the opportunity presented by wild but habituated dolphins. One of

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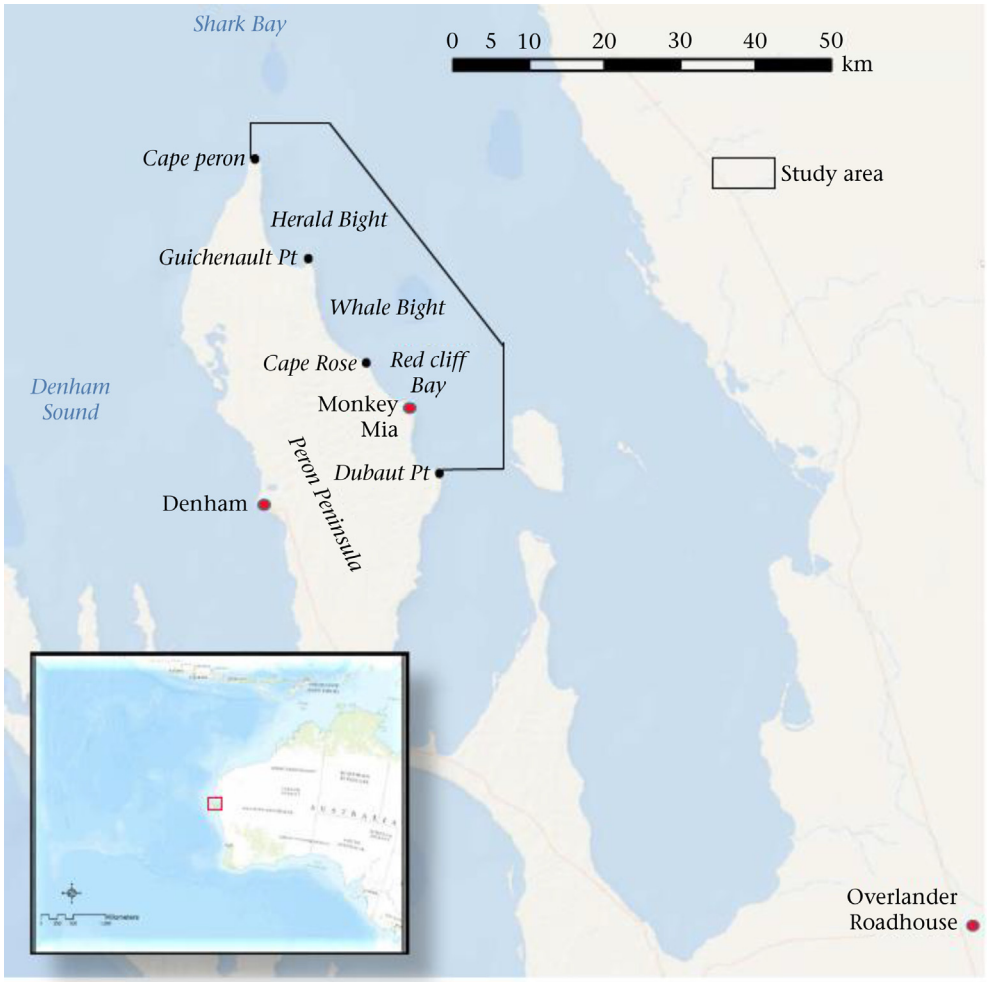

Figure 1. The Dolphin Alliance Project study area focused in and around Red Cliff Bay in the 1980s, extended north into Whale Bight in the 1990s, and enlarged to encompass the area outlined in black from 2001 onward. The area south and east of Cape Rose is mostly characterized by offshore flats divided by channels whereas the habitat north of Cape Rose is mostly open embayment plains.

us (Richard Connor) and Rachel Smolker took the bait and, in 1982, initiated the dolphin research program in Shark Bay (Connor & Smolker, 1985).

Smolker began systematic offshore observations in Shark Bay during 1984–1985, employing the 'survey' method (e.g. Wells, Irvine, & Scott, 1980; Würsig & Würsig, 1977), where researchers travel among groups of dolphins, stopping at each group long enough to record group composition (by photographing dorsal fins), predominant group activity, location, depth and a range of other data (see Supplementary Material). Surveys yielded valuable data on association, behaviour and habitat use but were not optimal for capturing the social interactions that constitute social relationships, leading to a deeper understanding of the social structure and mating system (Emlen & Oring, 1977; Hinde, 1976). Toward this end, Connor initiated focal individual follows in Shark Bay in 1986, initially on males and females before focusing on males exclusively in 1987. William Sherwin (University of New South Wales) initiated genetics research on the dolphins in the mid-1990s, via his Honours and then-doctoral student (Michael Krützen), who later joined Connor as co-director of *The Dolphin Alliance Project* (www.sharkbaydolphins.org), which focuses on male dolphin behavioural ecology and genetics in Shark Bay. A long-term dolphin database is maintained at the University of Zurich and University of Massachusetts Dartmouth.

Major advances in our understanding of the dolphin alliances coincided with significant expansions of our study area in the 1990s and 2000s. Hence we present a historical review of our key alliance discoveries by decade, including new analyses on male grouping patterns and alliance behaviour. First we present background information on life history, ecology, grouping and female behaviour sufficient to understand the context within which the alliances were documented.

LIFE HISTORY, ECOLOGY, GROUPING AND FEMALE BEHAVIOUR

Life History

The Shark Bay bottlenose dolphins are relatively small (about 2 m long) with minimum sexual size dimorphism compared to other *Tursiops* populations (Connor, Wells, Mann, & Read, 2000). After more than 30 years of observation, it is clear now that some male and female bottlenose dolphins in Shark Bay live into their 40s. In this and other life history variables the Shark Bay dolphins are similar to chimpanzees, *Pan troglodytes* (Connor & Vollmer, 2009). Females typically give birth to their first calf at age 12 years, and have interbirth intervals of 4 or more years, reflecting periods of dependency of 3–5 years and, rarely, longer (Connor, Wells, et al., 2000). Males typically begin consorting mature

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