A novel mammalian social structure in Indo-Pacific bottlenose dolphins (*Tursiops* sp.): complex male alliances in an open social network

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Terrestrial mammals with differentiated social relationships live in ‘semi-closed groups’ that occasionally accept new members emigrating from other groups. Bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia, exhibit a fission–fusion grouping pattern with strongly differentiated relationships, including nested male alliances. Previous studies failed to detect a group membership ‘boundary’, suggesting that the dolphins live in an open social network. However, two alternative hypotheses have not been excluded. The *community defence model* posits that the dolphins live in a large semi-closed ‘chimpanzee-like’ community defended by males and predicts that a dominant alliance(s) will range over the entire community range. The *mating season defence model* predicts that alliances will defend mating-season territories or sets of females. Here, both models are tested and rejected: no alliances ranged over the entire community range and alliances showed extensive overlap in mating season ranges and consorted females. The Shark Bay dolphins, therefore, present a combination of traits that is unique among mammals: complex male alliances in an open social network. The open social network of dolphins is linked to their relatively low costs of locomotion. This reveals a surprising and previously unrecognized convergence between adaptations reducing travel costs and complex intergroup–alliance relationships in dolphins, elephants and humans.

Keywords: alliances; ranges; social structure; social organization

1. INTRODUCTION

Mammalian social systems vary immensely along a range of variables [1]. However, two particular traits are always found together: complex social relationships and membership in a ‘semi-closed group’ with one or more reproductive females. In such groups, members of one sex (usually females) remain in their natal area or group, whereas members of the other sex disperse [2]. Semi-closed social groups are often described by familiar terms such as a ‘troop’ of baboons, a ‘pride’ of lions, a ‘community’ of chimpanzees or a ‘pack’ of wolves. In these societies, an individual’s bonds are normally limited to other group members, whereas interactions between individuals of different groups are typically hostile. Group defence may be performed by males (e.g. chimpanzees [3]), females (many primates [4]) or both (e.g. lions [5]).

A few species that feature semi-closed groups have what can be described as an ‘open social network’ above the group level, where affiliative interactions may extend to members of other groups with overlapping ranges.

For example, the African elephants’ (*Loxodonta africana*) social system is based on stable ‘family groups’ of female kin, and their offspring that associate with other female kin to form ‘bond groups’ that are, in turn, linked into larger ‘clans’ [6, 7]. Multi-level societies based on stable matrilineal groups are found in several odontocetes, including killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) [8, 9]. In fact, the behaviour and life history of elephants and sperm whales have converged to a remarkable degree [10].

The social system of Indo-Pacific bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia, features a fission–fusion grouping pattern with stronger associations between adult males than adult females and bisexual philopatry [11]. The male dolphins form nested alliances. Two or three males cooperate in ‘first-order’ alliances to form consortships with individual females [12, 13]. Teams of 4–14 males cooperate in ‘second-order’ alliances to attack other alliances and to defend against such attacks. Second-order alliances can persist intact for over 15 years and may be considered the core unit of male social organization in Shark Bay. Some second-order alliances have ‘third-order’ alliance relationships with other groups, which are also concerned with conflicts over females [14]. To mediate their bonds, males
use affiliative contact behaviours (petting and rubbing) and possibly synchrony [15]. This complex system of multi-level alliances has not been described in other populations of *Tursiops*, so further references to ‘dolphins’ are specific to the Shark Bay population.

Associations among adult female dolphins in Shark Bay are variable but never as strong as those between the most strongly bonded males [16]. There are no reports of females forming alliances against other females in Shark Bay, and in over 25 years, there has been only one observation of females forming a temporary coalition against young males [13]. Individual female ranges are not congruent but form an overlapping mosaic in our study area [17]. These findings indicate that the social structure in Shark Bay is not based on female defence of ranges or groups as is common in many mammals [18].

Although fission–fusion group formation is found in a wide range of species [19], the pattern of sex-specific bonds in the Shark Bay dolphins is much closer to that of common chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* spp.) than other terrestrial mammals [3,19]. However, there is no evidence that the male dolphins defend a community territory such as male chimpanzees and spider monkeys [3,20–23], suggesting an unprecedented combination of male alliance relationships in an otherwise open social network [24]. This issue is of general interest for two reasons. First, the relationship between social cognition and large brain evolution has received considerable attention [25], and animals with complex social relationships but living in an open social network would face novel cognitive challenges (reviewed by Connor [24]). In semi-closed social groups, individuals may not only know the other members of their group, but they may also learn the dominance rank and primary kin relationships of group members. Such ‘social knowledge’ may be critical to their reproductive success (e.g. they might refrain from forcibly taking food from a smaller individual if that individual has a larger sibling). In an open social network, the social knowledge individuals can acquire about others they encounter will be highly variable and limited for individuals encountered infrequently. Assessing risk in potential conflicts may be difficult: an opponent may have gained new allies since he or she was last encountered. Furthermore, discovering a novel social structure in dolphins raises questions about which aspects of their biology and ecology might permit such a deviation from the terrestrial ‘norm’, thus broadening our understanding of mammalian social evolution.

(a) Alternative models and predictions

Despite the apparent lack of a community boundary in Shark Bay [24], previous research has not been able to exclude two models based on Clutton-Brock’s [18] category of ‘multi-male groups with spatial defence by males’. The ‘community defence’ (CD) model is derived from the common chimpanzee/spider monkey social system, where individual females travel in smaller areas of a larger community range that is patrolled and defended by males [3,20,21]. Given the nested structure of dolphin alliances, the equivalent to a chimpanzee patrol might be performed by a group of male dolphins belonging to a single second-order alliance or even more than one second-order alliance. Thus, the CD model predicts: (i) that at least one or more second-order alliances will range over (=patrol) the entire study area (=community), and (ii) that these alliances will overlap with the ranges of all other second-order alliances in the community. We note that, given the hundreds of dolphins residing in our previous study area of 250 km², the dolphin community would have to be much larger than any known chimpanzee community. Travelling around such a large territory would be quite feasible for dolphins. Dolphins enjoy a low cost of locomotion and day ranges of odontocetes are typically an order of magnitude greater than those of similar-sized terrestrial mammals [26]. Typical travelling speeds of dolphins in our population are 3–5 km h⁻¹, which would allow them to traverse the full length of our study area along the peninsula (50 km) in a 12–18 h period.

The ‘mating season defence’ (MSD) model postulates that male groups defend smaller territories or sets of females during the mating season. For example, males might shift from using larger non-mating season ranges, where they concentrate on foraging to improve body condition, to smaller mating season ranges for female defence. The MSD model predicts that allied males will occupy exclusive ranges during the mating season months of September–December. However, observations off Scotland [27] suggest that groups of bottlenose dolphins might defend mobile ranges. A finding of overlapping mating season ranges might conceivably be an extinction of spatial defence shifts on a shorter timescale as mobile sets of females are defended by particular alliances. To allow for this variant of the MSD model, we also examined the extent to which alliances overlap in the females they consort with.

To test the predictions of the CD and MSD models, we examined ranging and behaviour of over 120 adult males in an expanded 600 km² study area (figure 1), in the period from 2001 to 2006. These males associated in 12 second-order alliances and five ‘lone trios’ (i.e. trios without second-order affiliations [14]).

2. METHODS

(a) Field observations

Male association, behavioural and ranging data were collected through surveys and focal follows during the same five-month field season for 6 years (2001–2006, from July through to November). This period covered the first three months (September to November) of the five-month peak breeding season, as well as August, when alliance behaviour and consortship rates increase [28,29]. Surveys represent brief encounters (at least 5 min) of dolphin groups during which we record a variety of data, including time and global positioning system (GPS) location, as well as group composition, based on photographic identification [30]. A group was defined as all individuals that were observed together based on a 10 m ‘chain rule’ [16]. Although care was taken to distribute the spatial search effort as evenly as possible throughout the study area, our ability to do so was somewhat limited by weather conditions.

Focal alliance follows ranged in duration from 1 to 8 h. During follows, we kept a continuous record of behaviour and group membership, with a focus on documenting consortships, following Connor et al. [31]. Members of second-order alliances formed first-order alliances (consorted females) with each other, cooperated in conflicts with other groups and generally shared half-weight association coefficients greater than 20 [12,16]. These associations were obvious in the field and distinct in cluster diagrams [14].

During the study, we observed that particular second-order alliances had third-order alliance relationships with other groups [14]. It is possible that such associations are based partly on joint defence of an area or females. Thus, to examine the question of whether allied males maintained exclusive access to a set of females (as predicted by the MSD model), we grouped first- and second-order alliances into putative third-order alliance groups (sensu [14]) and compared lists of consorted females between groups.

(b) Analysis
Data on male alliance membership were taken from surveys and focal alliance follows. GPS location data were analysed using ArcView v. 9.2 software. For each individual male, sighting points from the study period were plotted based on latitude and longitude, using a universal transverse Mercator projection with a WGS84 map datum. Hawth’s analysis tools for ArcGIS toolkit’s algorithms [32] were used to translate projected points into corresponding surface areas, which were spatially referenced. To avoid autocorrelation, a maximum of one sighting point per individual per day was used, thus enabling each sighting to be considered an independent data point. To calculate the total home range for each second-order alliance, we included sighting points for all the individual members of a given alliance during the study period, but limited each individual to one point per day.

To test the CD model, ranges were estimated using the minimum convex polygon (MCP) method. The MCP range estimation method is the most conservative test of the CD model because it includes outlier points and thus
maximizes the estimated degree of overlap between alliance ranges. To test the MSD model, we estimated alliance core ranges during the mating season using the fixed kernel density estimation (FKDE) method [33]. For the FKDE method, a smoothing factor ($h_{adj}$ [34]) of 1.574 was chosen as optimal, given the number and spacing of sighting points, to provide sufficiently continuous home range estimates, without overly inflating range size or artificially placing a part of the range on an impossible location (e.g. on land). FKDE output cell size was set at 100 m. We followed the common practice of using the 50 per cent point density volume contour to represent the core home range [35] of the animal, and 90 per cent volume contours were taken to represent the entire range for comparison with the MCP method.

For further details on methods and results, including analyses of individual male ranges with respect to sample size, the number of males in an alliance and a comparison with female ranges, see the electronic supplementary material.

3. RESULTS
(a) Tests of the community defence and mating season defence models

We found no evidence supporting either the CD or the MSD models. The key prediction of the CD model was that at least one second-order alliance would range over the entire study area. However, even with generous MCP range estimates, there were no individuals or alliances whose ranges overlapped all other alliances in the study area (figure 2). The largest FKDE-estimated alliance range size was 133 km$^2$, and the largest MCP-estimated range size was 229 km$^2$, compared with
the study area size of over 600 km$^2$ (table 1). Furthermore, the ranges of some second-order alliances did not overlap at all (figure 2).

The key prediction of the MSD model was that males in different second- or third-order alliances should show no or minimal overlap of ranges or female consorts during the mating season. However, conservative 50 per cent FKDE estimates of core ranges showed extensive mating season overlap among second-order alliances, including those that did not share a third-order alliance membership (e.g. alliances SJ and PB, PD and RR, BL and CB; figure 3). Data from a single mating season show the same pattern (see the electronic supplementary material).

There was also extensive overlap in the females consorted by different male groups. Sixty-five females were documented in three or more consortships (range 3–17, mean 6.4). Only one female, observed in three consortships, was observed with a single second-order alliance and only seven females (11%) were consorted by males from a single third-order alliance. Thirty-two (49%) of the 65 females were consorted by three or

Table 1. Average range sizes (in km$^2$) for lone trios and second-order alliances in Shark Bay.

<table>
<thead>
<tr>
<th>alliance name (alliance size)</th>
<th>mean</th>
<th>s.e.</th>
<th>n</th>
<th>minimum</th>
<th>maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>MCP</td>
<td>144.92</td>
<td>14.83</td>
<td>17</td>
<td>57.77</td>
<td>273.02</td>
</tr>
<tr>
<td>90% FKDE</td>
<td>92.31</td>
<td>6.78</td>
<td>17</td>
<td>48.15</td>
<td>132.90</td>
</tr>
<tr>
<td>50% FKDE</td>
<td>25.56</td>
<td>2.04</td>
<td>17</td>
<td>14.60</td>
<td>45.68</td>
</tr>
</tbody>
</table>

Figure 3. Alliance core ranges during the peak-mating season, calculated using the fixed kernel density estimation method.
more second-order alliances belonging to three or more third-order alliance groups. Thirty-one of those 32 females were observed in at least two consortships (range 2–12) in a single season. Over the course of that season, all 31 were consorted by males from more than one (range 2–5) second-order alliance, belonging to between two and four third-order alliances.

4. DISCUSSION
(a) A novel mammalian social system: an open social network or ‘unbounded’ dolphin society
We found no evidence that the large and complex social network in Shark Bay, comprising hundreds of bottlenose dolphins, is a closed group defended by males. We also found no evidence that males defend smaller ranges or groups of females within this network. Instead, there is extensive overlap in the ranges of alliances and in the females they consort with. Combined with earlier work on females, these results lead to the conclusion that Shark Bay bottlenose dolphins live in an open social network with a mosaic of overlapping female and male ranges.

The total extent of the Shark Bay dolphin social network is unknown, and it may be continuous throughout the dolphins’ habitat in the bay. A much larger social network is suggested by the fact that, in addition to the males that were the focus of our study, there were at least another 100 adult males that we encountered one or more times in different parts of the study area. We expect that the core ranges of these males partially overlap with or are beyond our study area.

It is unlikely that kinship can offer a complete explanation for the male dolphin network in Shark Bay. Male dolphins do not maintain strong bonds with their mothers and while they form male–male bonds from an early age [11], the second-order alliances ‘crystallize’ when males are in their teens, after a long juvenile period [36]. The combination of ubiquitous alliance formation among males and a slow life history where females give birth to single calves separated by several years militates against males being able to rely consistently on close kin for allies [24]. Relatives have been found among some close allies in smaller second-order alliances, but males were unrelated in one large, 14-member second-order alliance [37].

(b) Comparison with terrestrial mammals
The terrestrial mammal most often compared with bottlenose dolphins is the common chimpanzee (Pan troglodytes) [11,38]. Shark Bay bottlenose dolphins have a very ‘chimpanzee-like’ fission–fusion grouping pattern, stronger male–male than female–female associations and they have very similar life histories [39]. However, we found here that the dolphins do not live in semi-closed male-defended communities such as chimpanzees.

While the other great apes do not share as many features of social organization with the Shark Bay dolphins, their social boundaries may be less clearly defined or social interactions between groups more tolerant than in chimpanzees, whose intergroup relationships are exclusively hostile [3]. In striking contrast to common chimpanzees, some (but not all) bonobo (Pan paniscus) communities enjoy peaceful interactions when they meet [40]. A bounded chimpanzee-like community structure has not been found in orangutans (Pongo pygmaeus), whose ‘diffuse’ social system is described as ‘neighbourhoods, where residents know many others, but know them less well as the home range overlap decreases’[41]. Western gorillas (Gorilla gorilla) live in one-male groups, but have been described as having a ‘dispersed male network’ on the basis of tolerant interactions among related male silverbacks that have overlapping ranges [42]. However, in none of these species does the greater tolerance between groups translate to alliance formation between groups that might be comparable with the complex nested alliances we find in dolphins. Among other non-human primates, claims that Hamadryas baboons (Papio hamadryas) have more complex male alliances than those found in other baboons have been challenged [13]. Humans live in semi-closed groups and exhibit intergroup alliance formation. This is achieved, at least in part, by maintaining relationships with kin that have dispersed to other groups [43].

While it remains unclear if the nested intergroup relationships found in African elephants are commonly featured in an alliance context (e.g. two family groups against others), they do associate, like the dolphins, in a large open social network. But otherwise, elephant social organization is fundamentally different from the Shark Bay dolphin society. Unlike the dolphins, elephant society is based on stable units of female kin and their offspring [44], although individuals are capable of forming strong bonds with non-relatives when relatives are not available [45]. The core matrilineal units are apparently formed by a process of fission, as subordinate females become grandmothers [6,44]. The changes we observe in the male dolphins’ first-order and sometimes even their second-order alliance relationships [36] would not be expected in an elephant-like kinship system.

Outside of mammals, the most intriguing parallels with the dolphin social system are found among small parrots such as green-rumped parrotlets (Forpus passerinus), and coppers (Aratinga spp.). Although the basic unit of social structure is the male–female pair, these species exhibit an extensive fission–fusion grouping pattern, preferential associations beyond the pair bond [46] and have converged with the dolphins in the use of individually distinctive contact calls [46,47]. Young male green-rumped parrotlets are sometimes found in pairs before they find a mate [48]. Future studies should reveal whether these birds have an open social network or any alliance structure outside of the pair bond.

(c) Low cost of locomotion, overlapping ranges and nested alliances: convergence in dolphins, elephants and humans
It is interesting that mammalian brain size evolution produced peaks in such otherwise disparate taxa: elephants, humans and some odontocetes (dolphins and sperm whales). Connor [24] argued that the same selective environment was common to all three groups: an extreme degree of mutual dependence based on high infant vulnerability in species that are already investing heavily in each offspring. Given this mutual dependence, individuals were in reproductive competition with the same individuals their lives depend on, favouring increasingly sophisticated abilities in the arena of social cognition.

Another area where ‘the big three’ have apparently converged is in their low costs of locomotion. The low
cost of locomotion in dolphins has already been noted; elephants have the lowest cost of locomotion recorded for any terrestrial mammal [49], and the evolution of bipedal locomotion endowed humans with greatly reduced locomotion costs relative to the other apes [50]. Clearly, a lower cost of locomotion does not necessarily lead to complex social systems but it could have contributed to the evolution of enhanced social cognition and the complex intergroup–alliance relationships found in hominids, cetaceans and elephants. At a given population density, cheaper travel and concomitantly larger ranges would have increased the rate that individuals and groups encountered each other in competitive contexts, favouring larger groups and alliances [51], and perhaps intergroup relationships that are sometimes cooperative rather than hostile or merely tolerant. These changes would have directly impacted two factors that are thought to impose selection for enhanced social cognition: the number of social relationships an individual maintains [52], and the additional cognitive burden imposed by negotiating a multi-level group/alliance structure [13].

Humans maintain relationships with other groups by remaining in contact with dispersed kin and by cultural identity [53] and are thus said to be ‘released from the constraint of proximity’ [43]. However, multi-level alliance formation in humans was probably also favoured by their large overlapping ranges associated with the evolution of bipedal locomotion. Humans and bottlenose dolphins are the only two species that exhibit nested male alliances within a social network [12,24]. Some of the profound differences between human and dolphin social organization (e.g. dolphins do not exhibit pair bonds or male parental investment) may relate to the fact that humans are tied to a home base or hearth (see Wrangham [54]), whereas dolphins are not.

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