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ORIGINAL PAPER

Evidence for social role in a dolphin social network

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Abstract Social animals have to take into consideration the behaviour of conspecifics when making decisions to go by their daily lives. These decisions affect their fitness and there is therefore an evolutionary pressure to try making the right choices. In many instances individuals will make their own choices and the behaviour of the group will be a democratic integration of everyone's decision. However, in some instances it can be advantageous to follow the choice of a few individuals in the group if they have more information regarding the situation that has arisen. Here I provide early evidence that decisions about shifts in activity states in a population of bottlenose dolphin follow such a decision-making process. This unshared consensus is mediated by a non-vocal signal, which can be communicated globally within the dolphin school. These signals are emitted by individuals that tend to have more information about the behaviour of potential competitors because of their position in the social network. I hypothesise that this decision-making process emerged from the social structure of the population and the need to maintain mixed-sex schools.

Keywords Bottlenose dolphin · Unshared consensus · Social network · *Tursiops* · Behaviour · Sociality

Introduction

Individuals have to regularly make decisions that will affect their fitness (Conradt and Roper 2003; McGraw and Caswell 1996). In gregarious species these decisions are compounded by the need to interact with conspecifics in relation to intrinsic and extrinsic influences such as prey availability (Baird and Dill 1996; Fritz and de Garine Wichatitsky 1996; Lusseau et al. 2004; Templeton and Giraldeau 1996) or

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intra-specific competition (Connor et al. 2001; Gerard and Loisel 1995). These influences often result in the emergence of complex social behaviour (Arnold and Whiten 2003; Watts 1998, 2002) and social structure (Hinde 1976; Kappeler and van Schaik 2002; Koenig 2002; Wells et al. 1987), which facilitate the decision-making process and often the need to reach consensus between individuals within a group (Conradt and Roper 2005; de Waal 2000). Many social species have developed signals that help members of groups or aggregations to coordinate their activities (Black 1988; Poole et al. 1988; Stewart and Harcourt 1994). This decision process can results in conflicts (Conradt and Roper 2000, 2003) and no consensus has been reached on which mechanisms are driving this process (Conradt and Roper 2003, 2005; Couzin and Krause 2003; Couzin et al. 2005). Conradt and collaborators discriminate between democratic and despotic decision-making processes and argue that democratic processes are widespread because they lower the consensus cost by producing less extreme decisions (Conradt and Roper 2003). However, it is hypothesised that despotic decision-making processes, i.e. a small subset of individuals influencing disproportionably the behaviour of the whole group, can emerge from situations where some individuals are more knowledgeable about the situation than others. In that case the cost of decision is lowered by following information holders (Conradt and Roper 2003).

The bottlenose dolphin (*Tursiops* sp.) population residing in Doubtful Sound, New Zealand (Lusseau et al. 2003) presents an interesting model to test this hypothesis. Bottlenose dolphins live in fission-fusion societies and therefore individuals can make choices to join or leave a group (Mann et al. 2000). The social relationships of all individuals in the population have been mapped (Lusseau 2003b; Lusseau and Newman 2004) using a network representation approach which helped in defining the affiliation ‘‘distance’’ both between individuals and between clusters of individuals within the population (Lusseau and Newman 2004). Two social units (communities hereafter) were identified in this population using these techniques (Lusseau and Newman 2004).

Two behavioural events have been recently identified as signals of shifts in school’s activity state (Lusseau 2003a, 2006a, b). Side flopping (SF) is defined as a dolphin clearing its body entirely from the water and landing on its side and is only performed prior to the onset of travels. While upside-down lobtailing (ULT) is defined as a dolphin rolling to expose its ventral side at the water surface and slapping repeatedly the water surface with the dorsal side of its tail and is only observed before the school concludes travelling (Lusseau 2003a, 2006a, b). These behaviours are therefore reminiscent of other signals used by a variety of species to synchronise activities (Black 1988; Stewart and Harcourt 1994). While these signals are often used as a voting system in other species (Conradt and Roper 2005), it appears that SF and ULT are always performed by only one member of the school (Lusseau 2003a, 2006b). These events offer signals that can be emitted to all individuals within the school but which are not heard by non-school members because the sound produced by these percussive behaviours does not travel as far as vocalisations do (Finneran et al. 2000). These two non-vocal behavioural signals could be advantageous to minimise the cost of intra-specific competition from direct competition for food between the different communities present in the population. They can help synchronising the activities of the school without advertising it to non-school members. There is no sign of complete segregation of social units in bottlenose dolphins (Lusseau and Newman 2004; Lusseau et al. 2006; Wells et al. 1987).

The social structure of the Doubtful Sound bottlenose dolphin population is such that a large proportion of individuals within schools (41%) spent a significant amount of time together, hence it would be advantageous to not only have a signal that would allow activity synchronisation but also would not allow this synchronisation to be advertised outside the school (Lusseau et al. 2003). If this was the case, individuals that spent some time with members outside their communities would be more likely to have knowledge about these potential competitors and hence be more reliable in decision-making processes which involve competition evasion. Following their decisions would therefore lower the cost of choices and ultimately increase the fitness of school members (Conradt and Roper 2003).

Centrality measures on network graph can identify the location of individuals in relation with others (Lusseau and Newman 2004; Newman 2003; Wasserman and Faust 1994). They can therefore help identifying individuals that have social relationships spread *between* clusters of individuals as well as individuals that have a more central position *within* these clusters. I therefore tested the likelihood that these non-vocal behavioural events were performed by individuals that were more likely to have a better knowledge of the activities of other clusters of individuals.

Materials and methods

Field techniques

I collected behavioural data in Doubtful Sound, New Zealand (45°30′ S, 167°00′ E) between June 2000 and May 2002. Systematic surveys of the fjord were conducted to look for dolphin schools (Lusseau et al. 2003). Once a school was detected the identity of individuals in the school was determined using photo-identification (Würsig and Würsig 1977). A code of conduct was established for the observing vessel to minimise its effects on the focal schools (Schneider 1999). Studies showed that the behaviour of the focal schools was not affected by the presence of the observing vessel (Lusseau 2003c, 2006a). Side flops (SF) and upside-down lobtails (ULT) are rare events (0.012 sf/min and 0.016 ult/min of focal follows (Lusseau 2006b)); I therefore recorded the occurrence of SF and ULT in an *ad libitum* fashion while following the school (Altmann 1974; Mann 2000). SF were defined as jumps during which a dolphin cleared its entire body out of the water and landed on its side. ULT were defined as situations when a dolphin was upside-down stationary at the surface, belly pointing upwards, and forcefully slapped the water surface with its tail. Observations ended when the weather deteriorated, the focal school was lost, or the day ended, therefore the end of an observation period was not dependent on the behaviour of the focal school.

The gender of photo-identified individuals was assessed by direct observation of the genital slit using an underwater camera (Schneider 1999). Both the absence/presence of mammary slits and the distance between the genital and anal slits permitted to sex the animals (Schneider 1999). The identity of individuals performing the behavioural events was defined either through direct visual observations or from either photographs or videos. The marking rate in this population is high (Lusseau et al. 2003; Williams et al. 1993a) which means that practically all individuals can be recognised from marks on their dorsal fins. Therefore practically all the population (excluding calves) was equally likely to be recognised in this way, minimising sampling bias. Social relationships within the population have been previously described (Lusseau 2003b; Lusseau and Newman 2004) and this study is based on the same data, which is based on school membership obtained using photo-identification (Fig. 1). The resulting social network is defined by preferred companionships between individuals in the population (Lusseau 2003b).

Analytical techniques

Centrality measures (degree and betweenness) for each individual present in the network were calculated using Ucinet (Borgatti et al. 2002). The higher the betweenness (Freeman 1977), the more often an individual is found between clusters in the network graph. In other words, betweenness quantifies how much of a bottleneck an individual is in the network. It is defined using shortest path length. For each possible pair of individuals in a network it is possible to find the shortest path to go from one to another by travelling along the edges of the network, passing from node to node. The betweenness of an individual (node) is measured by counting how often that node is frequented when travelling between all possible pairs using shortest paths. Individuals with high betweenness tend to be information brokers in human societies (Girvan and Newman 2002) and potentially in bottlenose dolphin societies as well (Lusseau and Newman 2004). The degree of an individual (Freeman

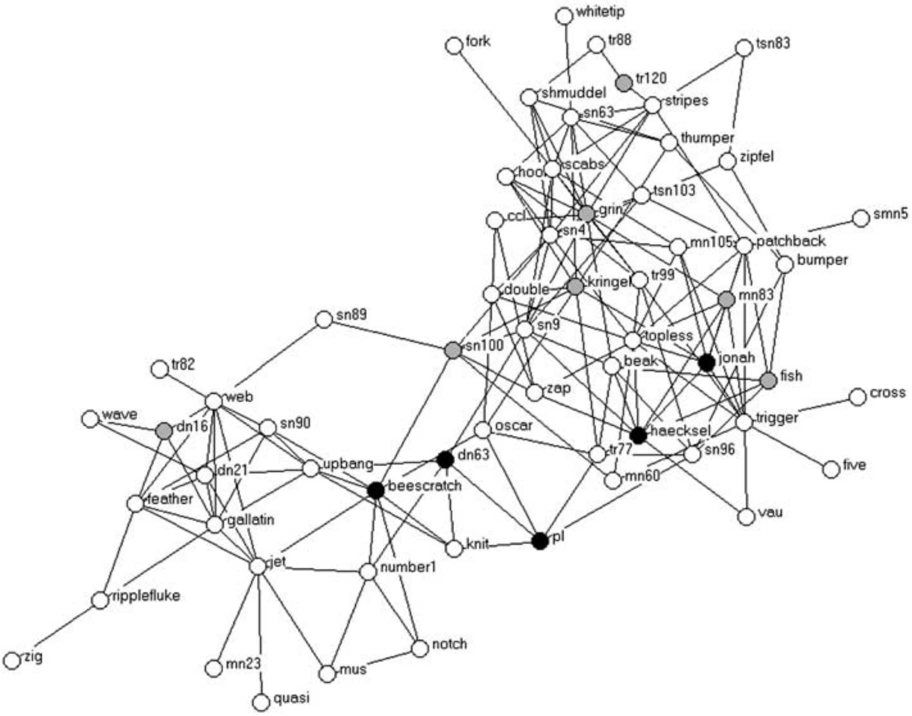

Fig. 1 Social network of bottlenose dolphins in Doubtful Sound, New Zealand; each vertex represents an individual and each edge represents a pair that was observed in the same school more often than expected by chance; see (Lusseau 2003b) for more details on how the social network was constructed. Dolphins observed SF are in black and the ones observed ULT are in grey

1979) is a measure of how much influence an individual can have on its peers: the more individuals that a dolphin is linked to, the more individuals it has the opportunity to affect. The degree of an individual is measured by counting the number of associates a dolphin has (number of edges). There are early indications that these measures are behaviourally meaningful in dolphin societies as the temporary disappearance of individuals with high betweenness may have led to groups of individuals temporarily spending less time together (Lusseau and Newman 2004). In addition, these centrality measures have proven useful to identify central individuals in other animal networks (Corner et al. 2003; Croft et al. 2005; Flack et al. 2006; Webb 2005). Randomisation tests were used to compare the difference in average centrality measures between individuals that were observed performing the behaviours and others to average differences in which individuals were randomly assigned as behaviour performer or not.

Since SF and ULT are rare events, it is possible that an individual may not have been observed performing them because we did not spend enough time with it. To eliminate this potential sampling bias, the random selections within the randomisation tests were weighted by the amount of time we spent observing each individual in relation to the total amount of time we spent observing dolphin schools.

Results

During the study period I spent 137 days (879.2 h) looking for dolphins. I followed focal groups for 716.5 h (over 133 days). During this time I was able to identify reliably the identity of individuals performing SF in 10 instances and performing ULT in 15 cases. Most SF were performed by males (9 out of 10). The likelihood that 9 out of 10 SF were performed by males and that females and males had equal chances to perform them was very low ($P = 0.001$, using a randomisation test with 1,000 iterations). In contrast, most ULT were performed by females (14 out of 15) and the likelihood that males and females were equally likely to perform them was also low ($P = 0.002$, 1,000 iterations).

All individuals were equally likely to be recognised when performing SF or ULT because of the distinct markings individuals bear on their dorsal fins. Only five males were identified performing the 10 SF (Fig. 1). A randomisation test (10,000 iterations) showed that the likelihood that all males in the population were equally likely to perform SF was low ($P = 0.0006$, likelihood that 10 SF were observed and 5 out of all males were identified performing them given the amount of time we spent observing each of them). Not all females seemed to perform ULT either (Fig. 1). Only seven females were identified performing the 15 ULT, which is highly unlikely if all females were equally likely to perform this behaviour ($P = 0.003$, 1,000 iterations randomisation test: likelihood that 15 ULT are performed by 7 females when drawn randomly from all the females in the population given the amount of time we spent observing each of them).

These tests show that SF tends to be a male-specific behavioural event and ULT a female-specific one. It is worth noting that both the SF performed by the female and the ULT performed by the male were not followed by changes in the school's behavioural state. In addition not all individuals seem to use these signals in the population. I therefore tested whether males that performed SF and females that performed ULT tended to have higher centrality measures in the social network.

The difference in degree, the number of partners an individual had on the social network, between SF males and non-SF males was small (0.29) and did not differ from random differences obtained by randomising who had been observed performing SF (1,000 iterations, $P = 0.382$, Fig. 2b). Similarly ULT females did not have a significantly higher degree than non-ULT females (difference = 2.58, 1,000 iterations, $P = 0.056$, Fig. 2d). However, both SF males and ULT females had significantly higher betweenness values (Fig. 3), a measure of the diversity of links an individual had, than non-SF males and non-ULT females respectively (males:difference = 4.50, 1,000 iterations, $P = 0.041$, Fig. 2a; females:difference = 5.20, 1,000 iterations, $P = 0.040$, Fig. 2c). These tests were ran 100 times to test the power of the randomisations and the same level of significance ($P > 0.05$ for degree and $P < 0.05$ for betweenness) was obtained in all 100 runs except for the female degree test which was significant in 2 instances. The degree and betweenness of both males and females were weakly correlated (Pearson's r: $r = 0.46$ and $P = 0.021$ and $r = 0.58$ and $P = 0.003$, respectively).

Discussion

This study provides some initial evidence on the decision-making processes, and the mechanisms involved to reach consensus, in situations where information is not equally shared by all individuals in fission-fusion societies. It appears that in this population unshared decision-making is used to synchronise the activity of school members using a signal that allow global communication at the school level but is

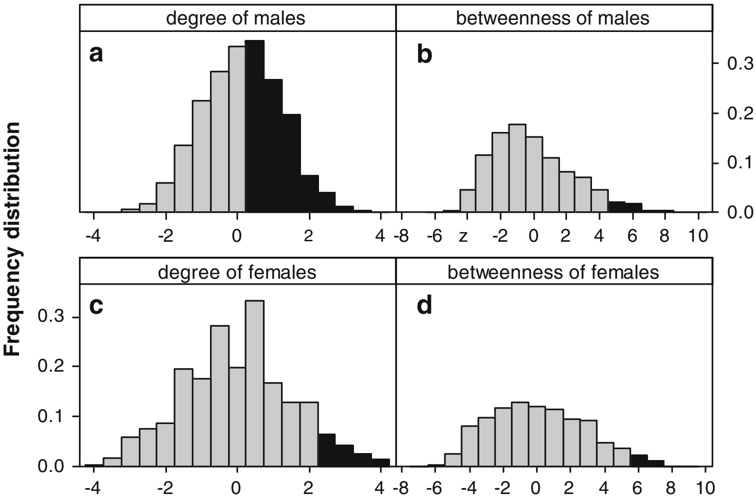

Fig. 2 Results of the four weighted randomisation tests looking at the difference in degree (**a** and **c**) and betweenness (**b** and **d**) of individual males observed SF versus others (**a** and **b**) and individual females observed ULT versus others (**c** and **d**). Thousand randomisations were performed for each test and each panel is a histogram of the resulting difference in degree and betweenness at each randomisation. In this analysis the likelihood that an individual was observed performing a behaviour in the random data was weighted by the amount of time spent with that individual in the field. The values that were higher than the observed differences are shown in black bars

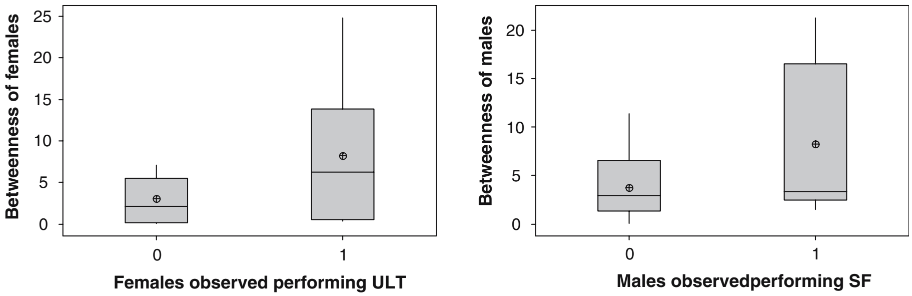

Fig. 3 Boxplot of betweenness for females (**a**) and males (**b**) depending on whether they were observed performing ULT or SF (value 1 on *x*-axis) or not (value 0 on *x*-axis). Lines in boxes are medians and symbols are means

advantageous in that it prevents advertisement of activity shift to non-school members.

SF and ULT are rare events and therefore could lack the necessary reinforcement to be a useful signal in the population. However, recent studies (Flack et al. 2006) show that rare events can still contribute to maintaining stable resource networks. It is possible that these events are only used when vocalisation is not possible because, for example, direct competitors are close by and this situation only arises rarely. Indeed, vocalisations can be heard up to several kilometres from the emitter and it might therefore be difficult to control to whom these vocalisations are advertised (Janik 2000). The sound produced by percussive behaviours such as SF and ULT do not propagate more than a few 100 m and would therefore not be heard by individuals that are further away (Finneran et al. 2000). There is circumstantial evidence that schools are rarely in the vicinity of one another in Doubtful Sound (Lusseau et al. 2003) but further studies are needed to confirm whether SF and ULT are more likely to occur when schools are close to one another.

Bottlenose dolphins in Doubtful Sound rely on reef-associated prey items that are produced within the fjord system and are spatially patchy but fixed (Lusseau and Wing 2006). These prey items tend to have a slow growth and there are good evidence that the dolphin population's carrying capacity is limited by food (Lusseau and Wing 2006). Intra-specific competition for food therefore plays an important role in defining the fitness of individuals, which could explain the evolution of the signalling system described here. Complex social behaviour have been described arising from selective forces in other bottlenose dolphin populations (Connor et al. 1999). Centrality measures are not related to age or sex in this population (Lusseau and Newman 2004). We are therefore left with the hypothesis that the behavioural role highlighted by this study is not associated with the individual but with its position in the social network, potentially indicating a social role (Flack and de Waal 2000). This hypothesis will be difficult to test empirically in the field because of the ethical issues surrounding playback and knockout experiments on free-ranging cetaceans. However, natural experiments, through the natural disappearance of individuals, could be helpful in testing this theory.

Signals associated with shift towards travelling were performed by males while signals associated with the ending of travelling bouts were carried out by females. The Doubtful Sound population live in mixed-sex school year-round which is unique for this species and rare for a fission-fusion society (Lusseau et al. 2003). The reasons for this are still largely unknown but may include long-term mate guarding, infanticide avoidance, long-term paternal role in young rearing, or lack of dispersal from the maternal unit (Lusseau et al. 2003). While sexual dimorphism is not pronounced in bottlenose dolphins (Tolley et al. 1995), some difference in metabolic costs still exist (Lusseau 2003c; Williams et al. 1993b) and cost of transport tends to be more expensive for females. These differences are enhanced by the extreme location of Doubtful Sound for the species (the population live at the southern limit of the species' range). This sexual discrimination in signal production could therefore be explained by the optimisation of the cost of transport for individuals allowing mixed-sex school to remain synchronous.

Individuals with high betweenness values in principle will have had more diverse affiliations within the social network and hence will be more knowledgeable about potential competitors because they have been more exposed to them. In addition, they may as well have knowledge about the patches recently visited by those and therefore would have a better understanding of the current quality of food patches. That is they would be more likely to know which food patches have been visited by those other groups and therefore would know which ones to avoid. Dietary analyses show that the Doubtful Sound population of bottlenose dolphins rely on reef-associated prey items which are resident to the fiord (Lusseau and Wing 2006). Therefore, having some understanding of which of those patches have been visited by other groups in the recent past provides a good proxy for patch quality. Following such individuals would be advantageous in decreasing travelling costs for all in the school. Individuals with high degree can indiscriminately reach more individuals within the network and may therefore be more related to the archetypical symbolic representation of leaders (Byrne 2000; Krause and Ruxton 2002). They therefore would have a good knowledge of individuals in their immediate vicinity, in their local cluster, but those can include both within and between ''global''cluster links. Following the Conradt–Roper framework (Conradt and Roper 2005) they would therefore be less reliable sources in decision-making processes regarding competition avoidance (scrambled or direct). The relative relationship between these two network statistics can explain the marginally similar results for degree and betweenness for females. However, for both males and females betweenness provided more explanation of the heterogeneity of the data than degree did.

Since signallers seem to be more likely to have preferred companionships (Lusseau 2003b) in several clusters of individuals, there can be several direct and indirect benefits for signalling. Further studies on the genetic relationship between the signallers and the members of the schools in which these individuals are observed signalling could help tease apart the roles of inclusive fitness and cooperation (Griffin and West 2002; Jennions and Macdonald 1994; West et al. 2001) in the evolution of these signals.

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