Social structure and behaviour of the Manta ray (*Manta birostris*) in the Republic of the Maldives

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Abstract

The present study confirms the presence of social structure within a population of manta rays found in the Republic of the Maldives. Many different species can be found occurring in groups and all are required, for at least some part of their lives, to meet conspecfics in order to mate. Associations were analysed between individuals within a population of Manta rays (*Manta birostris*) found in the Republic of the Maldives using a social network approach; with groups of individuals reflecting stable social communities. Social structure was explored at three levels: For all individuals within the population found in the Maldives over a period of many years (1996-2008), comparisons between years, and comparisons between observed behaviours at the time of observation. It was found that significant associations (and avoidances) occur within the population, with adult females being responsible for connecting the networks together; however this is restricted to behaviours other than feeding such as during cleaning, courtship and travelling behaviour. No significant result was obtained for individuals observed feeding together, with these groups reflecting simple aggregations in areas of high plankton concentrations; a finding similar to many other elasmobranches as they partake in so called feeding ‘frenzies’. True social structure, where individuals repeatedly associate with others over significant time periods has only been documented in a selection of species. Usually in vertebrates possessing high cognitive abilities, this behaviour has only recently started to be investigated in elasmobranches, and has not previously been described in any population of manta rays.

Keywords: *Manta birostris,* group living, social network theory, social structure

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Chapter 1

Introduction

Vertebrate social structure

Social structure may exist whenever animals live together in a group defined by stable interactions. It is seen in a variety of animal groups, from mammals, both terrestrial (Wittemyer *et al*., 2005) and marine (Gowans *et al*., 2001) to fish (Croft, 2006) and invertebrates (Michener, 1974) and is believed to result as a response to a variety of selective ecological factors (Gowans *et al*., 2001), including predation risk, the acquisition of food and mates and the transmission of information and disease. These factors, which may vary across time and space (Wittemyer *et al*., 2005), are key in determining the costs and benefits of group living. The benefits of living in such a way include reduced predation risk, the easier acquisition of food and mates, alloparental care of offspring and the transmission of information. The costs however, include increased competition for resources (food, space and mates), increased conspicuousness to predators, and the transmission of disease. It is a balance of all these factors which will determine the group living behaviour and social structure of any particular organism, with group formation only existing when the benefits outweigh the costs (Conner, 2000).

Many different species have been documented living in groups, and indeed all animals need to meet at least occasionally in order to breed, involving some form of social connectivity, however true social structure, at least for the purpose of this investigation, was defined as the repeated associations (or avoidances) between individuals within a population, which is not aggregating in response to a concentrated resource, or simply reflects the convergence of individuals to mate.

Group formation has been reported in a number of elasmobranch species (Klimley, 1987; Economakis & Lobel, 1998), but usually occurs as non-social aggregations around resources. In fact all cases reported in the literature thus far consider situations where numbers of individuals have been observed in close proximity to each other in response to external factors, without any repeated dyadic associations. These include predation (Holland *et al.*, 1993; Semeniuk, 2003), the acquisition of prey (Eibl-Eibesfeldt & Hass, 1959; Morrissey, 1991; Strasburg, 1958) and local environmental change. No cases of social learning have been reported in elasmobranches, with no examples of parental care of offspring. However, their relative brain-body ratios are comparable to those of birds and mammals (Northcutt, 1977), suggesting the possibility of elasmobranches being capable of complex behaviours similar to those of larger brained vertebrates (Guttridge & Gruber, 2008).

Predation

In many species it is the reduced risk of predation that is thought to be most fundamental in the evolution of sociality and group living (Molvar & Bowyer, 1994; Gosling, 1986; Jarman 1974; Gowans *et al.*, 2001) and indeed this has been found to be influential in the evolution of sociality in many species including Northern bottlenose whales (Gowans *et al.*, 2001), Moose (Molvar & Bowyer, 1994) and fish (Godin *et al.*, 1988).

Group living may reduce an individual's risk of predation in a number of ways. Firstly the encounter effect may lead to greater chances of detection by predators (Conner, 2000), favouring living in small groups, however particularly in marine environments it may be assumed that a group is no more likely to be detected by a predator than a solitary individual (Conner, 2000). Once detected by a predator, the dilution effect favours living in larger groups due to the reduced chance of an attack on any particular individual if the predator only consumes a few individual prey items (Turner & pitcher, 1986). If the predator is able to consume the entire group, e.g. Humpback whales (*Megaptera novaeangliae*) feeding on shoals of fish, then the rate of individual attack does not decline with increased group size, with no benefit gained from living in a group (Inman & Krebs, 1987). The dilution effect may also be applied to protection form conspecifics, specifically male harassment of females. Campagna *et al.* (1992) observed greater pup loss in Southern sea lions (*Otaria byronia*) due to male harassment, for females who arrived early at breeding grounds compared to those that arrived later due to the diluted risks in the presence of many other females. Similar observations have been made in humpback whales (*Megaptera novaeangliae*), with pregnant females being the last to arrive at breeding grounds to avoid harassment (Clapham, 2000).

A further effect on predation is known as the confusion effect, where individual capture rate per attack is reduced due to the difficulty for predators to capture an individual within a group (Milinski, 1977). This mechanism is particularly apparent while observing shoals of fish or flocks of birds evade a predator. As a response to disturbances by predators, cetaceans have been observed moving closer together compacting the group (Norris *et al.*, 1994; Whitehead & Glass, 1985) in a similar way to schooling fish (Pitcher & Parrish, 1993). It is suggested that this is beneficial as cetaceans may be more able to respond to the changes in direction and speed of the pod, usually by vision. Fish are able to do this in a similar way using the lateral line system. A further disadvantage to the predator is not being able to single out an individual for attack (Hobson, 1978). Further explanations for this compaction of a group in response to a predatory attack include the selfish herd hypothesis, where overall group compaction occurs as a result of each individual selecting a location within the group (usually the centre) which minimizes their individual chance of attack (Hamilton, 1971).

In contrast to the compaction of a group, some species employ the opposite strategy by scattering. Some predators have used the compaction behaviour of their prey as an effective means of prey capture, for example baleen whales engulfing entire mouthfuls of fish, so as a response to this type of predation it may be beneficial to scatter rather that compact. This type of response has been documented in dolphin species in response to the cooperative hunting techniques of killer whales (Acevedo-Gutierrez *et al.*, 1997).

Group living not only reduces the chance of attack and capture by a predator, but may also aid in the detection of a predator before an attack has begun (Uetz & Hieber, 1994), possibly even preventing it happen. This is particularly true if the predator is an ambush hunter. Group members may alert others to the presence of a predator passively, via behavioural changes as they monitor and evade the predator themselves, or actively by giving an alarm call. In an extreme case of predator vigilance, sentinel behaviour is found in a variety of avian and mammalian taxa (Conner, 2000) and refers to a non-foraging individual positioned in a location where it may more easily observe approaching predators as the rest of the group forages for food (Horrocks & Hunte, 1986).

Further benefits may be derived from the group in response to a predatory attack if individuals engage in predator mobbing behaviour. Approaching a predator may seem risky; however after being approached by prey, a predator that has lost the element of surprise may be dissuaded from an attack. More intense pursuit behaviour by prey animals may also confer some level of fitness, signalling to the predator that the individual is in good condition and will be difficult to capture. Such behaviour has been observed in Thompson's gazelle (*Gazella thomsoni*) 'stotting' in response to attacks by cheetahs (*Acinonyx jubatus*) (Caro, 1994). More intense still is the mobbing behaviour exhibited by some species of birds and cetaceans, where a predator is physically attacked and harassed until it leaves the area (Mann & Barnett, 1999; Conner & Smolker, 1990).

Group formation in response to predation has been observed in a number of elasmobranches. Scalloped hammerhead pups in Hawaii form aggregations during the day as they rest in nurseries which may provide protection from predators (Holland *et al.*, 1993). Similar behaviours have also been observed in Cowtail stingrays (*Pastinachus sepen*) in Shark bay, Australia (Semeniuk, 2003), where individual rays rest alone in water of high visibility but group together in conditions of low visibility. Experimental evidence for this behaviour being a response to predation risk is convincing. Firstly rays were found to preferentially settle near models with artificially extended tails (presumably due to its increased mechanical detection of predators) and secondly, it was found that rays in groups tended to adopt geometries which maximised the predator detection area (Carrier *et al*., 2004).

Due to their relatively large size and speed in the water manta rays do not have many natural predators; however bites are sometimes seen on individuals. Although whether these bites are recent or were incurred at a younger age and haven't healed is still hard to determine. The only two predators known to prey on the manta ray are the tiger shark (*Galeocerdo cuvier*) and the killer whale (*Orcinus orca*), both of which grow large enough and are potentially fast enough to prey on them. Geographic variations in the attack rate observed in manta rays certainly exists with individuals from Mozambique showing a high frequency of injuries; conversely individuals from the Republic of Maldives do show signs of predation but these occur at a much lower frequency. To date however quantitative comparisons of attack rates between populations have not been carried out.

The acquisition of resources

The acquisition of resources has also been highlighted as an important factor driving group living and social structure (Johnson *et al*., 2002), with behavioural ecologist's long recognising the relationship between social behaviour and the distribution and predictability of resources (Clutton-Brock & Harvey, 1977; Crook, 1964). The benefits of group living to attain resources may take many forms, from group hunting in wolves to bring down larger prey (Drzejewski *et al*., 2002), to the increased foraging rate of prey species, as less time needs to be spent looking out for predators (Milinski & Heller, 1978).

Although many species of sharks are solitary foragers, in some cases groups of sharks will come together to feed. This behaviour has been observed in blacktip reef sharks (*Carcharinus melanopterus*), lemon sharks (*Negaprion brevirostris*), oceanic whitetip sharks (*Carcharinus longimarus*) and thresher sharks (*Alopias*). In each case groups of individuals were observed apparently ‘herding’ prey items such as fish and squid together (Eibl-Eibesfeldt & Hass, 1959; Morrissey, 1991; Strasburg, 1958). Whether these cases are reflective of cooperation is arguable as they could simply reflect the aggregation of individuals around a common food source. Indeed many so called cooperative foraging examples could be explained as simple feeding ‘frenzies’, where individuals are highly motivated to feed and may be seen in numbers from a few individuals to hundreds of sharks (Carrier, 2004), however these feeding bouts tend to end abruptly (Nelson, 1969) and do not resemble any form of social structure.

Manta rays (*Manta birostris*) are often observed feeding together in groups, utilising a chain formation, individuals will feed in a line following others. The exact purpose of this has yet to be proven and although similar behaviours are observed during courtship, it seems this behaviour is linked to prey acquisition, possibly aiding in directing water flow and food into the mouth (Stevens, pers. Comm.)

Further benefits include the increased access to mates such as that seen in lion prides, where one or sometimes two males will live in a group with many females fathering multiple offspring. Defending them from other males, they will attain an inclusive fitness far higher than would be possible if each male had to search out each female and guard each cub individually (Clutton-Brock, 1989).

Learning

Social learning has long been of interest to ethologists and behavioural ecologists, as it seems to allow animals too rapidly and efficiently learn about their environment due to the reduced costs of mistakes and exploration (Laland & Williams, 1997). There are a number of examples of social learning documented in a variety of animals groups, such as the washing of sweet potatoes in Japanese macaques (*Macaca fuscata)* (Kawai, 1965), and the spread of milk bottle top opening seen in British tits, *Parus* spp. (Hinde & Fisher, 1951).

Most experimental evidence for social learning has come from controlled laboratory experiments (Galef, 1988b; Heyes & Dawson, 1990; Nicol & Pope, 1994) which have identified several ways in which learning can occur, only some of which rely on complex cognitive abilities (Galef, 1988a; Whiten & Ham, 1992; Heyes, 1994). Most cases documented seem to be as a result of very simple processes (Galef, 1988a) such as 'local enhancement' (Thorpe, 1956), where an animals actions may simply draw the attention of others to a particular stimulus or event in the local environment (Laland & Williams, 1997). However experimental evidence suggest that these 'tip offs' can lead to learning with a subsequent spread of behaviour throughout a group (Galef, 1988a).

This copying behaviour or ‘local enhancement’ has also been demonstrated in respect to mate choice in some fish species (Guppies, reef fish), where females may copy other conspecifics in choosing a mate (Dugatkin & Godin, 1992; 1993), possibly learning which males are more ‘desirable’, possessing the best genes.

Linked to the other benefits of group living already mentioned, learning in social groups may aid in increased foraging success (Ryer & Olla, 1991; 1992) and increased awareness of predators (Suboski *et al*., 1990) with many gregarious and long-lived species such as gorillas (*Gorilla gorilla*), elephants (*Loxodonta africanus*) and dolphins (*Tursiops truncates*) relying on information transport within the social group to effectively exploit their environment (Janik, 2000; Conradt & Roper, 2003; Lusseau, 2003).

Competition

Where competition with conspecifics or members of other species exists, group formation may be selected for as members of the same group cooperatively defend resources (Wranghm, 1982). This is particularly true of food sources if they occur in a patchy distribution with the ability to support only a limited number of individuals. Where females usually join to defend food sources (Gompper, 1996), for males it is the acquisition of females to mate with that drives cooperative defence (Wrangham, 1980). Living in a group however inevitably incurs some level of cost in respect to intraspecifc competition, but individuals may be more willing to share prey items or foraging areas with relatives, a mechanism known as kin altruism.

Disease

Grouping behaviour may reduce the risk of non-socially transmitted disease and parasite burden via the dilution effect (Mooring & Hart, 1992). This dilution effect has been observed in both horses and dolphins where parasite burden was at its greatest when individuals were in small groups, with this burden reducing in larger groups (Duncan & Vigne, 1979; Conner, 2000). The body of an elasmobranch offers a diversity of sites suitable for use by parasites and indeed every organ system found in elasmobranches has been found to contain parasites (Carrier *et al*., 2004). Conversely a cost of group living is the increased transmission of socially transmitted diseases, which may increase with increased group size.

Environmental challenges

A further benefit of group living may be seen when individuals face challenging environments. Some species such as emperor penguins (*Aptenodytes forsteri*) huddle together to keep warm during the winter months, without such behaviour an individual animal will surly die (Conner, 2000). Others, such as many aquatic and bird species may benefit from the reduced costs of locomotion while swimming or flying in a group (Abrahams & Colgon, 1985; Pitcher & Parrish, 1993). Clark (1991) studied bowhead whales *(Balaena mysticetus)* in the Bering Sea, observing groups of up to 15 whales navigating together over a large area of 4-8 square miles, suggesting that the echoes created from other whales vocalisations aided in assessing ice conditions and reducing the costs of locomotion to the individual.

All of the examples considered thus far are those where the individual benefits (and pays some costs) from the presence or behaviour of others, a situation known as mutualistic group formation (Conner, 2000) more reflective of social structure. However it is possible to find other types of group formation in many species, which form independently of any benefits derived from others in the group. Examples of this non-mutualistic group formation include aggregations formed in areas of highly concentrated food sources (Alexander, 1974), or predator refuges and even energetically favourable spots (e.g. basking areas or shelter form cold) where the resources concerned and the areas in which they are found are sufficient enough for individuals to tolerate each other. It is this distinction between a mutualistic and non-mutualistic groups which many authors use to differentiate between social and non-social aggregations (Conner, 2000; Norris & Schilt, 1988) with the former being referred to as groups and the later aggregations. In social groups it is reasonable to assume that in order to derive benefits from other individuals, close proximity is necessary, making these social groups easily distinguishable from non-social aggregations, which may occur over larger scales (Conner, 2000); however care should be taken while considering scale as an indicator of sociality. As described previously some species (i.e. cetaceans) that are able to communicate over large distances may remain socially connected despite large scale group dispersal.

It is important to consider that such boundaries and definitions rarely occur in nature, with the possibility of small mutualistic groups occurring within larger non-mutualistic aggregations. Whitehead & Weilgart (2000) observed this arrangement while studying sperm whales (*Physeter macrocephalus*) off the Galapagos Islands, noting four levels of spatial organisation; stable units of roughly ten related females and calves, associations between units lasting over a period of days, temporary aggregations of around forty individuals over an area of 15 km^2 and finally large concentrations of thousands of individuals occurring over an area of 1,000 km^2. Whitehead & Weilgart (2000) go further to explain the reasons for each level of grouping suggesting that the first (lowest) level may be due to the care and protection of dependant offspring, the second may result in improved foraging efficiency and the third and forth levels, resembling non-mutualistic aggregations, possibly as a result of varying spatial scales of food concentration.

Overview of the costs and benefits of group living

The different factors driving group living in animals have been explored. This focus has been on the mechanisms with examples rather than the ecological circumstances of particular species. The circumstances driving group living behaviour in any species is usually a combination of these factors rather than one acting in isolation. Both the costs and benefits (see appendix 1) have been discussed and it is important to remember that both may be acting simultaneously at different levels, with group formation usually occurring only when the benefits of such behaviours outweigh the costs. For a full review of the mechanisms described here please refer to Krause & Ruxton (2002). Although some groups form only briefly, usually in response to concentrated resources, some portray a more stable structure. Many different species, both terrestrial and marine, vertebrates and invertebrates spend at least some part of their lives in close association with conspecifics (Ebensperger & Bozinovic, 2000). The structure of these social relationships varies greatly in time and space, from stable long term groups to temporary aggregations in response to concentrated resources. It is this difference between temporary aggregations and long term grouping which highlights the difference between non-social and social groups. Social groups are expected to portray some degree of repetition, with individuals being able to meet (or avoid) each other on repeated occasions. Further, associations between individuals are expected to have some level of temporal stability.

Knowledge of the social structure exhibited by groups of animals is an important part of understanding an animal's biology. Social structure defines an important range of ecological factors; that is those between nearby conspecifics (Whitehead, 1997); this may include competition, cooperation and dominance. Thus social structure is an important factor in population biology, influencing gene flows among and between populations as well as spatial distributions (Wilson, 1975).

Social structure is also correlatively seen with increased levels of cognition and communication, possible even being an evolutionary determinant in these processes (Byrne & Whitten, 1988). A rich social life has been described in many mammal species including elephants (Wittemyer *et al*., 2005), primates (Whiten, 2000) and cetaceans (Conner *et al*., 1998), but its presence in elasmobranches is yet to be explored (Carrier *et al*., 2004). A current method for exploring the social structure of animal groups and one which has advanced our understanding of social interaction in animal populations (Guttridge & Gruber, 2008), is the use of social network theory. This method has recently been developed and used in investigations into a number of animal groups (Eisfeld & Robinson, date unknown; Lusseau, 2003 Wittemyer *et al.*, 2005; Croft *et al.*, 2004; 2005), and has enabled a framework in which to study social behaviour as well as allowing the quantification of inter-individual associations (Guttridge & Gruber, 2008).

Social network theory

The basic component of any social network is the dyadic association between pairs of individuals (Whitehead, 1997). Until recently the majority of work in the field of social structure has only considered these dyadic interactions (dyads refer to two associated individuals); however it has become clear that these interactions rarely occur in isolation, and the importance of studying these dyadic interactions within the context of the whole population is beginning to be considered (Croft *et al.*, 2005).

One way of considering a complex arrangement of dyadic interactions is the use of network theory. A network is essentially a number of nodes connected to each other in a particular arrangement via edges (Croft *et al.*, 2008). Graphically, nodes usually represent individuals (but may also represent behaviours) and edges represent an interaction or association.

It may be beneficial to gain some understanding of the different properties that each node within the network may possess. Standard network measures such path length, cluster coefficients, node degree and node betweeness allow a deeper understanding of a networks structure and the importance of the individuals within it. The presence or absence of a specific individual may have important implications on the resulting structure of a network. Furthermore the links of any one individual to another in a network may vary greatly, some being ‘well connected’ and others not so, with the removal of such ‘well connected’ individuals resulting in the lengthening of information pathways between individuals (Lusseau, 2003) (figure 1).

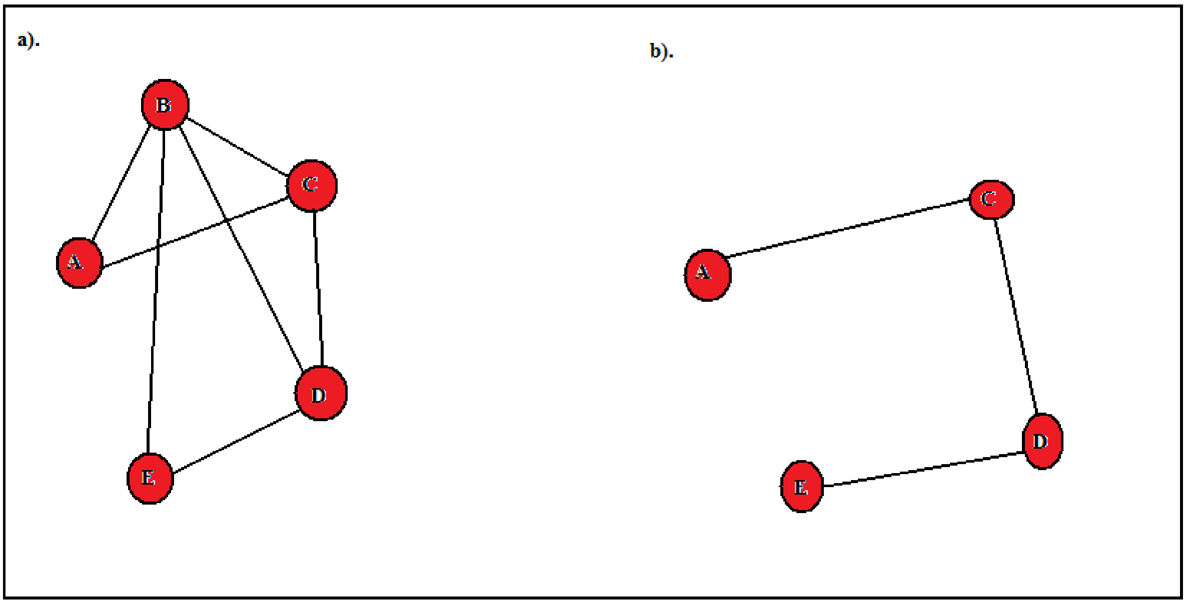

Figure 1. Illustrative example of a simple model network demonstrating the importance of certain nodes. Red circles indicate nodes (individuals) and black lines represent edges (associations). A). shows the complete network with associations and information (or disease) able to pass from A to E across the shortest path, via B. b). shows the network after the removal of node B, the path for information (or disease) to travel from A to E becomes much longer.

Certain individuals (known as cut points) are responsible for connecting others within the network, with their removal resulting in the separation of individuals from the larger community or further, the division of the community into separate components (figure

2) (Barthelemy, 2004). It is these individuals that are responsible for connecting the network together and thus responsible for maintaining any observed social structure within a population.

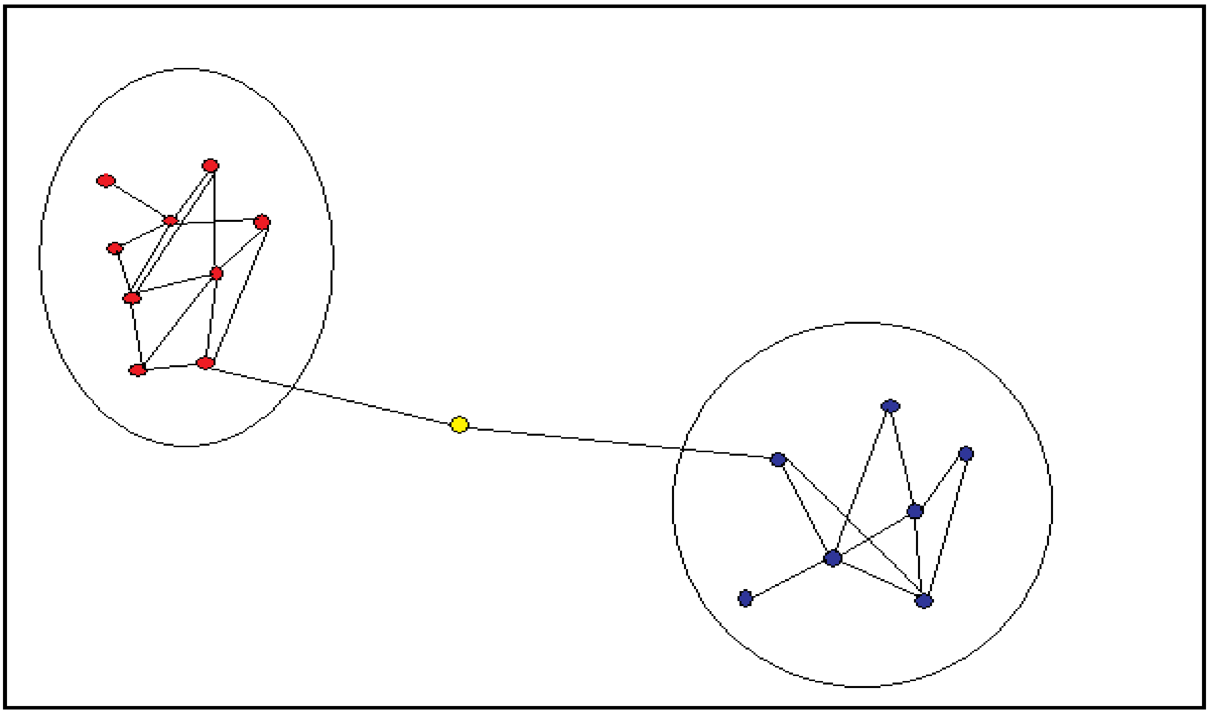

Figure 2. The yellow node is a cut point. Having a small connectivity and a high level of betweeness, it connects the red group and the blue group in the community. Its removal will result in the separation of the single community into two distinct ones (figure adapted from Barthelemy (2004).

The clustering coefficient, complementary to path length is another measure of a networks average structure, being derived from local considerations of the networks structure around each of the nodes (Croft *et al.*, 2008). Node degree is simply a measure of the number of edges connected to it. A measure of 'connectedness', individuals with a high degree are important in a network in respect to the transfer of information (or disease). For example let us consider that an individual produces and innovative behaviour e.g. the washing of sweet potatoes observed in Japanese macaques (*Macaca fuscata*) (Kawai, 1965; Itani & Nishimura, 1973), the degree of the innovator will be important in determining the likelihood of this new behaviour spreading throughout the population. If the innovator has a high degree and therefore many connections to others in the population, the behaviour is likely to spread, if it has a low degree it is likely to not, or if it does, it will almost certainly occur at a slower rate.

The degree of a node is a simple measure of its centrality, with those possessing a high degree and therefore many connections usually occupying central positions within the network, and those with a low degree usually being found on the periphery (Croft *et al.*, 2008). However there are more sensitive measures of an individual nodes centrality such as node betweeness. The betweeness of an individual node *i* is defined as “the total number of shortest paths between pairs of nodes (other than *i*) that pass through *i*” (Croft *et al.*, 2008). By calculating node betweeness it is possible to determine which individuals play key roles in the network in respect to the flow of information and/or disease.

The use of network theory is highly versatile and has long been used by physicians, mathematicians and social psychologists in many areas of study; however it has only recently been applied to the study of sociality in animals and is still relatively uncommon (Croft *et al.*, 2004; 2008). There are many systems which use a network approach with pair-wise connections such as power grids (Xu *et al.*, 2004), transport systems (Sen *et al.*, 2003) and the World Wide Web (Tadic, 2001) as it is capable of describing both the small and large scale properties of many interconnected individuals (Croft *et al.*, 2004).

Examples of the use of network theory in the study of animal social structure are varied, involving both marine and terrestrial species and captive and wild animals. Any study involving captive or easily approachable animals would be able to attain detailed observations of interactions, as the study population has a limited area in which to roam and are likely to be habituated to the presence of an observer (see Kuroda, 1980). In contrast studies involving wild populations bring with them a unique set of problems which need to be overcome. Firstly the individual animals used in the investigation need to be resighted, the greater the number of resightings the more confidence can be placed in any observed patterns of interaction and association. A further problem exists in being able to view a definitive interaction. As mentioned this will be much easier when observing captive animals, however this becomes much more challenging in the wild. One method commonly used is the replacement of a specific interaction with an association measure, where interactions are assumed to occur under defined conditions (Whitehead, 1997; Whitehead & Dufault, 1999).

Examples of these ‘replacement measures’ include nearest neighbour measures, where individuals observed next to each other in a group are defined as associating, distance measure, i.e. individuals within a defined distance of one another are defined as associating, and the ‘Gambit of the group’ where individuals observed in the same location during a set sampling period are defined as associating. The later example is commonly employed in studies involving large aquatic animals which typically roam over large areas and are known to mostly interact underwater, making them difficult to observe (Whitehead, 1997).

Examples of studies that have employed these methods include those by Croft *et al.* (2004; 2005) who used a network approach to explore the social structure of groups of Guppies (*Poecilia reticulate*). Individuals were marked with a fluorescent dye in order to be able recognise them again in future captures, with the final guppy network being found to be highly structured using a variety of network measures such as path length, degree, and cluster coefficients. It is important to remember however that this finding exists in the particular population investigated and does not necessarily represent similar patterns in other guppy populations or populations of any other fish species. Intra-specific comparisons between populations as well as comparisons between similar species would provide an exciting area of research and a greater insight into the development of such social systems.

Social network analysis has also been applied to the study of many cetacean (Eisfeld & Robinson, date unknown; Lusseau, 2003) and terrestrial mammal species (Wittemyer *et al.*, 2005). In investigations into the properties of dolphin social groups, Lusseau (2003) applied a network approach to determine the structure within a population of bottlenose dolphins (*Tursiops truncates*) in Doubtful sound. It was found that not all individuals were equal in their role in society, with certain individuals representing 'hubs' or centres within the network through which all other associations were linked.

The study species

The manta ray (*Manta birostris*) (plate 1), part of the Mobulidae family, is the world's largest species of ray and one of the world's largest species of fish (Yano *et al*., 1999). Previous work has considered this species to include both the smaller resident manta rays and the larger oceanic manta ray (see Yano *et al*., 1999); however recent work has defined these as two separate species (Marshall, unpublished data). The resident manta ray (*Manta birostris*) used in this study grow to a disc width of up to 4.0 meters. Feeding solely on planktonic organisms, it acquires food by filter feeding through the water column; taking large amounts of water into the mouth and filtering out prey items as water passes over specialised gill rackers and exits via the gill; a feeding mechanism known as ram feeding (Sims, 1999) similar to that of other elasmobranches such as the whale shark (*Rhincodon typus*), basking shark (*Cetorhinus maximus*) and the more elusive megamouth shark (*Megachasm pelagios*) (Moss, 1977).

Predominantly tropical this species is found globally in waters around the equator (plate 2), with occasional sightings in temperate regions (Last & Stevens, 1994). Seasonality in distribution and abundance has been reported (Notarbartolo-di-Sciara & Hillyer, 1989) with suggested ties to the distribution and abundance of plankton (Stevens, Pers. Comm.). Like other filter-feeding elasmobranches, manta rays are opportunistic as they forage on food sources that are often spatio-temporally patchy (Taylor *et al*., 1983; Colman, 1997; Sims, 1999), travelling large distances in search of food. Manta rays are known to live for at least 20 years (Homma *et al*., 1999), with an average fecundity of 1 (Bigelow & Schroeder, 1953; Homma *et al*., 1999), making this species, like all other species of elasmobranch, particularly vulnerable to overfishing.

Despite their occurrence in many regions of the world, their aesthetic value and their importance to the eco-tourism and diving industry, little published information exists on many aspects of the biology of this species (Yano *et al*., 1999), with the first conference dedicated to manta ray research occurring in 2008 (American elasmobranch association).

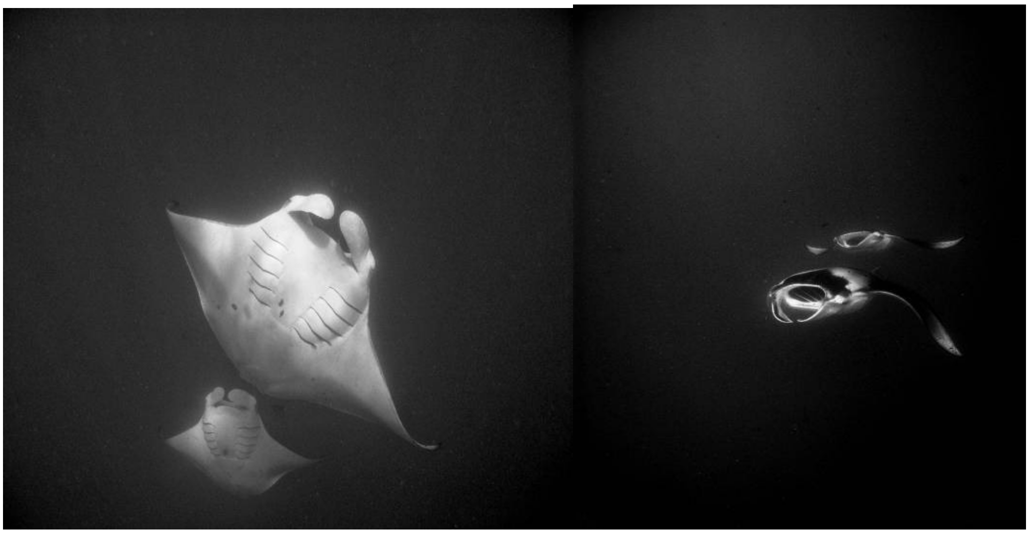

Plate 1. The manta ray (*Manta birostris)* is found in tropical regions around the world. (Photos: Gareth MacGlennon).

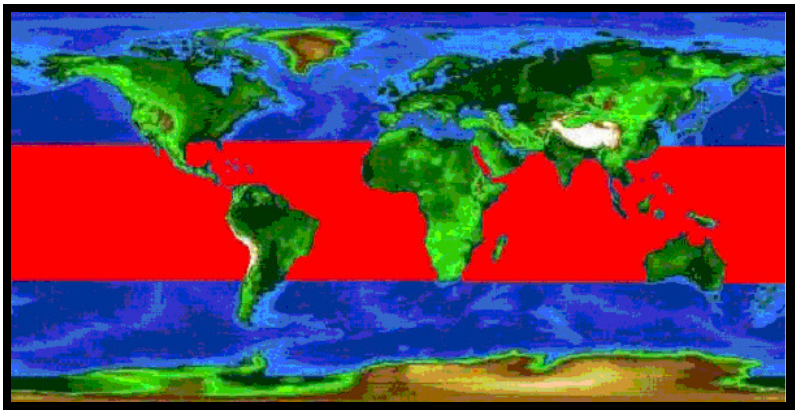

Plate 2. Map depicting the global distribution of *Manta birostris* around the equator. (Map courtesy of MMRP).

Officially listed as 'near threatened' (IUCN, 2007), many countries including the Maldives lack sufficient legal protection for the manta ray, with some countries such as the Philippines, Mexico, Mozambique, Madagascar, India, Sri Lanka, Brazil, Tanzania and Indonesia operating specific fisheries for this species; mainly for their meat, fins, liver and branchial filaments (IUCN, 2007).

The study area

The Republic of the Maldives (plate 3) is an archipelago of coral atolls. Spanning the equator, they cover 1,000 Km from North to South and 100 Km from East to West, with water making up 99% of all territory. This area presents itself as an ideal location for any study on this otherwise relatively unknown species due to the presence of a year round resident population, estimated to be made up of tens of thousands of individuals and relatively low levels of mortality due to anthropogenic processes.

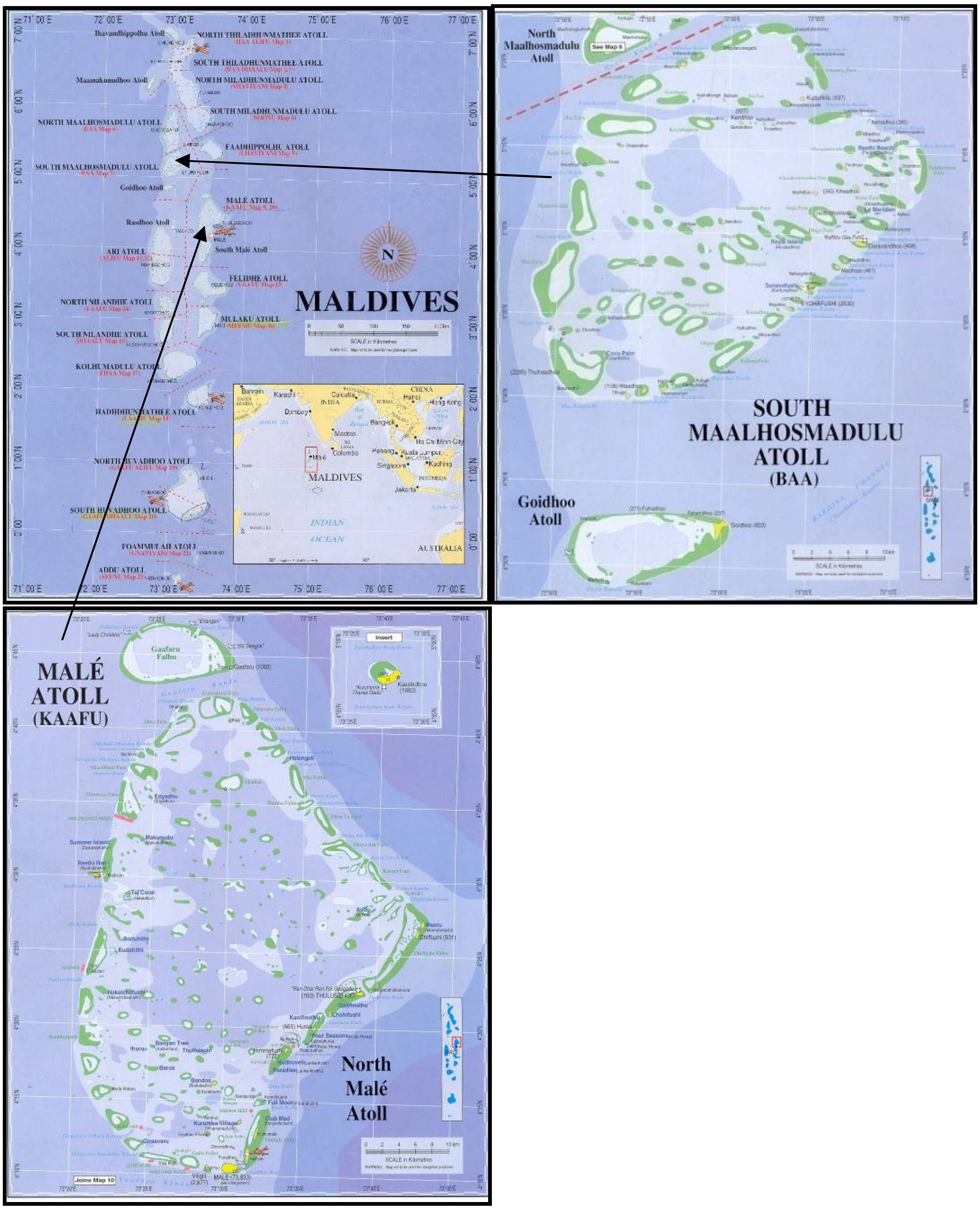

Plate 3. Top left, map of the Maldives. Top right, map of Baa atoll located in the West central Maldives. Bottom, map of North Male atoll located in East Central Maldives (Maps. Tim Godfrey).

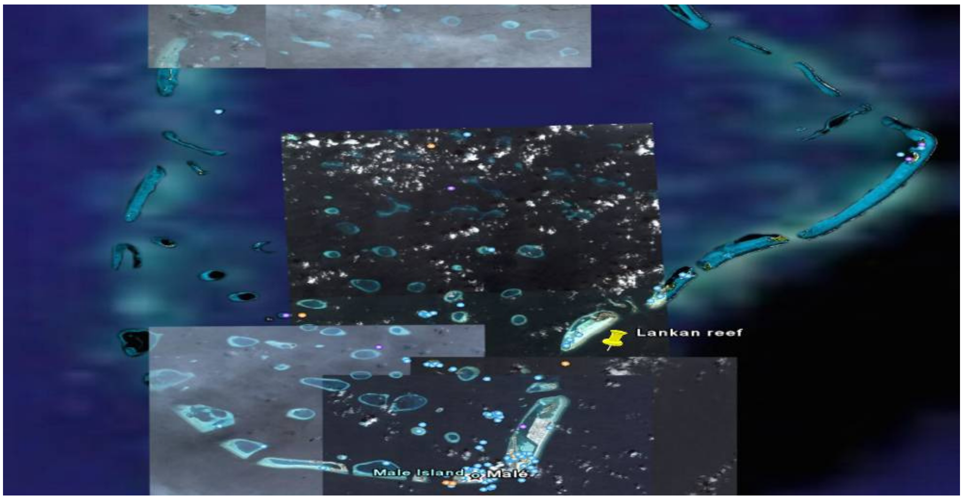

Plate 4. Top, Satellite image of Hanifaru (5° 10'26"N/73° 8'42"E), a lagoon with frequent manta ray sightings both cleaning and feeding. Bottom, satellite image of Lankan reef (4° 16'47"N/73° 34'18E), located on the outer edge of North Male atoll this reef is an important location for manta ray cleaning and mating (Satellite images. Google earth).

Samples were collected from various areas around the Maldives, however due to frequent sightings; two particular areas were frequently used to collect much of the data. Hanifaru (plate 4) is a relatively small lagoon found on the outer East edge of Baa atoll. Sightings of manta rays have been frequent in this area due to the presence of both cleaning stations and concentrated food supplies. Acoustic Doppler Current Profiling (ADCP) data has revealed strong currents from deep water outside the atoll frequently entering this lagoon, bringing with it high levels of zooplankton. Due to the shape of this lagoon zooplankton congregates in high densities attracting many manta rays and other plankton feeders such as whale sharks to feed. Lankan reef (plate 4) is located on the outer East edge of North Male atoll and has long been recognised as an important area for manta ray cleaning and mating; with both behaviours being frequently documented (Maldivian Manta Ray Project, MMRP).

Outline of objectives

This project aims to investigate the social structure within the Maldivian population of manta rays in three ways; across a long time period of many years, by comparing between years and comparing between behaviours with the following objectives:

1. Investigation into the general manta ray biology within the Republic of the Maldives, such as sex and age ratios.
2. Social structure for the entire known population of manta rays in the Maldives will be explored over a long time period (1996 – 2008).
3. Further exploration will be carried out to explore the core structure of the network and identify key individuals.
4. Social structure for the entire known population of manta rays will be compared between years (2006 - 2008).
5. Social structure for the entire population of manta rays will be compared by specific behaviours observed (Cleaning and feeding) over a long time period (1996 – 2008).
6. Potential reasons for any patterns and findings will be discussed.

Chapter 2

Materials and Methods

The Maldivian manta ray project (MMRP) was set up in 2005, after which a detailed database was developed on individual manta ray locations and movements around the Maldives for a number of years. Although officially started in 2005, data (photographs) from sightings previous to this was collected from third parties and added to the existing database. Mostly consisting of data collected by trained employees and volunteers of the project, too date over 1,000 individual manta rays have been observed and identified. Observations are made throughout the year over many locations spanning much of the central atolls.

Identifying individuals

In any study of social structure and networks, the ability to identify individuals is imperative (Croft *et al.*, 2008), and in this study identification was facilitated by the unique spot pattern arrangement found on the ventral side of each manta ray (see Yano *et al.*, 1999) (plate 5, a.). Specifically the branchial area located between the gills, these spot patterns are documented to be not only unique to each individual, but permanent marks that do not change over time (Stevens, pers. Comm.). Confidence was placed in this method with the resighting of two manta rays, M93 and M12, first recorded in the publication 'The Maldives, home of the children of the sea' in 1990, then subsequently recorded many years later in 2005 and 2007 respectively, each with no change in spot pattern. Identification was further aided by the position of unique scars and injuries seen on many rays (plate 5, b.). This technique for identification has been used in the study of many species (Whitehead & Dufault, 1999; Whitehead, 1994), including bottlenose whales (*Hyperoodon ampullatus*) (Gowans & Whitehead, 2001), whale sharks (*Rhincodon typus*) (Meeken *et al.*, 2006) and bottlenose dolphins (Lusseau, 2003). Although computer recognition software exists (e.g. I3S) and has been used effectively in other species (see Shorrocks & Croft, 2008), these programs are still ineffective in the automated identification of manta rays. For this reason identification was conducted by eye via comparisons with a 'branchial gallery', a database containing information and images of all known individuals.

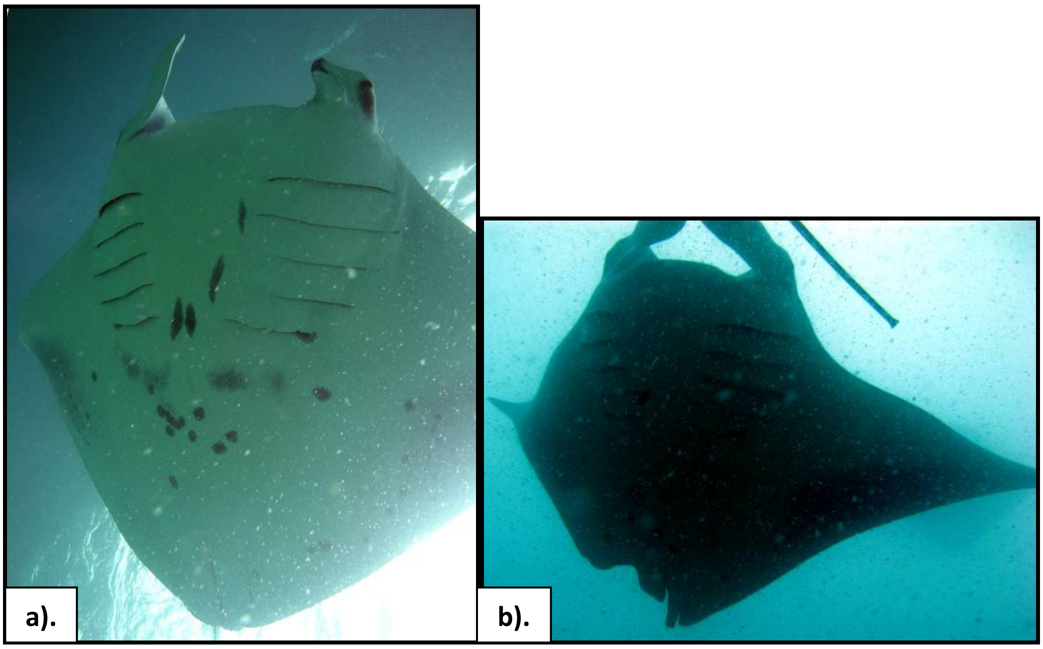

Plate 5. A). The unique spot pattern found on the branchial area on the ventral side of M578, also note the missing left cephalic fin. B). the shape, size and position of unique scars also aid in identifying individuals (Photo: Gareth MacGlennon, 2008).

In order to reduce the chance of errors in results, identification was conducted by only trained and experienced persons to avoid pseudo replication. Accuracy tests were conducted during the initial stages of the investigation to ensure that confidence could be placed on any subsequent identifications made. This was carried out by having a third party select multiple images of randomly chosen individuals. Subsequent identification, using the existing branchial database was then carried out by the investigator. Due to the prominent differences in spot patterns as well as the possession of scars and reproductive organs (males only), accurate identification was maintained throughout the investigation. Out of 200 images, an average of 5 (2.5 % average over 3 tests) were miss identified, with errors only occurring while using low quality images or images taken at angles not clearly displaying the branchial area. For this reason images of this type were rejected, with only high quality images clearly displaying identifying marks being used during identification and analysis.

Sex was determined by the presence or absence of claspers (male reproductive organs) around the anal fins. This was aided by the identification of mating scars on the left pectoral fin of females. Age was determined in males by disc size (length from tip of left to tip of right pectoral fin, in adults usually >2m) and the length of claspers, which for adults (6-8 years) extend out from the anal fin (IUCN, 2007). Female age was identified by disc size (again usually in adults >2m) and the presence of mating scars found on the left pectoral fin indicating age sufficient for mating behaviour.

Data collection

Data was primarily collected via photographic and videographic evidence taken during manta ray encounters over a period of many years (1996 – 2008) at a variety of locations around the Maldives, although due to logistical constraints, sampling was predominantly carried out in areas within the central atolls. Manta rays were found by searching known areas for feeding or cleaning behaviour (where the water's surface is commonly broken) in a 9 metre dhoni (traditional Maldivian boat) rented from a locally inhabited island. Usually visible from the surface, this effort was also aided by the help of local inhabitants and local dive centres contacting us with sightings information. Every effort was made to search for manta rays each day during the study period, however due to local weather conditions at the time this was not always possible. Photographic evidence was obtained using an 8 mega pixel Sea & Sea underwater digital camera with a wide angle lens while either scuba diving or free diving and videographic evidence was provided by Scuba zoo, a locally based underwater filming company.

Any photographs taken were organised by date and location and added to the existing database of identified manta rays. Any rays that had not already been identified were given an I.D. number and its information logged along with date, location and behaviour in the existing database.

To assess the sex ratios seen in our samples a Chi square test was carried out comparing observed numbers of males and females with the numbers expected in a normal population. The initial expected sex ratio in a normal manta ray population was assumed to be 50/50 male and female, with the null hypothesis expecting the observed and expected frequencies of sex in our population to agree. The numbers of individual resightings were also calculated and displayed to demonstrate the resighting rate during the investigation.

$\chi^2 = \sum \frac{(O - E)^2}{E}$ (Chi square test, O = observed value, E = expected value)

Assessing rates of association and exploring group structure across all years

The ‘Gambit of the group’ was used as the measure of association; a measure used in many other investigations involving marine species, it compensates for the extreme difficulty in observing specific social interactions between dyads (Whitehead *et al.*, 2000). This measure of interaction has some important implications to consider; however they may be justified if most interactions take place within groups (see Whitehead & Dufault, 1999). Since there is no evidence of acoustic communication in manta rays it is reasonable to assume that any interaction would have to occur while in close proximity and thus the ‘Gambit of the group’ can be used as a suitable measure of interaction.

Data was taken from the existing database and placed into an Excel spreadsheet listing all individuals seen together in a group with corresponding date, location and behaviour. The data from this spreadsheet was then analysed using SOCPROG 2.3 (after Whitehead, 1999) to determine social structure and the significance of associations. Developed to run in Matlab 6.5, release 13 by Hal Whitehead (1999) this program was created to analyse the social organisation of animal groups. The sample period was set to a day, counting all individuals seen in the same location during the period of a day as having an association.

After producing graphs that demonstrate sampling efficiency, SOCPROG was used to calculate the significance of the observed associations within our population. This was done by producing an association matrix and after 10,000 permutations (after stabilisation of the P value) the sum of associations index was used to calculate the mean association rate between dyads and the standard deviations of results. A measure of the exact number of times individuals were seen together, this association index was used due to the absence of any known bias in sampling, but due to the difficulties involved in the sampling environment coupled with variations in individual boldness it was not always possible to identify all the individuals within the group.

After saving the network obtained from the association index the data was saved as a vna file and opened in a program used for visual representation of networks, NetDraw (Borgatti, 2002). This software was then used to construct network association graphs. Filtering the network at a value of 1 (sum of associations) removed all associations below this level, leaving a more structured network of stronger associations.

After using the spring embedding function to optimise the layout of the network, the Girvan-Newman function (2002), which uses “edge betweeness” as a measure to determine edges that are most likely to join communities, was used to form a network graph to demonstrate grouping in the population placing individuals into communities.

$Q = \sum_{t=1}^{g} (e_{tt} - a_t^2)$ (Girvan and Newman function, 2002)

Further exploration of the network

Using the Chi square method used previously the sex ratio within the initial network was compared considering the skewed sex ratio found within the total Maldivian population. Further sex ratio analysis was carried out on intra-community differences (communities found by the Newman-Girvan analysis).

The original network graph using data from all individuals and behaviours over the entire study period (1996 – 2008) was further filtered to explore the core structure. Filtering thresholds were increased by 1 association each time to a total of 7 associations, with any differences in network composition being highlighted and tested statistically.

Network measures such as node betweeness, node degree and correlation coefficients were calculated using NetDraw and Ucinet for each individual within the network and displayed either as graphs for comparisons or as a table in the appendix.

Comparisons over years

Statistical analysis and the construction of network graphs were the same as for all years, however the data was split according the year of collection. Although the total data set was made up of data from 1996 to 2008, only the last 3 years (2006, 2007 and 2008) were considered due to the availability of more data. The results of each three analyses were tabulated for comparison and the three network graphs were placed alongside each other, also for comparison.

Cut points were calculated using the function key in NetDraw. This highlighted individuals occupying unique places in the network connecting other individuals to the larger group that would otherwise not be connected without the association with the cut point individual. Individuals forming cut points in the network were tabulated along with their sex and age.

Comparisons between behaviours

Statistical analysis and the construction of network graphs were the same as for all years, however the data was split according the behaviour observed at the time of observation. Two categories were formed, Cleaning (which also involved other behaviours such as courtship and travelling together) and feeding. Again results from these analyses were tabulated for comparison along with network graphs displaying groups and cut points.

Chapter 3

Results

Of all the known population of manta rays in the Republic of Maldives many more females have been identified than males indicating a significantly skewed sex ratio (figure 3), furthermore adult individuals were observed more often than juveniles (figure 4).

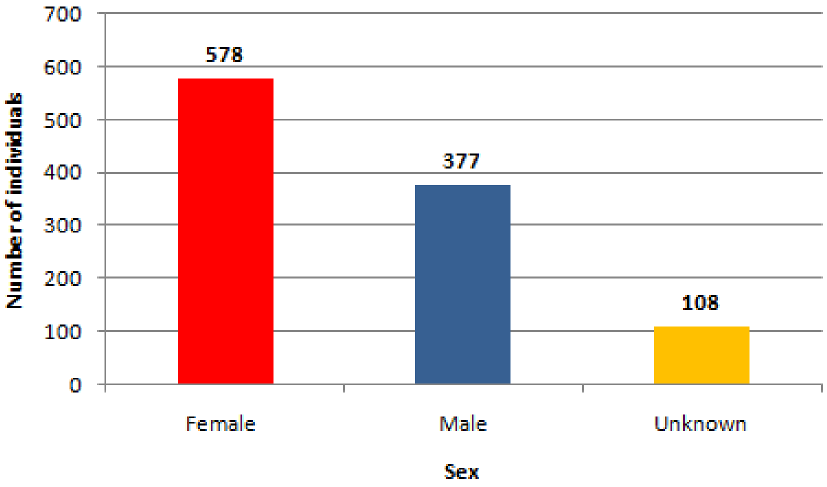

Figure 3. Sex ratio of all individuals within the known population of manta rays in the Republic of the Maldives. Chi square = 42.305 with 1 degree of freedom (P<0.001).

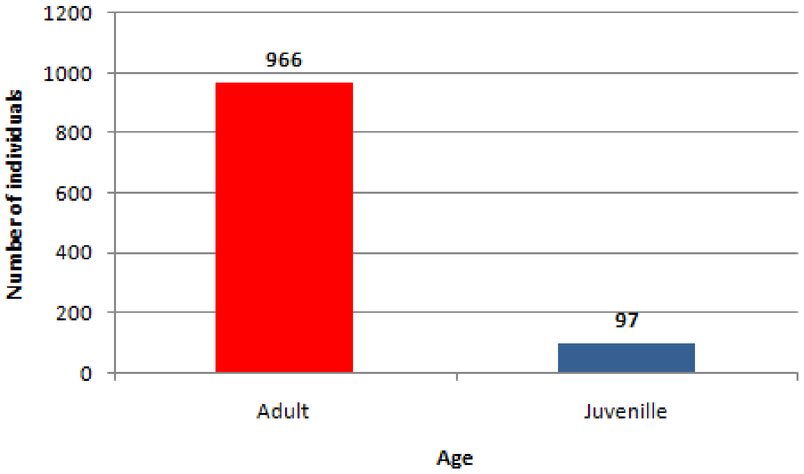

Figure 4. Age of all individuals within the known population of manta rays in the Republic of the Maldives.

Being able to disperse over a large area is key to the ability for any individual within the population to be able to associate with (or avoid) any other. Figure 5 highlights the number of individuals which have been documented in more than one atoll, indicating a high dispersal ability to move outside their original atoll, and thus the ability to associate with all other individuals in the known population. Another important aspect to any study of social structure is the ability to resight individuals over time. A large proportion of the population was observed at least twice, with some individuals being observed more than 10 times during the investigation, although in reduced numbers (figure 6).

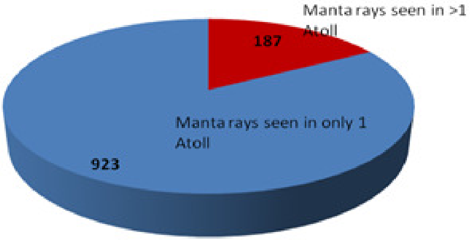

Figure 5. Numbers of manta rays seen in more than one atoll indicating large scale movments.

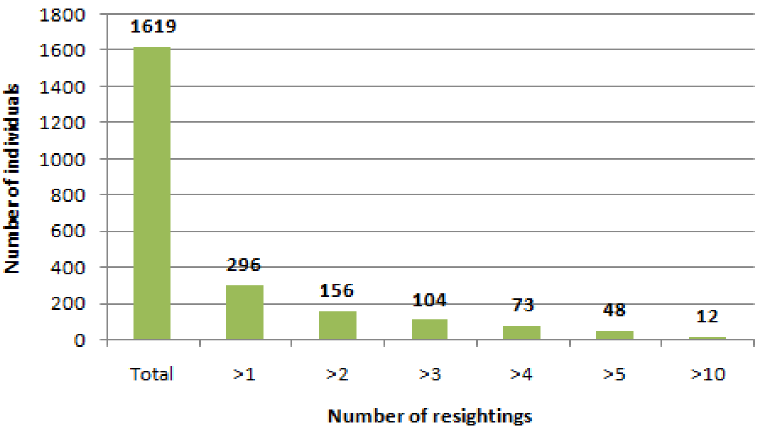

Figure 6. The cumulative number of individuals observed at increasing levels. The total column refers to the total number of sightings throughout the investigation. The average resighting rate per individual was 2.08.

Population sampling: Associations across all years and behaviours

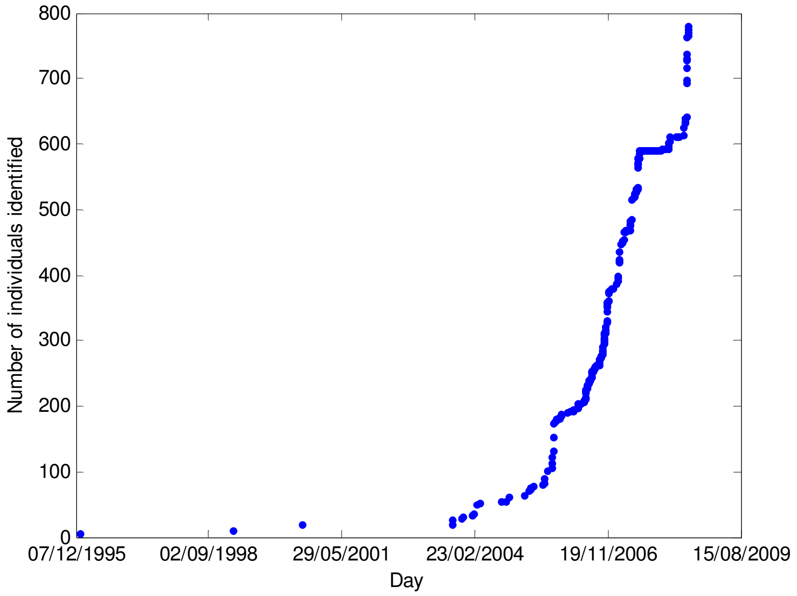

Figure 7. The number of individuals identified over time (321 sampling periods).

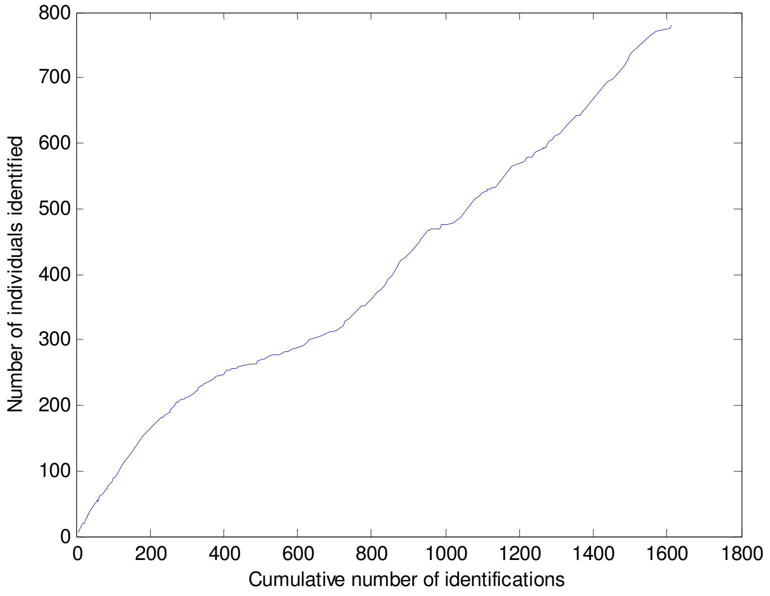

Figure 8. The number of individuals identified against cumulative number of identifications (observations), this graph demonstrates sampling efficiency with a sampling period of a day and the mean number of individuals identified per sampling period as 0.007 (0.7 %).

During the investigation the identification of individuals increased with time (figure 7). During the first years of the study very few individuals were identified until 2004/2005, after which identification of individuals rose dramatically. For the rest of the investigation, identification of new individuals remained high until the end, indicating incomplete sampling of the population, with an average individual resighting rate across the whole study period of 2.08 (figure 6). Although unevenly distributed, this pattern demonstrates a linear relationship between time and individuals being identified.

The rate at which new individuals were identified also increased with the rate of cumulative identifications (sampling effort) (figure 8). There is a gradual incline across the graph suggesting the slow but consistent identification of new individuals throughout the study period. The incline of the graph suggests that there may be more individuals in the population which were not sampled.

Testing significance of association patterns: Associations across all years and behaviours

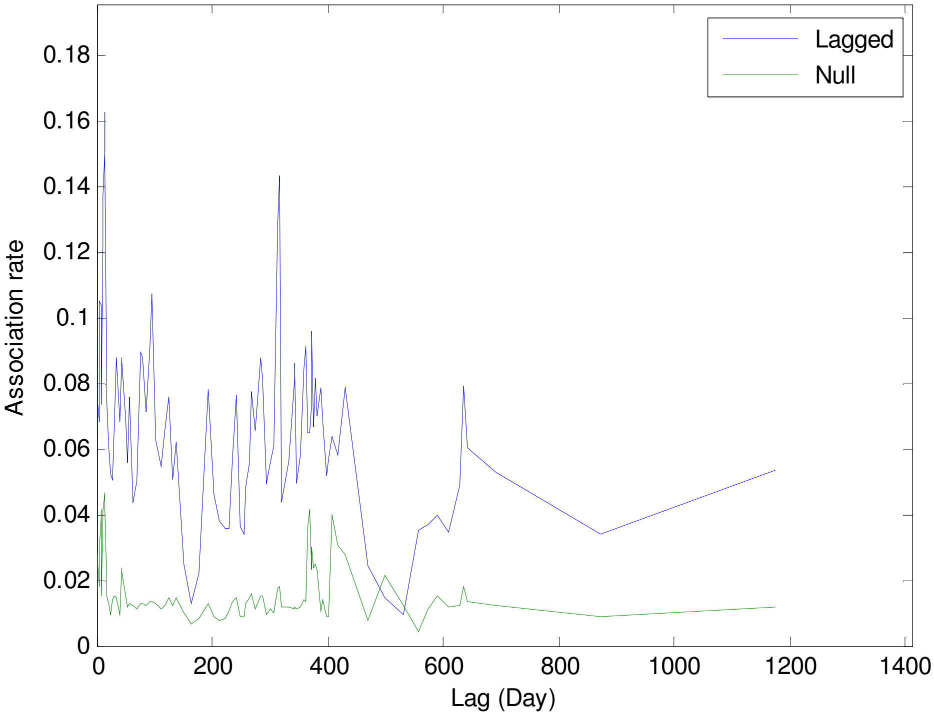

Figure 9. The association rates of both observed data (lagged) and expected data (null). (P value <0.001). This graph demonstrates the probability of associations being repeated in the future i.e. associations lasting over a longer time period. When lagged association rate is equal to null association rate, there is no preferential associations over time (SOCPROG user manual).

A higher observed association rate was observed than that expected if all associations occurred equally and at random (figure 9). The null association line remains low with two small peaks around day 400. The lagged association line however, starts much higher with large fluctuations and a large peak at around day 300. This pattern may be due to the sampling strategy used, discussed in the methods; it was sometimes difficult to find the groups due to the environment in which they exist, also they were not always seen towards the end of the investigation. The mean association per dyad was 0.041, a relatively low rate of association, with the mean number of individuals identified per sampling period being 0.007 (0.7 %).

There were significant non-random associations between dyads over long time periods but not over short periods (table 1) with the mean association between dyads being 0.05 after a 1000 day period (figure 9). The presence of a greater proportion of non-zero elements in the random data compared to the observed data (table 1) suggests the presence of preferential avoidance within the population.

If the mean association indices for the observed data were significantly lower than the random data the null hypothesis that there is no preferential association over shorter time periods was rejected. If the standard deviation of the mean association indices for the observed data was significantly higher than the random data the null hypothesis that there is no preferential association over longer time periods was rejected. The presence of preferential avoidance is highlighted by a greater proportion of non-zero elements in the random data to the observed data (Gowans, *et al.*, 2001).

Table 1. Mean association indices, standard deviations and non-zero proportions for observed and random data.

	Mean association index	SD of mean association index	Proportion of non-zero elements
Observed data	0.041	0.217	0.038
Random	0.041	0.215	0.038

data			
P value	0.030	0.999	0.001

Population structure

Network graphs displaying the structure of the whole population of known manta rays found in the Republic of Maldives were constructed using data from 01/01/96 until

16/07/08 (figures 10-13). Comparing Figures 10 and 11 illustrates the importance of filtering the data to remove associations in the network that were below a value of 1, using the sum of associations as an association index. This has removed all associations that were only observed once during the study period, leaving a more structured network.

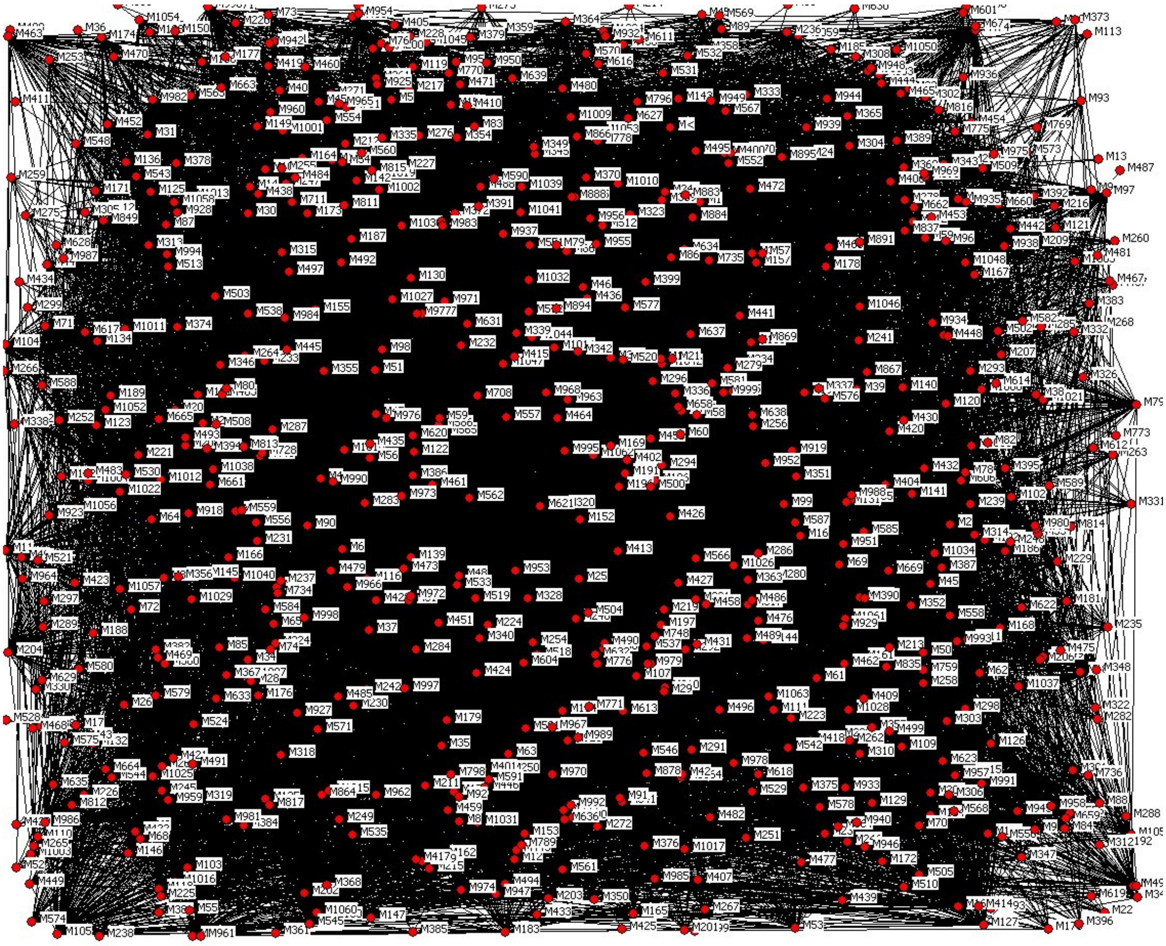

Figure 10. Network diagram illustrating the unfiltered network of all individuals seen during the study period. Individuals are represented by red nodes and ID number. Lines between nodes indicate an association.

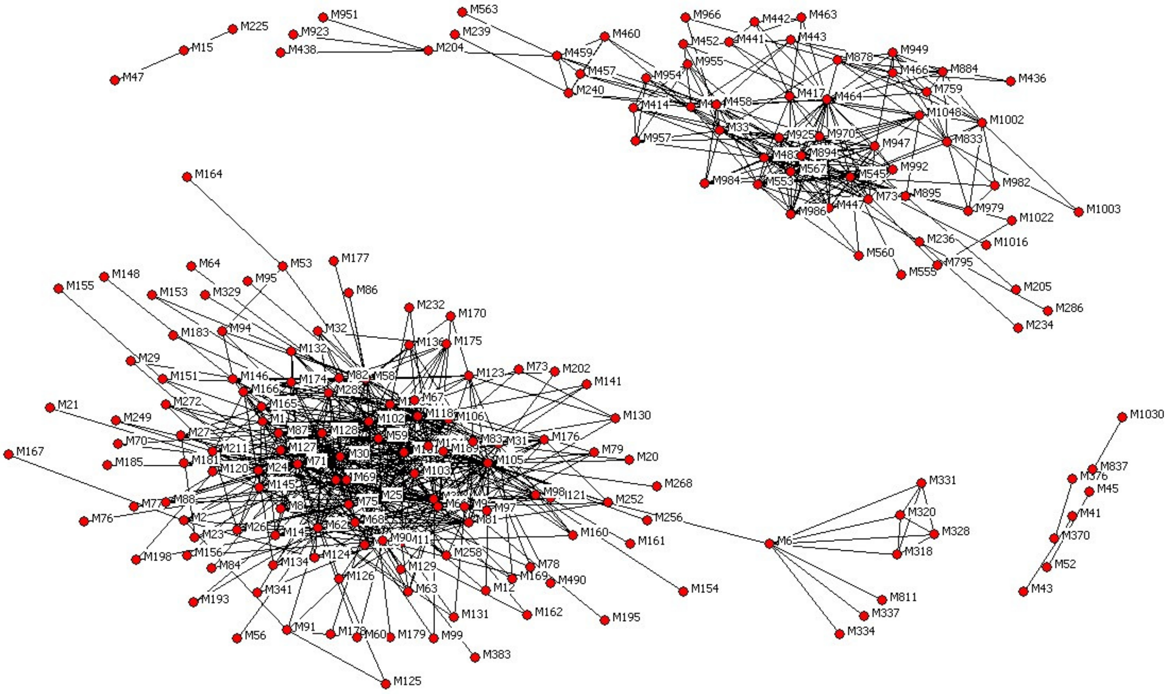

Figure 11. The same network has been filtered at a value of 1 to remove all associations that occurred only once during the study period. The remaining nodes have been organised using the spring embedding function which optimises the layout for further analysis.

After filtering (figure 11), 577 nodes and their associations have been removed indicating that a large proportion of the network consisted of weak associations (i.e. those only observed once the study period). Remaining nodes have been arranged into groups using spring-embedding to optimise the network layout (figure 11), however further division in the population is possible and is highlighted in figure 12. Using the Girvan-Newman function the population was organised into 8 communities based on measures of betweeness with a modularity index of 0.438 being found within the population.

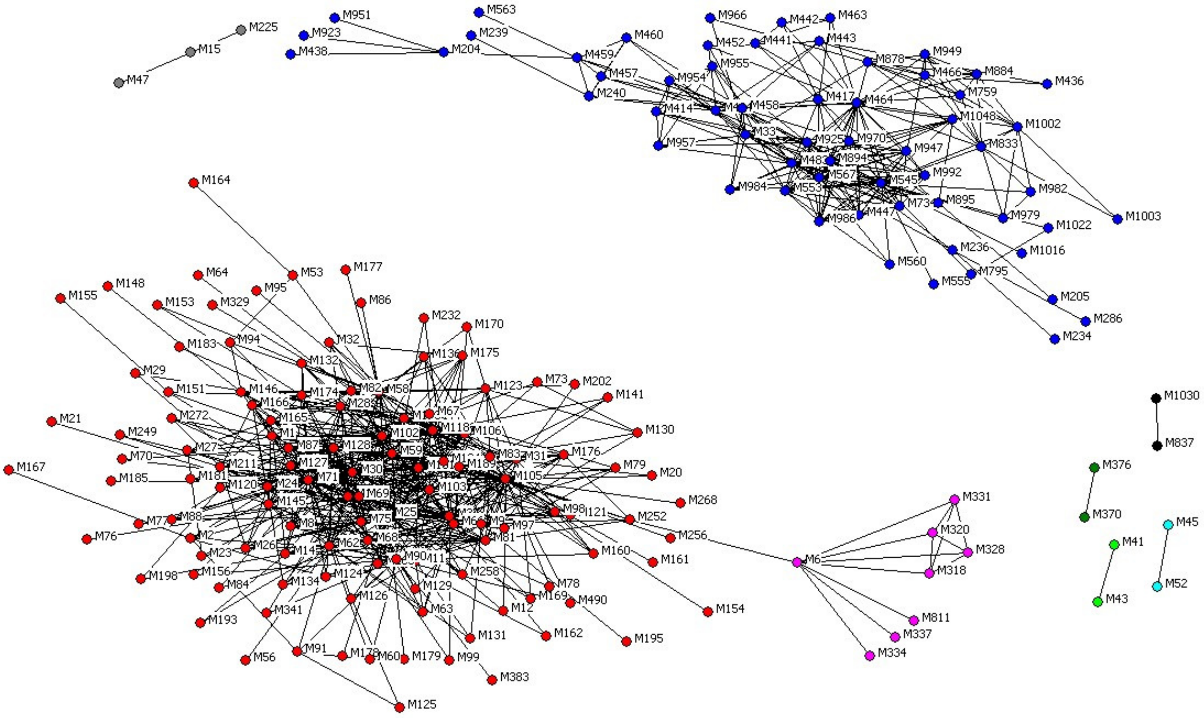

Figure 12. The community breakdown as given by the Newman-Girvan clustering analysis. Communities consisting of single individuals have been removed. Node colour refers to community membership. The analysis found 589 clusters, 8 communities and Q=0.445.

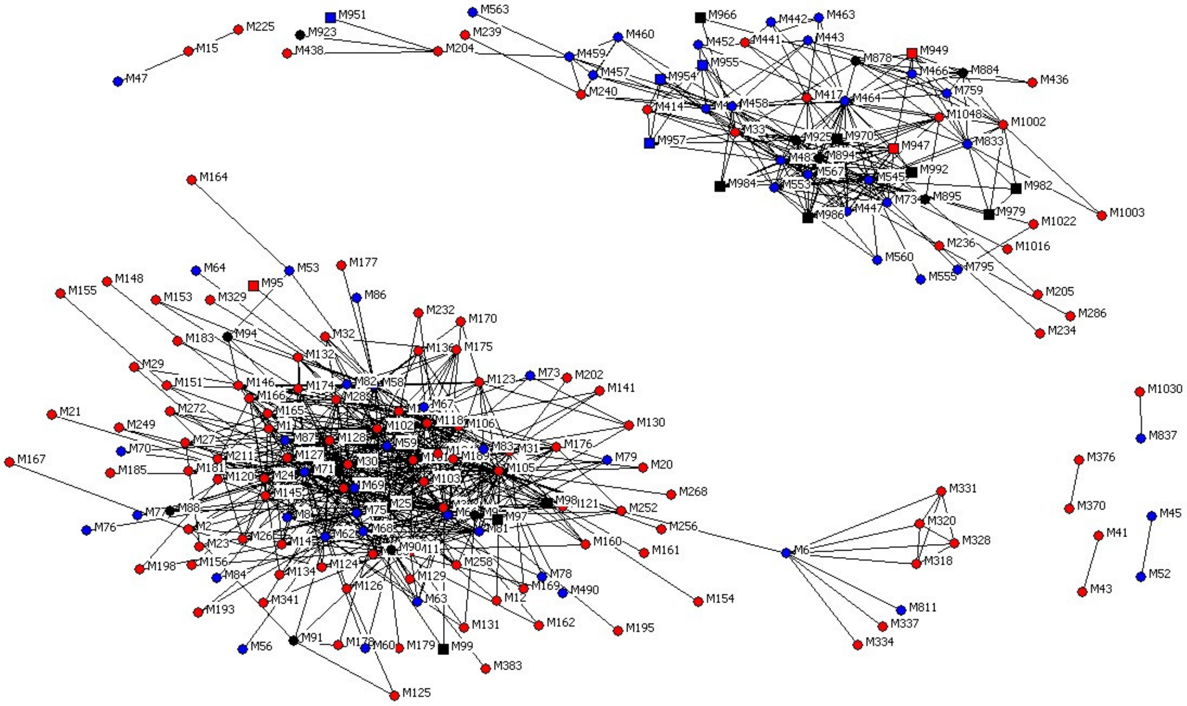

Figure 13. The same community breakdown however with node colour and shape representing node (individual) attributes. Blue=Male, Red=Female and Black=Unknown. Circle=Adult and Square=Juvenile.

It is clear that the populations social structure is made up of both males and females, except for three single sex dyadic pairs (figure 13), although stated previously there are more females present in the population. The presence of juveniles is restricted to the two larger communities where they can be seen throughout, however none are seen in any of the smaller communities. The number of females and males present in the network were compared while accounting for the original skewed sex ratio in the population, again there were significantly more females present in the network than that expected (figure 14).

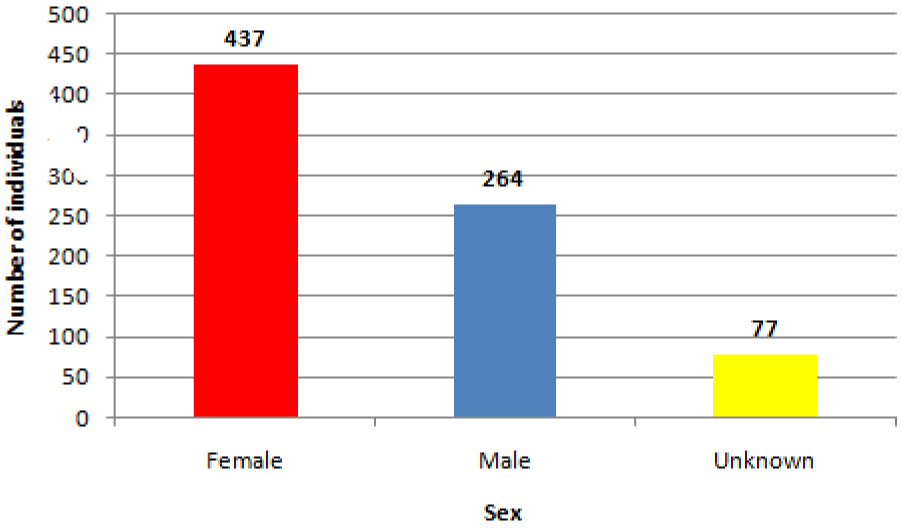

Figure 14. Graph demonstrating the observed sex ratio within the social network (all years and behaviours). Accounting for the skewed sex ratio observed in the Maldivian population of manta rays there are still significantly more females than males. Chi square=5.913 with 1 degree of freedom (P = <0.05).

Discovering the presence of a greater number of females within the whole network leads to the question of where they are found in the network. Sex ratios were compared for each of the 8 communities previously discovered in the network by the Girvan-Newman analysis and are displayed in figure 15 for comparison. A chi square test was conducted on each of these communities while accounting for the original skewed sex ratio, with significantly more females being observed in 4 of the communities (table 2).

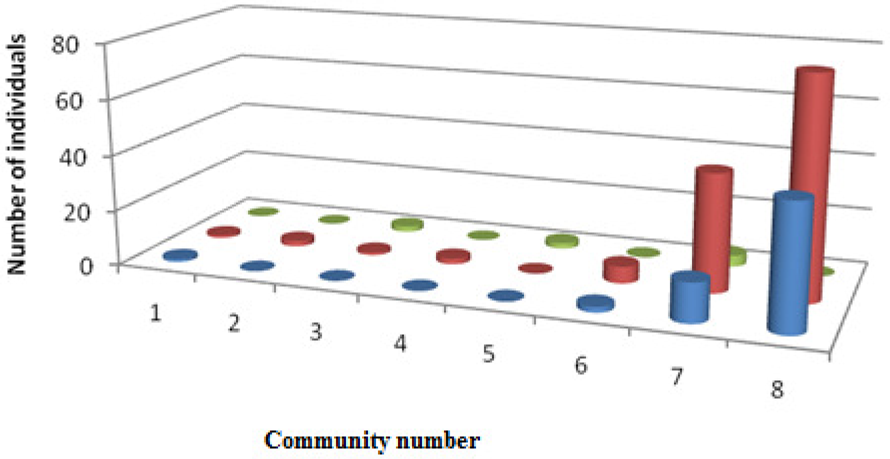

Figure 15. Graph displaying intra-community sex ratio as defined by the Girvan-Newman analysis. Blue indicates males, red indicates females and green indicates individuals of unknown sex.

Table 2. Displays figures from figure 15 with accompanying results from chi square tests and significance levels.

Community	Male	Female	Unknown	
1	1	1	0	No significant difference
2	0	2	0	No significant difference
3	0	1	2	No significant difference
4	0	2	0	Chi squared = 4.004 with 1 degree of freedom (P = <0.05)
5	2	0	0	Chi squared = 6.000 with 1 degree of freedom (P=<0.05)
6	2	6	0	No significant difference
7	14	42	4	No significant difference
8	44	78	0	Chi squared = 7.961 with 1 degree of freedom (P = <0.01)

Further exploration of the networks

By further exploring the network it is possible to discover more detail on the makeup of the network and the key individuals responsible for holding it together by highlighting repeated pair wise associations. The original network (figure 11) was filtered at increasing levels (increasing association strength, AS) to reveal the core structure. This was carried out by increasing the filtering threshold at increasing levels to a maximum of seven, where only two individuals remain.

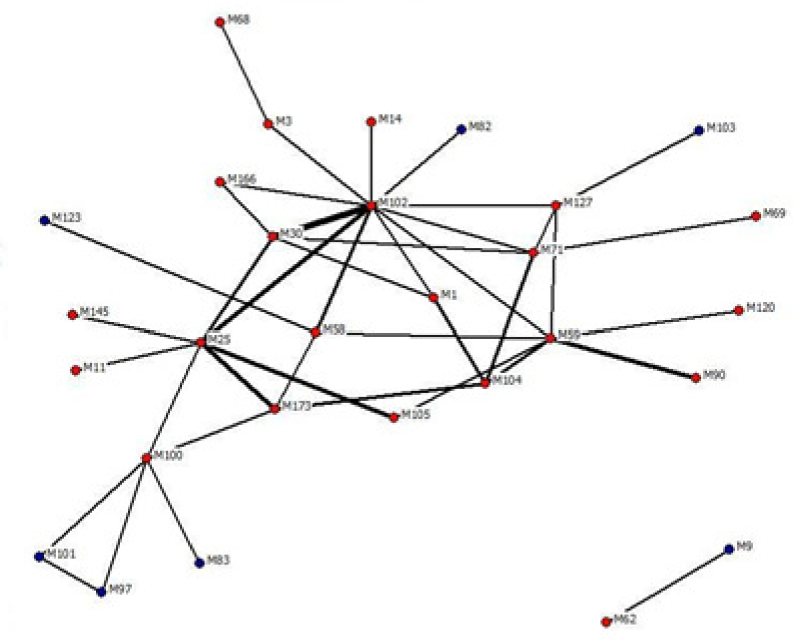

Figure 16. The original network diagram from figure 13, however filtering has been increased to AS> 3. Node colour and shape refers to individual attributes (Blue=Male, Red=Female and Black=Unknown, Circle=Adult and Square=Juvenile). Line thickness is directly proportional to strength of association.

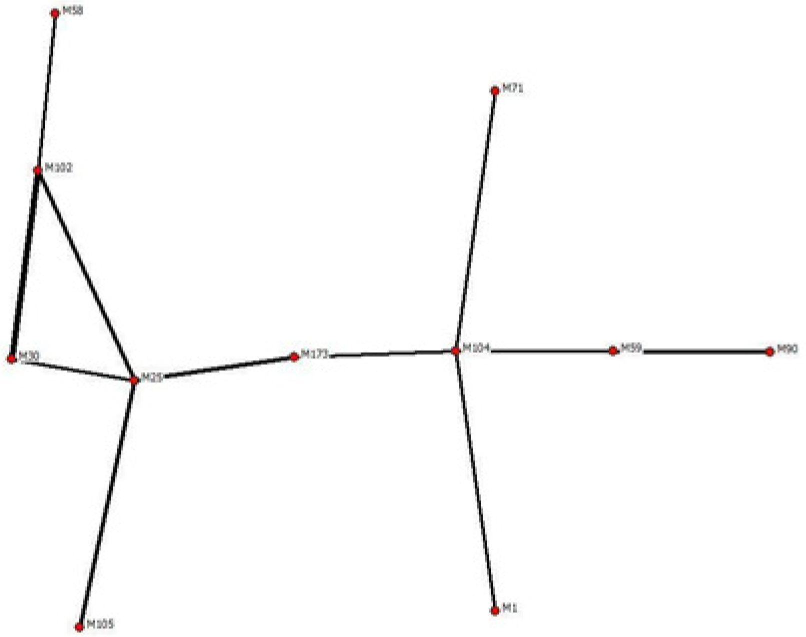

Figure 17. The original network diagram from figure 13, however filtering has been increased to AS>4. Node colour and shape refers to individual attributes (Blue=Male, Red=Female and Black=Unknown, Circle=Adult and Square=Juvenile). Line thickness is directly proportional to strength of association.

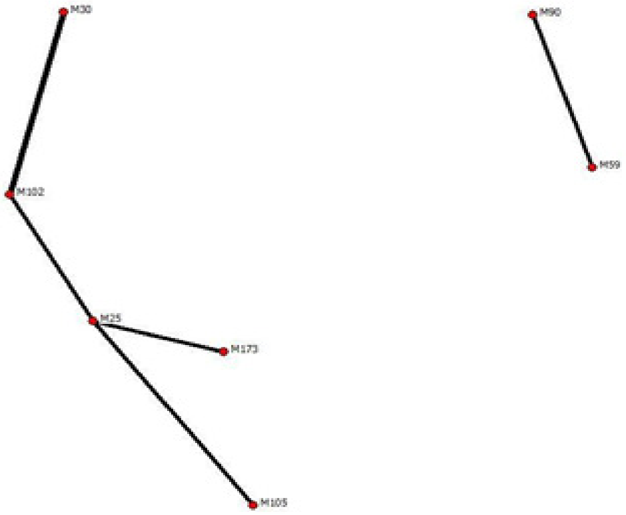

Figure 18. The original network diagram from figure 13, however filtering has been increased to AS>5. Node colour and shape refers to individual attributes (Blue=Male, Red=Female and Black=Unknown, Circle=Adult and Square=Juvenile). Line thickness is directly proportional to strength of association.

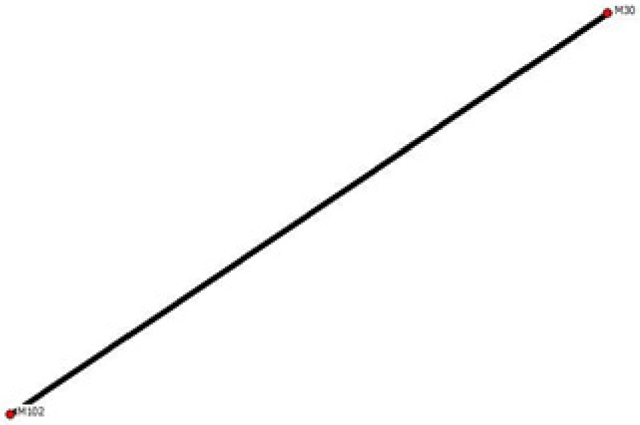

Figure 19. The original network diagram from figure 13, however filtering has been increased to AS>7. Node colour and shape refers to individual attributes (Blue=Male, Red=Female and Black=Unknown, Circle=Adult and Square=Juvenile). Line thickness is directly proportional to strength of association.

After filtering the network at increasing levels the number of individuals remaining in the network dramatically reduces. Remaining nodes (individuals) are primarily adult females. Filtered at 3 associations, figure 16 shows only 7 males out of 29 individuals, all of which are located on the periphery of the network, only connected by adult females with no male-male associations. Increasing the filtering threshold further (figure 17) (Filtered at 4 associations) the network is made up of only adult females (11 in total). After 5 associations the remaining network has been divided into 2 communities (figure 18) and eventually after 7 associations the network is reduced to a single dyadic association between 2 adult females (M30 & M102) (figure 19).

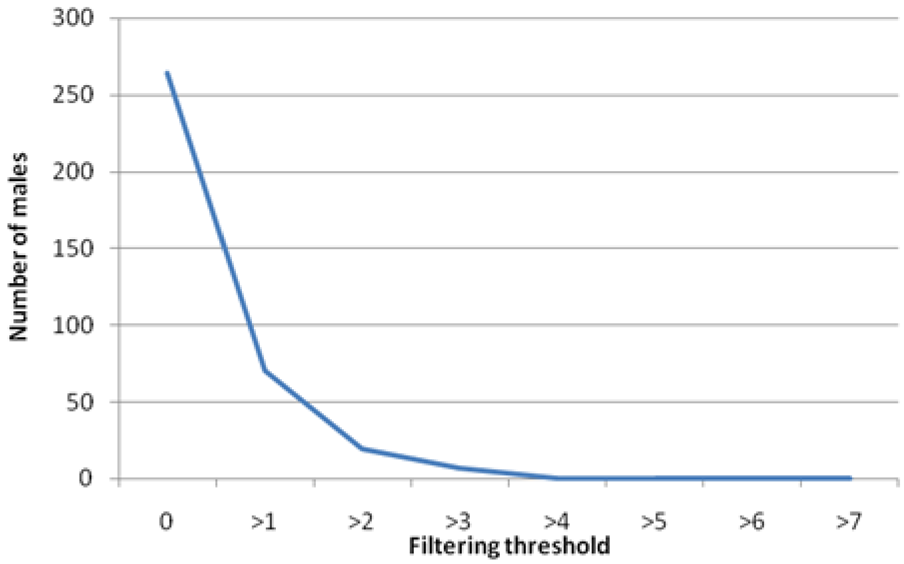

Figure 20. Graph demonstrating the decline in numbers of males within the network at increasing filtering thresholds. (Pearson's correlation test r = -.720, n = 8, P = <0.05).

As the filtering threshold increases, the number of males present within the network declines (figure 20). After conducting a Pearson's correlation test, a strong negative correlation (defined by Cohan, 1988 (appendix 2)) can be seen between the numbers of males present in the network and increasing filtering thresholds

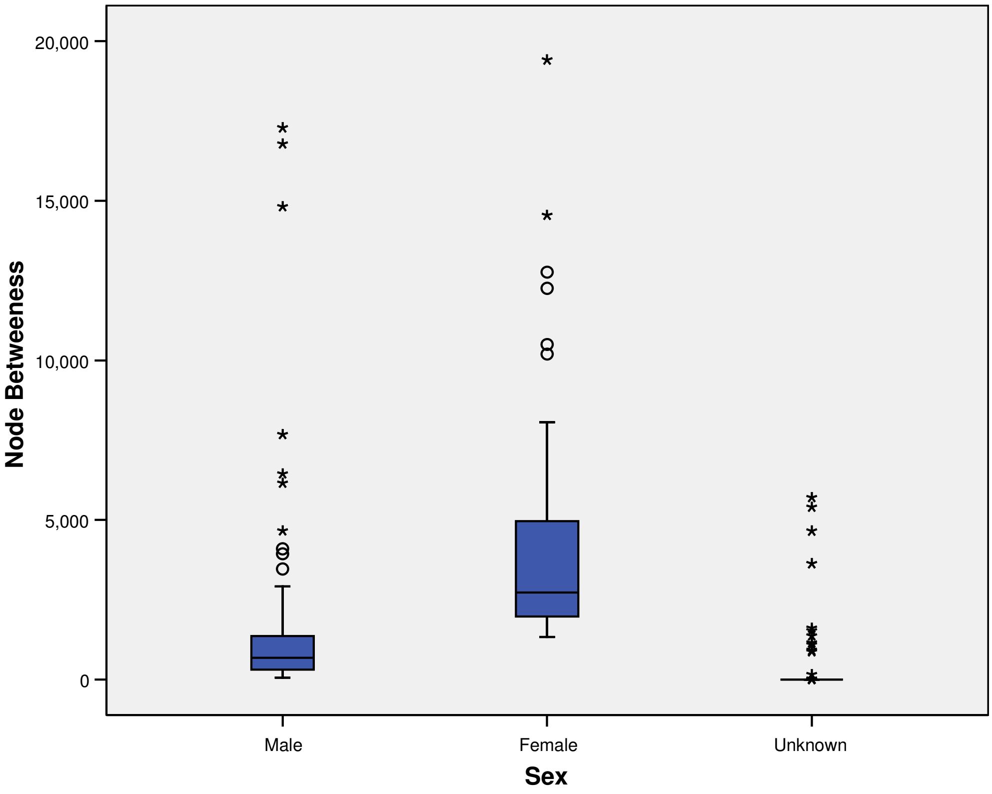

Figure 21. Node betweeness measures for males, females and individuals of unknown sex. Each individual in the network was considered with results displaying means (Line within box), standard deviations (spread of box), inter-quartile range (lines above and below box) and outliers (stars and circles).

Node betweeness values were calculated for each individual using the analysis software Ucinet (figure 20). Females within the network possess greater betweeness values compared to males and individuals of unknown sex.

Comparisons between years

The social structure of the population of manta rays found in the Republic of the Maldives was compared over a three year period from 2006 – 2008. Over long time scales (several years) demographic effects, such as birth and death along with immigration and emigration from the study area, may cause changes in the social network structure, making comparisons over these time scales useful. Although the overall data set consisted of associations from 1996 – 2008, the amount of available data was much greater for the last three years of the investigation, for this reason it is only these years which have been used for comparison. Associations between individuals were calculated for each of the three years considered, the results of which are presented in table 3.

Table 3. Mean association indices, standard deviations and proportions of non-zero elements across the three year period.

Year	Mean association index		
	Observed data	Random data	P value
2006	0.076	0.076	0.527
2007	0.060	0.060	0.044
2008	0.156	0.156	0.479
	SD of mean association index		
	Observed data	Random data	P value
2006	0.297	0.296	0.998
2007	0.283	0.280	0.999
2008	0.380	0.379	0.870
	Proportion of non-zero elements		
	Observed data	Random data	P value
2006	0.068	0.068	0.001
2007	0.051	0.052	0.000
2008	0.151	0.151	0.146

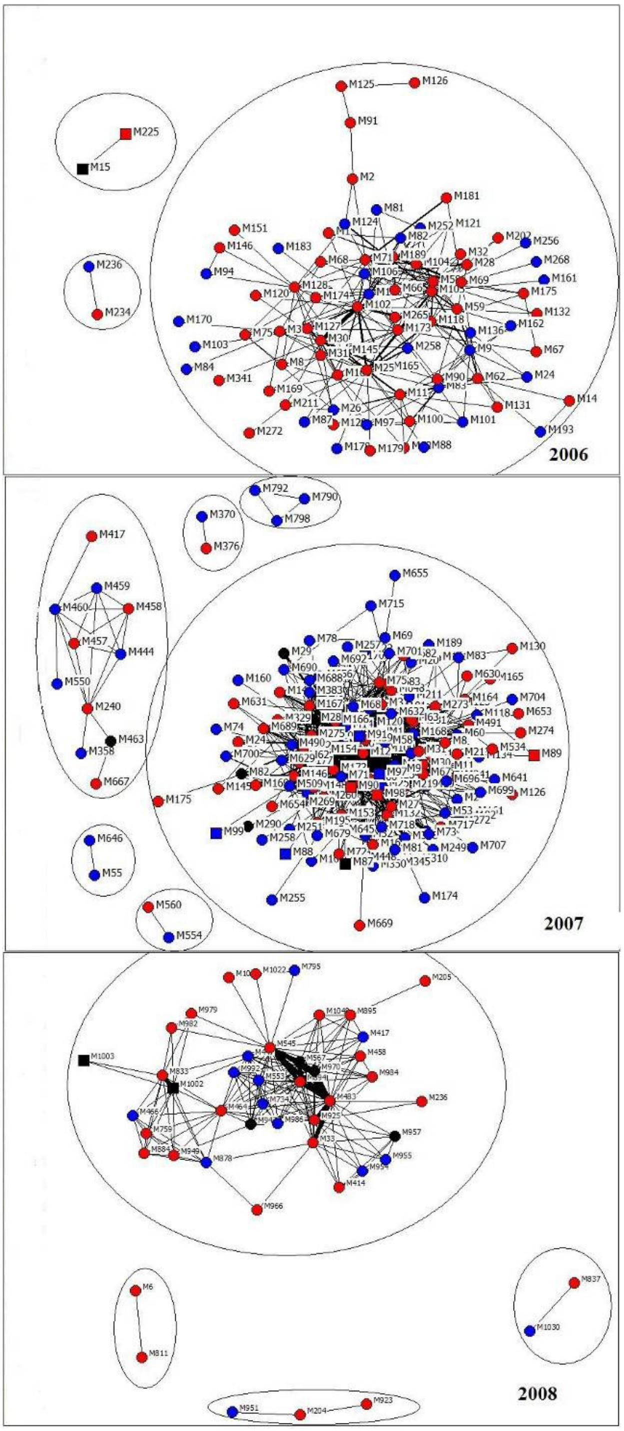

Figure 22. Comparative diagrams across a three year period illustrating the social dynamics of the population of manta rays found in the Republic of the Maldives. Colours indicate sex (Blue=Male, Red= Female and Black=Unknown), node shape indicates age (Circle=Adult and Square=Juvenile). Circles around groups indicate communities as indicated by the Girvan-Newman clustering analysis. Edge thickness is directly proportional to tie strength with thicker lines representing stronger associations.

As before, networks were filtered at a value of 1 and spring embedded to optimise layout. Communities indicated by the Girvan-Newman clustering analysis (enclosed in circles) differ across the three years (figure 22 and table 3), with the greatest number occurring in 2007, conversely the fewest number were seen in 2006. Furthermore the number of clusters and modularity index also fluctuates across the three years with the greatest number of clusters also being seen in 2007 and the least number of clusters occurring in 2006. Associations of varied strength occur in each of the three years with the core of the network being made up of stronger associations (represented by thicker lines, figure 22).

Table 4. Summarising table of figure 22. A community is defined as a set of nodes which are connected via at least one association. Clusters represent groups produced by the Girvan-Newman clustering analysis with Q being the modularity index. (Where Q=1 represents a population split into perfect clusters, possessing many intra-group edges and no between cluster edges, Q=0 represents a population with no clusters and associations between dyads occurring at random).

Year	Communities	Clusters	Q
2006	3	208	0.280
2007	6	448	0.059
2008	4	230	0.293

Most of the individuals within the investigation were only observed during one year of study, however a substantial amount were seen in two of the years and some individuals were seen in all three years investigated although in reduced numbers (figure 23).

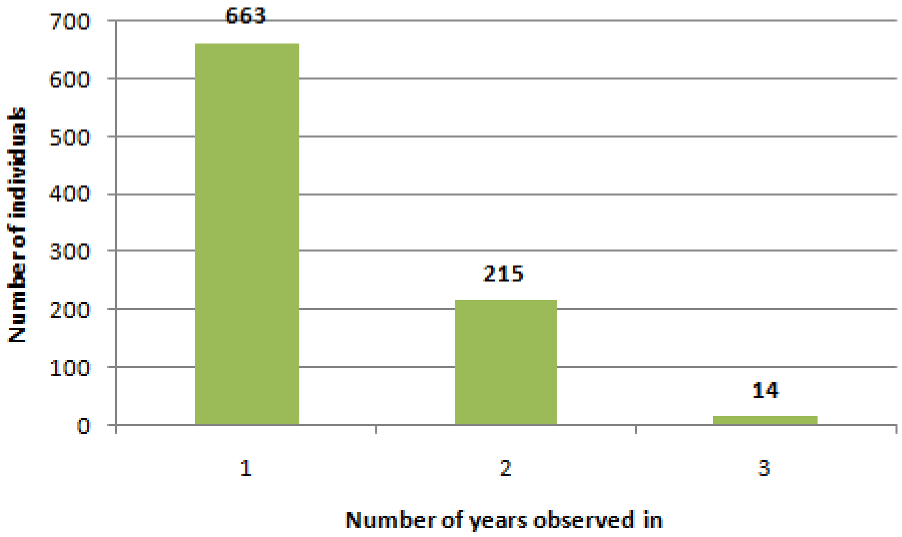

Figure 23. The proportion of individuals identified in one, two or three of the networks (different years).

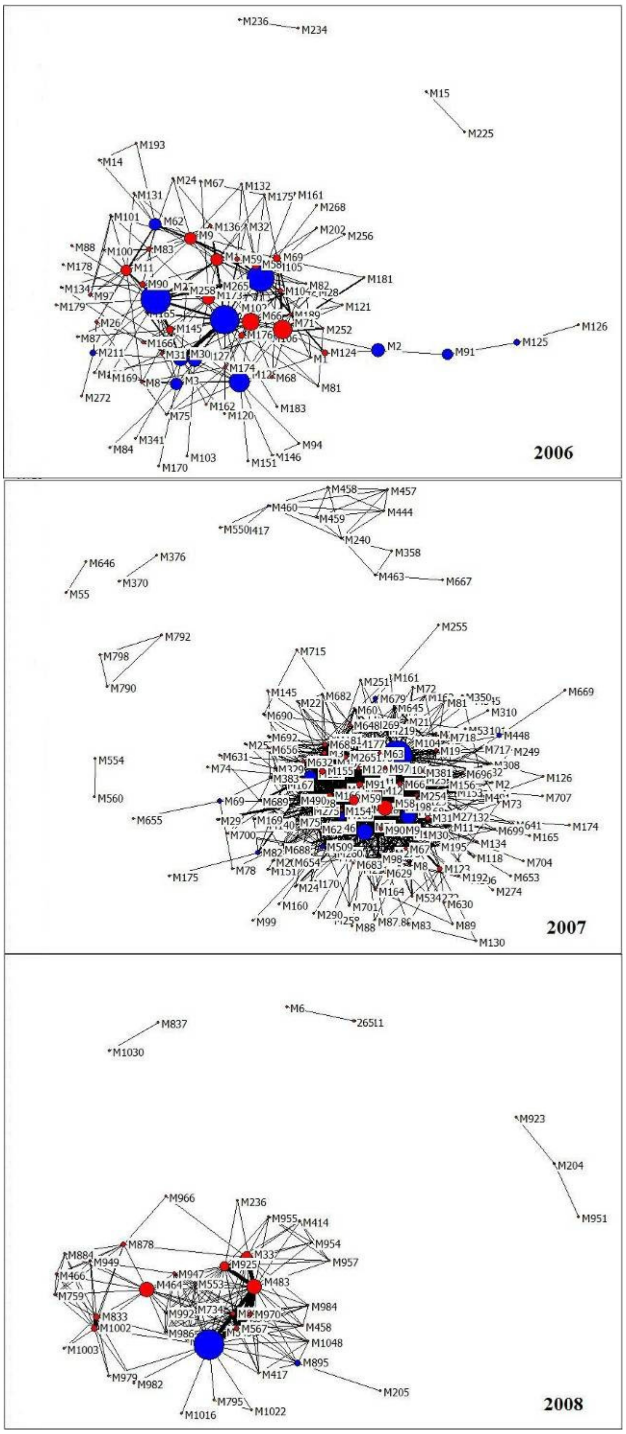

Figure 24. Comparative diagrams across the same three year period highlighting cut points in the network. Blue nodes indicate individuals which form a cut point, being the only link between other individuals in the network. Node size represents value of betweeness as calculated by the Girvan-Newman function, larger nodes possess larger values of betweeness. Edge thickness is directly proportional to tie strength with thicker lines representing stronger associations.

Cut points are indicative of individuals who occupy unique places in the network, being the only connection between other individuals and the community. Figure 24 highlights those individuals forming cut points in the network across the three years and table 5 lists these individuals along with their sex and age. It is clear that different individuals form cut points each year, the majority of which are adult females (27 out of 30). The numbers of cut points also vary across the three years with more being found in 2006 and 2007 compared to 2008.

Table 5. Individuals forming cut points across the three year period along with their sex and age.

Year	Individual ID	Sex	Age
2006	M2	Female	Adult
	M3	Female	Adult
	M25	Female	Adult
	M30	Female	Adult
	M62	Female	Adult
	M91	Female	Adult
	M102	Female	Adult
	M105	Female	Adult
	M125	Female	Adult
	M127	Female	Adult
	M128	Female	Adult
	M211	Female	Adult
2007	M25	Female	Adult
	M69	Female	Adult
	M71	Female	Adult
	M82	Male	Adult
	M104	Female	Adult
	M105	Female	Adult
	M127	Female	Adult
	M132	Female	Adult
	M168	Female	Adult
	M240	Female	Adult
	M448	Female	Adult
	M460	Female	Adult
	M463	Female	Adult
	M509	Male	Adult
	M679	Female	Adult
2008	M204	Male	Adult
	M545	Female	Adult
	M895	Female	Adult

Comparisons between behaviours

The original data set was split according to the observed behaviour at the time of encounter and analysed as above. Two groups were formed, cleaning (also including courtship and all other behaviours) and feeding. Associations between individuals were calculated for each behaviour considered, the results of which are presented in table 6.

Table 6. Association indices, standard deviations and proportion of non-zero elements for all years across different behaviours

Behaviour	Mean association index		
	Observed data	Random data	P value
Cleaning	0.059	0.060	0.001
Feeding	0.074	0.074	0.498
	SD of mean association index		
	Observed data	Random data	P value
Cleaning	0.295	0.298	0.000
Feeding	0.271	0.271	0.848
	Proportion of non-zero elements		
	Observed data	Random data	P value
Cleaning	0.048	0.050	0.000
Feeding	0.072	0.072	0.194

A mantel test was carried out to calculate the correlation between the two matrices constructed using the association data of individuals observed cleaning and feeding together. The two matrices have a correlation of 0.032 (P=<0.05), a relatively low correlation suggesting that the associations making up the two matrices are different.

Network diagrams were drawn for each of the behavioural groups and displayed as previously, the first demonstrating community membership, with nodes indicating individual attributes (sex and age), and the second displaying nodes of various sizes according to their measure of betweeness with cut points in the network.

Cleaning

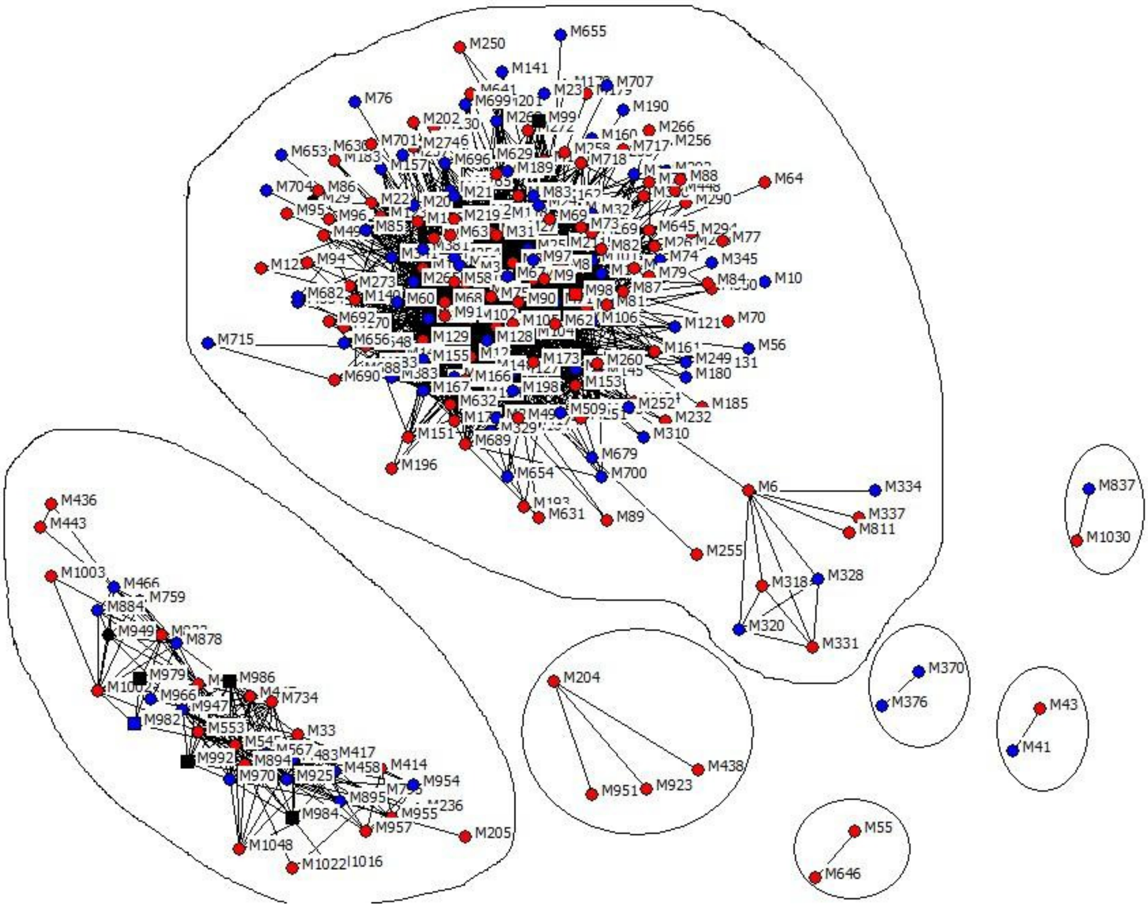

Figure 25. Network diagram illustrating the social structure of all individuals seen cleaning together over the whole study period (1996 – 2008). Node colour indicates sex (Blue=Male, Red=Female and Black= Unknown). Node shape indicates age (Circle=Adult, Square=Juvenile). Circles around groups indicate communities as indicated by the Girvan-Newman clustering analysis. There were 545 clusters, 6 communities and Q=0.176, clusters of solitary individuals have been removed.

Considering only individuals seen cleaning (as well as courtship and travelling) (figure 25), the network displays two large communities consisting of many individuals and five smaller communities consisting of two or three individuals. Again the presence of both males and females can be seen throughout the network and the presence of juveniles can also be seen, although in reduced numbers and restricted to the two larger communities.

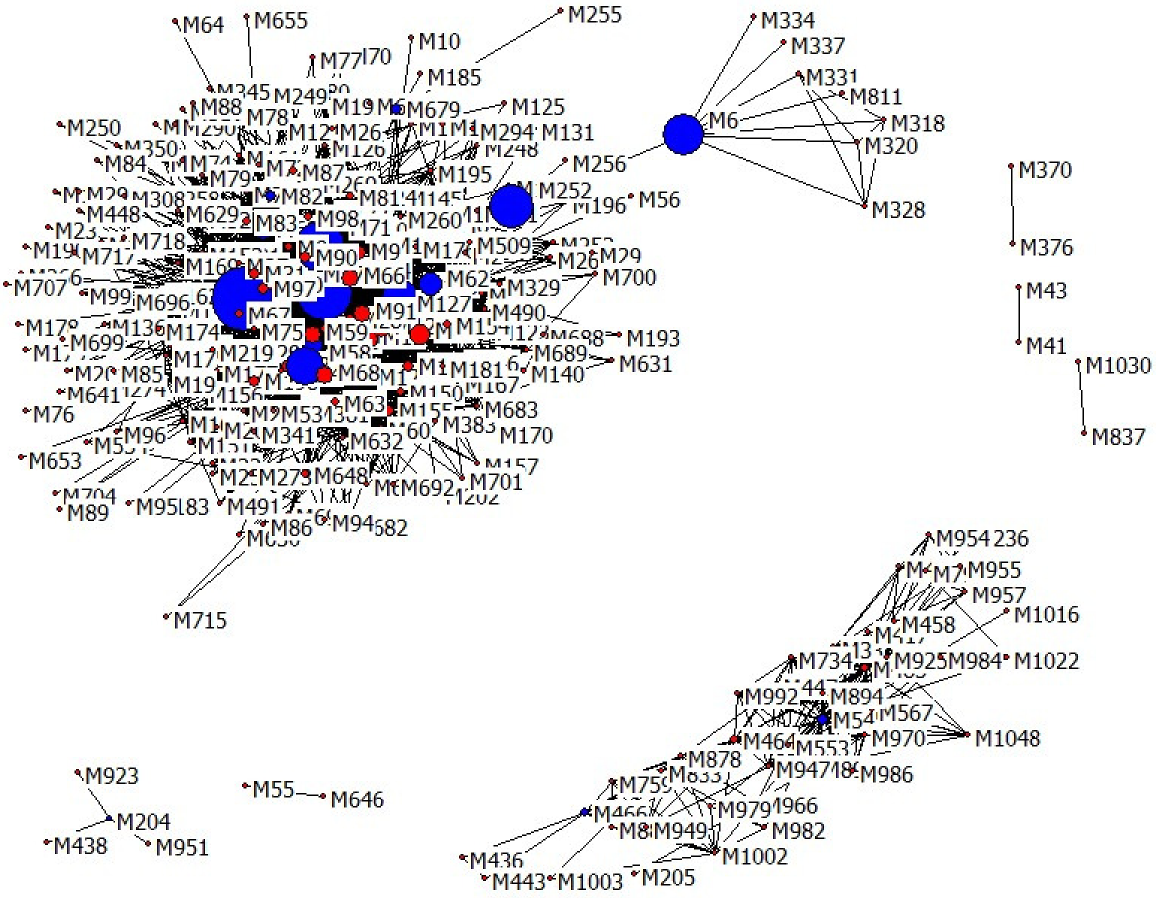

Figure 26. Network diagram illustrating key individuals forming cut points within the population (marked in blue). Node size represents value of betweeness as calculated by the Girvan-Newman function, larger nodes possess larger values of betweeness. Edge thickness is directly proportional to tie strength with thicker lines representing stronger associations.

After changing the nodes to represent measures of betweeness, it is possible to see that this measure is heterogeneous throughout the network with some individuals having much higher values than others (figure 26). Furthermore the presence of a number of cut points can be seen in the network, the majority of which were adult females (table 7).

Feeding

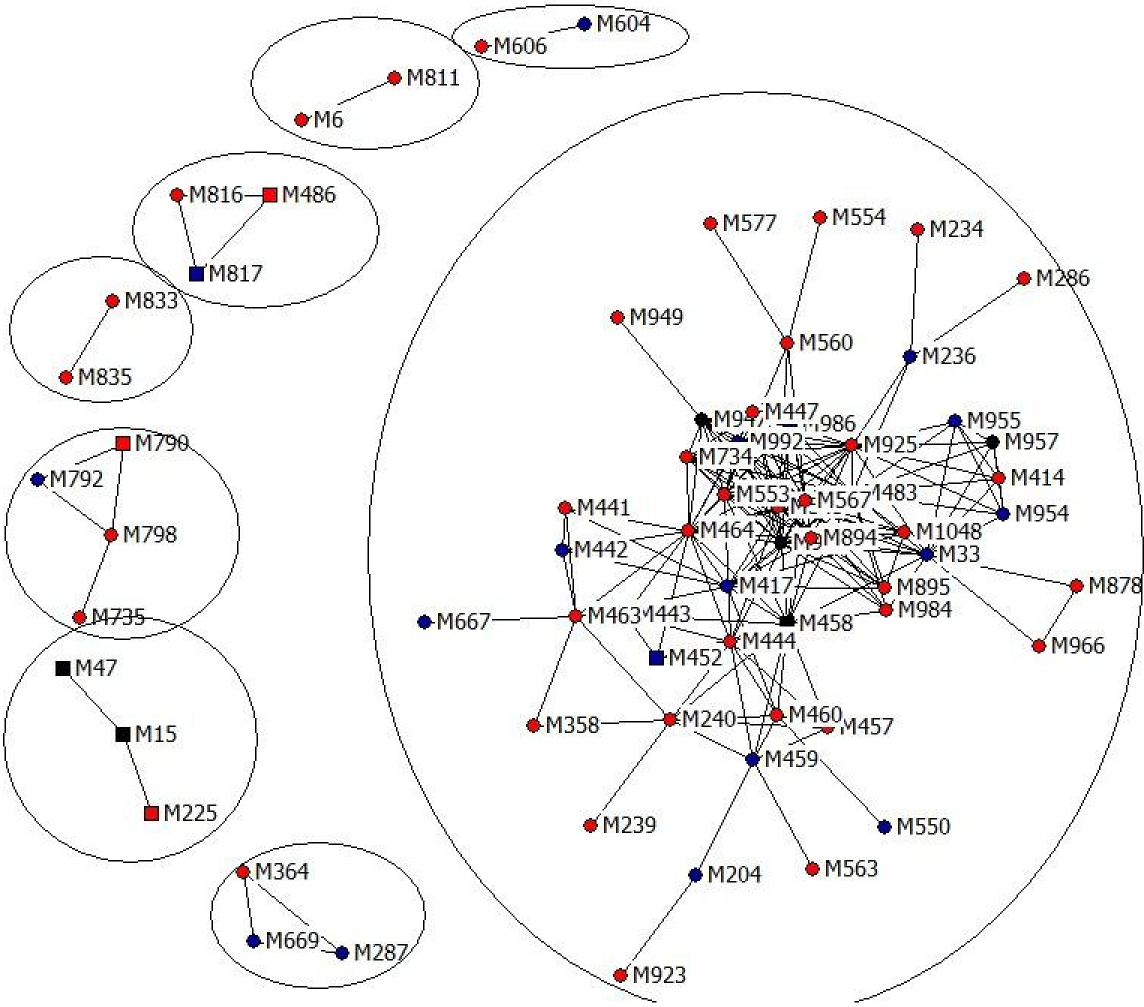

Figure 27. Network diagram illustrating the social structure of all individuals seen feeding together over the entire study period (1996 – 2008). Node colour indicates sex (Blue=Male, Red=Female and Black=Unknown). Node shape indicates age (Circle=Adult, Square=Juvenile). Circles around groups indicate communities as indicated by the Girvan-Newman clustering analysis. There were 394 clusters, 8 communities and Q=0.305, clusters of solitary individuals have been removed.

When considering only those individuals seen feeding together (figure 27) one large community can be seen with seven smaller communities containing only a few individuals. Again the presence of both males and females can be seen, although this time both adults and juveniles can be found in the smaller communities.

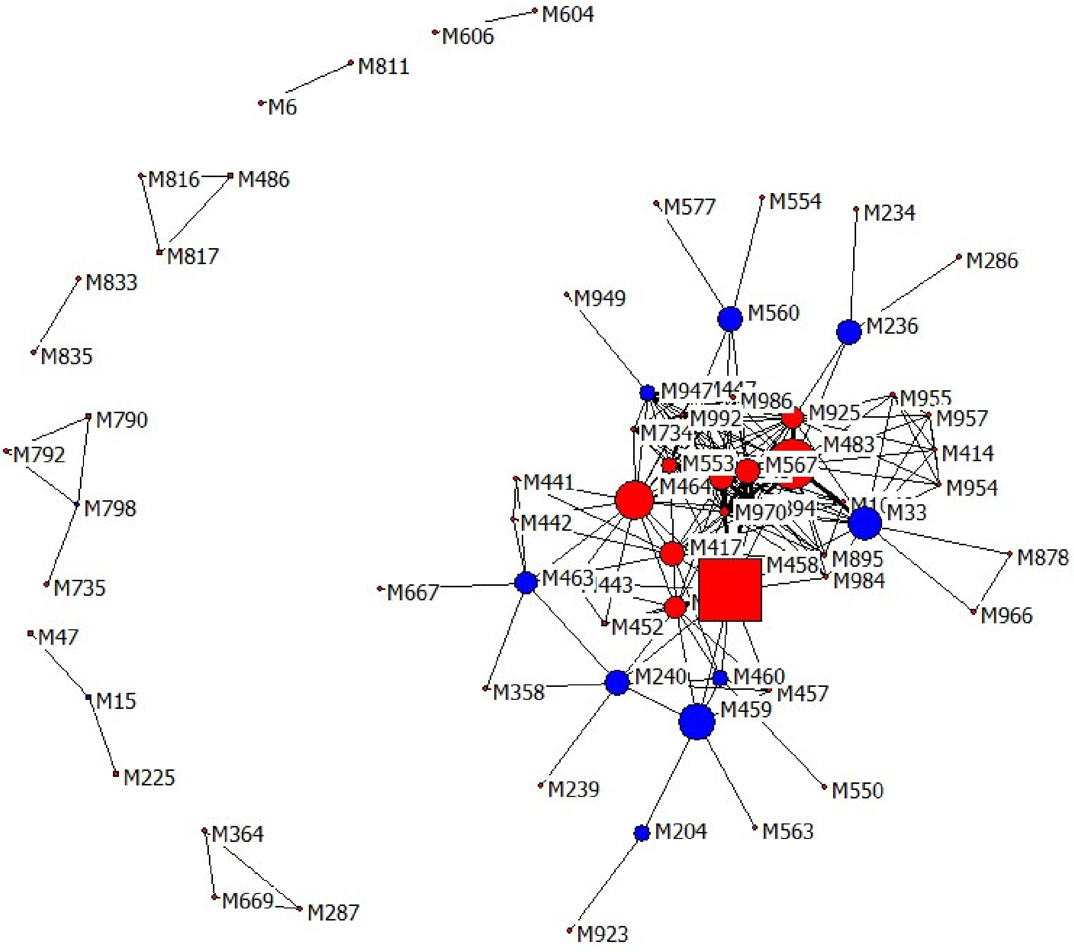

Figure 28. Network diagram illustrating key individuals forming cut points within the population (marked in blue). Node size represents value of betweeness as calculated by the Girvan-Newman function, larger nodes possess larger values of betweeness. Edge thickness is directly proportional to tie strength with thicker lines representing stronger associations.

As before there is variation in the measure of betweeness in the network and the presence of a number of cut points (figure 28), this time however they consisted of almost equal numbers of males and females (table 7).

Table 7. Individuals forming cut points across the different behaviours with their sex and age.

Behaviour	Individual ID	Sex	Age
Cleaning	M6	Female	Adult
	M25	Female	Adult
	M58	Female	Adult
	M62	Female	Adult

	M69	Female	Adult
	M71	Female	Adult
	M82	Male	Adult
	M100	Female	Adult
	M102	Female	Adult
	M104	Female	Adult
	M105	Female	Adult
	M168	Female	Adult
	M204	Male	Adult
	M252	Male	Adult
	M466	Female	Adult
	M895	Female	Adult
Feeding	M15	Unknown	Juvenile
	M33	Male	Adult
	M204	Male	Adult
	M236	Male	Adult
	M240	Female	Adult
	M459	Male	Adult
	M460	Female	Adult
	M463	Female	Adult
	M560	Female	Adult
	M798	Female	Adult
	M947	Unknown	Adult

Chapter 4

Discussion

The present study confirms the presence of social structure in a population of manta rays found in the Republic of the Maldives. Many other elasmobranch species have been documented forming aggregations in response to concentrated food sources or seeking refuge from environmental changes, and indeed some of the results obtained in this study demonstrate this same behaviour within this species. However for the first time significant repeated associations and avoidances resembling a more detailed social structure have been documented allowing the creation of social network diagrams to explore this previously unknown behaviour.

Survey effort

As discussed in the methodology survey effort greatly increased after 2005 when the Maldivian manta ray project became more firmly established. Data preceding this date was collected and analysed but remains sporadic compared to data collected after 2005. For this reason the identification of new individuals within the population rose dramatically between 2005 and 2008, and is more likely to be due to the greatly increased sampling effort carried out between these years compared to years previous to 2005 and not due to any sudden increase in population size.

Comparisons between years were constrained to only involve data from the last 3 years of investigation (2006-2008), where a more detailed data set exists. For comparisons between behaviours and for the analysis of social structure using all dates and behaviours the whole data set was used consisting of sightings from 1996-2008.

There is a clear skew in the sex ratio of observed manta rays within the Maldivian population, with more females being observed than males. Currently there is little data on the reproductive biology of this species (Duffy & Abbott, 2003) with no definitively known sex ratio. For this reason initial comparisons in the numbers of males and females were calculated assuming a normal population ratio of 50:50 male and female. Furthermore the majority of identified individuals within the database consist of adults with far fewer juveniles being observed, although this may simply represent patterns of boldness, where adults will more readily accept the presence of divers and snorkelers allowing photographic I.D shots to be taken, with juveniles remaining more elusive.

For any two individuals to associate it is fair to assume that they must be able to make some form of contact with each other. Whether by sound, which underwater may travel over large distances allowing seemingly dispersed individuals to remain in social contact (e.g. cetaceans), by sight or even by physical contact requiring individuals to be within a restricted spatial proximity. Like all elasmobranches, there is no evidence to support acoustic communication in this species, so for any two rays to be socially connected they would be required to occupy similar areas. Sightings of known individuals from different atolls were analysed finding that although most individuals remain observed in only one atoll, a number of individuals are regularly observed in a number of atolls, demonstrating an ability to travel large distances and having the potential to associate with (or avoid) all other individuals within the Maldivian population, a key aspect in justifying the measure of association used (Gambit of the group) when using the whole dataset to calculate association rates.

A further requirement for any study of social structure is the repeated sightings of individuals. During the investigation many of the identified individuals within the database were resighted at least three times with some being resighted over ten times, although the number of individuals resighted this often is much lower.

Aggregations or socially structured groups?

Significant associations over long time periods (see Gowans, *et al.*, 2001) were observed in the population, demonstrated by a higher observed association rate compared to that expected if all associations occurred at random (null). Furthermore the presence of a greater proportion of non-zero elements within the random data suggests the presence of preferential avoidance between individuals. These results were seen when considering the whole data set (1996-2008) and in the 2006 and 2007 networks; conversely no significant result was found when considering observations during 2008 alone. The reason for this however may simply be due to insufficient data for this year. The data sets for 2006 and 2007 consist of observations throughout the entire year, however for 2008 observations stopped towards the end of July.

Long term demographic effects such as birth, death, immigration and emigration may alter the composition of a population's social structure over longer time periods making it useful to compare differences over these time scales. By comparing three different years (2006-2008) it is clear that the social structure of the population changes dramatically, with different numbers of communities and different individuals being observed in the networks. This may be due to actual changes in individual choice (who to associate with and who to avoid) or may be due to the observation of different individuals in different years due to the natural effects mentioned or sampling strategies.

The number of individuals observed in only one year is much higher than that of individuals observed in two or three of the years reflecting a low rate of resighting over a period of years.

These findings suggest that the observed network of associating individuals is indeed more reflective of social groups rather than simple aggregations in response to concentrated resources.

The construction of network graphs allows visual representation of these observed associations and were constructed for associations observed between all individuals observed together in a group. After filtering the network many of the individuals were removed revealing a structured network more closely representing the true social structure within the population; however the removal of those individuals only observed in association together once should not be overlooked. It is worth considering that due to the particular constraints on observation, such as environmental conditions and differences in individual boldness, some associations may have been observed more than others. It was certainly found that some individuals were more accepting of divers and snorkelers than others, regularly approaching within distances allowing clear identification photographs to be taken, whereas others were more elusive, only appearing a few times in the photographic evidence.

In all of the networks males and females appear spread throughout, with no clear division based on sex. Juveniles were restricted to the largest communities, possibly due to the added protection form predators or the need to learn specific behaviours from their adult conspecfics, however social learning has not previously been documented in any elasmobranch species. Further exploration of the network reveals the presence of significantly more females within the networks even while accounting for the initial skewed sex ratio discovered within the total Maldivian population.

Further still, exploring the sex ratio of each of the networks communities reveals significantly more females than expected in a number of the communities. After increasing the levels of filtration in the data, the number of males present within the network dramatically reduced with a strong correlation between increasing filtering thresholds and a reduction in male numbers. The exact reason for this skewed sex ratio is unclear, but may possibly be due to male dispersal while females remain in areas for longer periods, strengthening their social bonds. Similar observations have been made in aggregations of hammerhead sharks, where females form schools and move offshore at a smaller size to males (Klimley, 1987), resulting in greater predation success on pelagic fishes and subsequent increased growth rates. Reasons for this include possible differences in maturation between sexes, with males maturing at a smaller size. The increased growth rate of females therefore allows maturation of both sexes at similar stages in their lifecycles (Klimely, 1987).

When exploring the networks structure at increasing filtering thresholds it became apparent that adult females made up the core of the networks structure. Betweeness values, a measure of an individual’s connectivity within the network, were much greater for females than males further supporting the idea of adult females being key in the maintenance of the networks structure and thus the maintenance of social structure within the population.

After exploring the distribution of cut point individuals within the networks it is possible to see that these individuals are spread heterogeneously throughout and are made up of different individuals in different years. A common trend however is that cut point individuals are primarily adult females, a finding consistent over the three years. This makes sense when considering the greater values of betweeness for females mentioned previously.

The importance of females in elasmobranch groups has also been observed in basking sharks (*Cetorhinus maximus*), where females have been regularly seen in leading positions amongst schools of sharks (Sims *et al.*, 2000), and grey reef sharks (*Carcharinus amblyrhynchos*) where females have been observed forming polarized schools (Economakis & Lobel, 1998). In a study into the aggregation behaviour of grey reef sharks in the Marshall Islands, Economakis & Lobel (1998) identified three types of grouping: lone individuals, loose aggregations and polarized schools. Reasons for females predominantly making up these polarized schools include their role as courtship and pre-pupping groups. Taylor (1993) made similar observations in Hawaii suggesting that pregnant females were grouping in shallow areas of higher ambient water temperatures aiding embryonic development.

Thermoregulatory behaviour has been suggested to occur in a number of shark species where females seek out warmer water (Castro, 1993; Morrissey & Gruber, 1993; Carey & Scharold, 1990) and as a result end up aggregating in a common area. The purpose of this may be due to several reasons including faster embryonic development, the increased growth rate of females, refuge from male harassment during breeding season and the use of such areas as centre landmarks from which foraging routes branch. No such obvious changes in water temperature, or segregation by sex was observed during the present investigation, suggesting that this isn’t a factor driving the aggregation of females, although this is yet to be fully explored.

Non-social feeding, social cleaning

After separating the original data set to differentiate between the specific behaviours of the rays documented at the time of observation, significant association between dyads was found occurring over short time periods (see Gowans, *et al.*, 2001) with significant avoidance during cleaning behaviour. No significant results were obtained for individuals seen feeding together during the investigation.

Like the original network diagram, both networks demonstrate males and females making up most of the communities. In the cleaning network, juveniles are again restricted to the larger communities, however in the feeding network juveniles may be seen in a number of the smaller communities. Cut point individuals may be seen throughout, and again these are different individuals in both of the networks. As before most of the cut point individuals in the cleaning network are made up of adult females whereas in the feeding network there are equal numbers of males and females. This finding further supports the theory that adult females are responsible for holding together the structure of the networks as they can be seen forming cut points in all of the networks which show significant associations but are less frequent in the network where no significant association exists (feeding).

Although evidence of any true social structure in elasmobranches is lacking in the literature, with most aggregations being linked to courtship or feeding behaviour, some authors have reported aggregations for other reasons (Harvey-Clark *et al.*, 1999; Sims *et al.*, 2000; Wilson, 2004). Explanations for these behaviours include the protection from predators (McKibben & Nelson, 1986) and conservation of energy. Whilst some studies involving basking sharks speculate that these aggregations predominantly represent group courtship behaviour (see Harvey-Clark *et al.*, 1999; Sims *et al.*, 2000), other authors have found they may occur outside of known breeding seasons (Wilson, 2004) highlighting other possible causes.

It would appear that during activities such as cleaning, courtship and travelling, individual manta rays are actively choosing their associates, with networks drawn from observations of these behaviours reflecting true social structure. Similar observations have been made in basking sharks off the coast of the U.K. where close following behaviour was documented with no links to feeding behaviour (Sims *et al.*, 2000). Unlike the present study however, these social affiliations involved both males and females and at times of the year when courtship and mating behaviour has also been documented.

Manta rays were observed breaching frequently during the investigation, the exact purpose of which is poorly understood. This behaviour could simply aid in the removal of ectoparisites or may have some ties to social communication. Breaching has been observed in both basking sharks and great white sharks (*Carcharodon Carcharias*) where it is thought to function as a form of social communication during courtship activities (Sims *et al.*, 2000; Pyle *et al.*, 1996). However in the present study, no subsequent courtship behaviour was observed after any breaching events.

Conversely, whilst feeding it appears that there is no preference in associations as each individual ray tries to attain sufficient amounts of food. Non-social aggregations in areas of high food sources have been observed in a number of other elasmobranches including those feeding on high concentrations of zooplankton such as whale sharks and basking sharks. Heyman *et al.* (2001) found whale sharks to aggregate in a predictable manner, coinciding seasonally and temporally with fish spawning aggregations of the coast of Belize. Similar observations have been made involving whale shark aggregations in Australia (Taylor, 1996), where a peak in whale shark numbers was observed 2 weeks after the peak in coral spawning activity. Basking sharks, another large filter feeding elasmobranch, are known to aggregate in the Gulf of Maine, where they feed from spring until autumn (Owen, 1984), and have also been observed forming loose aggregations in areas of high plankton concentration off the U.K coast (Sims *et al.*, 2000).

High concentrations of zooplankton are commonly found in the nutrient rich waters of seasonal and temperate seas, however they may also be found in oceanic zones of upwelling and convergence (Tait, 1980), even in tropical regions. The location of one of the key sites used in this study, Hanifaru lagoon, is located on the outer edge of Baa atoll. The unique topography of this area allows upwelling currents from deep water to enter the lagoon, bringing with it high concentrations of zooplankton mostly made up of deep water copepods. Pilot studies using Acoustic Doppler Current Profiling (ADCP) have found a unique eddy in the currents around the lagoons entrance, allowing zooplankton to accumulate in this area during specific tidal conditions (Stevens pers. Comm.). Plankton samples collected at times of mass manta ray feeding events agree with this, being made up almost entirely of deep water copepods although they also contained a number of other species, mostly in larval stage.

Few of the individuals observed cleaning together were also observed feeding together, with correlation tests involving both of the behaviours investigated finding a low correlation between the two association matrices. This further suggests that feeding is exclusively an activity involving an individual's need to feed with no relation to social affiliation.

Conclusions and implications of observed social structure

Although social behaviour has been documented in other elasmobranch species, this has predominantly been linked to courtship behaviour. In the present investigation individuals observed cleaning together were not differentiated from individuals observed undergoing courtship behaviour, and it is arguable that any significant observed associations presented here also occurred as a result of courtship behaviour due to this lack of differentiation. The initial network diagrams show both male and females whose associations may be due to courtship behaviour, however unlike other examples in the literature, a key finding in the present study was that involving repeated pairwise associations between individuals. This would infer that individuals are repeatedly choosing the same individuals to mate with, or are at least entering courtship behaviour with the same individuals on more than one occasion.

After further exploration of the networks structure it was found that it is predominantly adult females which make up the core of the networks structure, possessing the greatest number of repeated associations, suggesting a much richer social structure with stronger social bonds.

It is unclear why adult females in this species would have a stronger, more structured social life compared to males. Similar observations in other elasmobranch species have been made with possible explanations such as reduced male harassment and increased embryonic development in areas of higher ambient water temperatures. No such areas of higher ambient water temperatures and aggregations made up of entirely adult females have been discovered in the Maldives, suggesting other possible reasons for this observed behaviour.

Juveniles were never seen alone or in juvenile only groups, explanations for this includes the possibility of increased protection from predators and possible social learning in respect to feeding and cleaning sites. Although social learning has not been demonstrated in any other elasmobranch, it is possible that juveniles may learn the locations of desired feeding and cleaning grounds by simply following adults, reflecting a simple copying behaviour which physiologically speaking, many elasmobranches should be capable of achieving.

There has been a lot of research into the functions of elasmobranch aggregations (Sims et al., 2001), however very little is known about many of the aspects responsible for developing them including the interactions between individuals within groups; the mechanisms underlying social recognition; the factors (morphological, behavioural or ecological) that affect associations, and the influence that these associations have on the overall organization, structure, and complexity of the group (Guttridge & Gruber, 2008).

The findings reported here have great implications in respect to any management and conservation strategies employed on this species. It would appear that adult females are responsible for connecting the social structure together, with their removal leading to the fragmentation of any such social groups. This may be a good result in respect to the management of any socially transmitted disease; however at present this does not appear to be a significant threat to this species in this area. Instead this finding should be considered by those responsible for any management such as governments and those utilising this species as a resource such as fisherman in order to conserve wild populations.

Further suggestions as a result of this study include the official listing of Hanifaru lagoon as a marine protected area with subsequent enforcement. Currently there are no other documented cases of aggregations of this species occurring at this scale anywhere else in the world. With the ever expanding tourism industry in the Maldives and the increase in both diving and wildlife tours, it is inevitable that human pressure in this area will increase. The implications of this are hard to define at this point, however an area such as this should be protected before any negative impacts can take effect.

Future research

The present study has demonstrated a unique behaviour in this species by demonstrating significant social structure within the Maldivian population. However reasons for observed patterns remain difficult to determine, a situation hindered by a general lack of published work on this species. Many aspects of this species biology remain unexplored, leading to the possibility of future research in areas not only linked to this research, but in a wide range of areas.

One such area of research and one which has great relevance to the present study would be in discovering how manta rays find areas of high zooplankton on which to feed. During the present investigation individuals were repeatedly observed feeding in a select number of locations. How these individuals find these areas, whether by chance as they follow plankton gradients, passively ending in areas of accumulation, or by active choice due to an understanding of the area and a memory of where to find good feeding patches, would provide a worthy area of research. Similar behaviours where individuals arrive predictably in areas of high plankton concentrations have been documented in whale sharks (Heyman *et al.*, 2001) and basking sharks (Sims *et al.*, 2000). Sims *et al.* (2000) suggests that basking sharks may simply follow plankton gradients along coastal fronts, by chance ending up in areas of rich feeding in which other sharks are likely to be, leading to opportunities for courtship behaviour. In contrast, Heyman *et al.* (2001) suggest that whale sharks may actively locate feeding grounds using a combination of olfactory and visual cues, the exact mechanism by which this may occur however has not been discovered.

Whilst observing individuals feeding in groups, clustering behaviour known as feeding chains, where individuals line up behind one another and feed in a line, was repeatedly observed. Nearest neighbour studies, those looking at which individual is found nearest to others in a group may reveal a deeper level of social structure not explored in the present study.

A further area of research would include inter-population studies, where social structure can be explored in other manta ray populations around the world, with subsequent comparisons of any patterns found. Although some manta rays are known to be highly mobile, moving over large distances, many have been found to be resident with most individuals remaining in specific geographical locations (Dewer *et al.*, 2008). Due to the lack or low level of interbreeding, this may lead to the possible development of unique behaviours amongst distinct populations.

Molecular studies may provide unique insights into many aspects of an animal's biology and have indeed been employed in the investigation into a wide variety of research areas in many species. Similar techniques could be used to investigate the relatedness of individuals within the Maldivian population, discovering any distinct subpopulations which may be present, as well as providing possible explanations into any observed patterns of social structure. Due to an average fecundity of 1 young in this species, it is unlikely that the adult females observed in strong association in this investigation are closely related, at least at the sibling level. However it would be worth exploring genetic relatedness and comparing these results with the observed social connectedness documented here.

A distinct skew in sex ratio was documented in the Maldivian population. Whether this is due to actual differences within the population or due to sampling strategies is uncertain. However this finding was based on photographic evidence collected over a number of years allowing more confidence to be placed in this result. Comparisons with other populations would provide a better understanding of why this is occurring and weather this is a unique situation within the Maldivian population or is found in other populations globally. Satellite tracking of both males and females would provide insight into the different behaviours they display, with females seeming more site fidelic allowing the development of stronger bonds with others, and males being relatively unsocial displaying only weak social bonds with others.

References

Abrahams, M.V. & Colgon, P.W. (1985). Risk of predation, hydrodynamic efficiency, and their influence on school structure. *Environmental biology of fish*. **13:** 195-202.

Acevedo-Gutierrez, A., Brennan, B., Rodriques, P., Thomas, M. (1997). Resightings and behaviour of false killer whales (Pseudorca crassidens) in Costa Rica. *Marine mammal science*. **13:** 307-314.

Alexander, R.D. (1974). The evolution of social behaviour. *Annual review of ecological systems*. **5:** 325-383.

Barthelemy, M. (2004). Betweeness centrality in large complex networks. *The European physical journal B*. **38:** 163-168.

Bigelow, H.B. & Schroeder, W.C. (1953). Fishes of the western North Atlantic. No. 1, Part 2. Sawfishes, guitarfishes, skates, rays, and chimaeroids. Sears Foundation for Marine Research. Yale University.

Borgatti, S.P. (2002). NetDraw: Graph visualisation software. Harvard: Analytic technologies.

Borgatti, S.P., Everett, M.G. and Freeman, L.C. (2002). Ucinet for Windows: Software for Social Network Analysis. Harvard, MA: Analytic Technologies.

Campagna, C., Bisioli, C., Quintana, F., Perez, F., Vila, A. (1992). Group breeding in sea lions: Pups survive better in colonies. *Animal behaviour*. **43**: 541-548.

Carey, F.G. & Scharold, J.V. (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine biology*. **106:** 329-342.

Carrier, J.C., Pratt, J.H.L., Martin, L.K. (1994). Group reproductive behaviours in free-living nurse sharks, *Ginglymostoma cirratum. Copeia*. **1994:** 646-656.

Carrier, J.C., Musick, J.A., Heithaus, M.R. (2004). *Biology of sharks and their relatives*. CRC marine biology series.

Caro, T.M. (1994). *Cheetahs of the Serengeti plains*. Chicago: University of Chicago press.

Castro, J.I. (1993). The biology of the finetooth shark, *Carcharhinus isodon. Environmental biology of fishes*. **36:** 219-232.

Clapham, P.J. (2000). *Cetacean societies. Field studies of whales and dolphins*. University of Chicago press.

Clark, C.W. (1991). Moving with the herd. *Natural history*. **38**.

Clutton-Brock, T.H. (1989). Mammalian mating systems. *Proceedings of the royal society of London*. **236:** 339-372.

Clutton-Brock, T.H & Harvey, P.H. (1977). Primate ecology and social organisation. *Journal of zoology*. **183**: 1-39.

Cohan, J. (1988). Statistical power analysis for the behavioural sciences. Hillsdale, NJ: Erlbaum.

Colman, J.G. (1997). A review of the biology and ecology of the whale shark. *Journal of fish biology*. **51**: 1219-1234.

Conner, R.C. (2000). *Cetacean societies. Field studies of whales and dolphins*. University of Chicago press.

Conner, R.C. & Smolker, R.A. (1990). Quantitative description of a rare behavioural event: A bottlenose dolphins behaviour towards her deceased offspring. *The bottlenose dolphin*. San Diago: Academic press.

Conner, R.C., Mann, J., Tyack, P.L., Whitehead, H. (1998). Social evolution in toothed whales. *Trends in evolution and ecology*. **13:** 228-232.

Conradt, L. & Roper, T.J. (2003). Group decision-making in animals. *Nature*. **421:** 155-158.

Croft, D.P., Krause, J., James, R. (2004). Social networks in the guppy (*Poecilia reticulate*). *Proceedings of the royal society of London*. **271:** 516-519.

Croft, D.P., James, R., Ward, A.J.W., Botham, M.S., Mawdsley, D., Krause, J. (2005). Assortive interactions and social networks in fish. *Oecologia*. **143:** 211-219.

Croft, D.P., James, R., Krause, J. (2008). *Exploring animal social networks*. Princeton university press.

Crook, J.H (1964). The evolution of social organisation and visual communication in weaverbirds (*Ploceinae*). *Behaviour*. **10:** 1-178.

Dewar, H., Mous, P., Domeier, M., Muljadi, A., Pet, J., Whitty, J. (2008). Movements and site fidelity of the giant manta ray, *Manta birostris,* in the Komodo Marine Park, Indonesia. *Marine biology*. **155:** 121-133.

Duffy, C.A.J. & Abbott, D. (2003). Sightings of mobulid rays from Northern New Zealand, with confirmation of the occurrence of *Manta birostris* in New Zealand waters. *New Zealand journal of marine and freshwater research*. **37**: 715-721.

Drzejewski, W.J., Schmidt, K., Theuerkauf, J.R., Drzejewska, B.J., Selva, N., Zub, K., Szymura, L. (2002). Kill rates and predation by wolves on ungulate populations in Bialowiez, a primeval forest (Poland). *Ecology*. **83**: 1341–1356.

Dugatkin, L.A. & Godin, J.G.J. (1992). Reversal of mate choice by copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal society London.* **249:** 179–184.

Dugatkin, L.A. & Godin, J.G.J. (1993). Female mate copying in the guppy (*Poecilia reticulata*): age dependent effects. *Behavioural Ecology.* **4:** 289–292.

Duncan, P. & Vigne, N. (1979). The effect of group size in horses on the rate of attacks by blood-sucking flies. *Animal behaviour.* **27**: 623-625.

Ebensperger, L.A. & Bozinovic, F. (2000). Communal burrowing in the hystricognath rodant, *Octdon degus*: a benefit of sociality. *Behavioural ecology and socio-biology.* **47:** 365-369.

Economakis, A.E. & Lobel, P.S. (1998). Aggregation behaviour of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston atoll, Central Pacific ocean. *Environmental biology of fishes.* **51:** 129-139.

Eibl-Eibesfedlt, I. & Hass, H. (1959). Erfahrungen mit Haien. *Z. Tierpsychol.* **16:** 733-746. Not seen, cited in Nelson (1977).

Eisfeld, S.M. & Robinson, K.P. (date unknown). The sociality of bottlenose dolphins in the outer Southern Moray Firth, NE Scotland: Implications for current management proposals? Cetacean research unit, Baniff, Scotland.

Galef Jr., B.G. (1988a). Imitation in animals: history, definitions and interpretation of the data from the psychological laboratory. *Social Learning: Psychological and Biological Perspectives* (Ed. by T. Zentall & B. G. Galef Jr.), pp. 3–28. Hillsdale, New Jersey: Erlbaum.

Galef Jr., B.G. (1988b). Communication of information concerning distant diets in a social, central-place foraging species: *Rattus norvegicus*. *Social Learning: Psychological and Biological Perspectives* (Ed. by T. Zentall & B. G. Galef Jr.), pp. 119–139.

Godfrey, T. (2004). *Atlas of the Maldives- A reference for travellers, divers and sailors*. 4th ed., Atoll editions.

Godin, J., Classon, L.J., Abrahams, M.V. (1988). Group vigilance and shoal size in a small characin fish. *Behaviour*. 104:29-40.

Gompper, M.E. (1996). Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behavioural ecology*. **7**: 251-263.

Gosling, L.M. (1986). The evolution of the mating strategies in male antelopes. *Ecological aspects of social evolution: birds and mammals*. University Princeton press.

Gowans, S. & Whitehead, H. (2001). Photographic identification of Northern bottlenose whales (*Hyperoodon amullatus*): Sources of heterogeneity from natural marks. *Marine mammal science*. **17**: 76-93.

Gowans, S., Whitehead, H., Hooker, S. (2001). Social organisation in northern bottlenose whales, *Hyperoodon ampullatus*: Not driven by deep water foraging? *Animal behaviour.* **62**: 369-377.

Guttridge, T. & Gruber, S.H. (2008). The Social Organization of the Lemon Shark, *Negaprion brevirostris.* Bimini biological field station.

Hamilton, W.D. (1971). The geometry of the selfish herd. *Journal of theoretical biology*. **31:** 295-311,

Harvey-Clark, C.J., Stobo, W.T., Helle, E., Mattson, M. (1999). Putative mating behaviour in basking sharks off the Nova Scotia coast. *Copeia*. **1999:** 780-782.
Heyes, C.M. (1994). Social learning in animals: categories and mechanisms. *Biological review.* **69:** 207–231.

Heyes, C.M. & Dawson, G.R. (1990). A demonstration of observational learning in rats using a bidirectional control. *Journal of experimental psychology.* **42:** 59–71.

Heyman, W.D., Graham, R.T., Kjerfve, B., Johannes, R.E. (2001). Whale shark *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine ecology progress series*. **215:** 275-282.

Hinde, R.A. & Fisher, J. (1951). Further observations on the opening of milk bottles by birds. *Br. Birds*, **44:** 393–396.

Hobson, E.S. (1978). Aggregating as a defence against predators in aquatic and terrestrial environments. *Contrasts in behaviour*. New York Wiley

Holland, K.N., Wetherbee, B.M., Peterson, J.D., Lowe, C.G. (1993). Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia*. **1993:** 495-502.

Homma, K., Maruyama, T., Itoh, T., Ishihara, H., Uchida, S. (1999) Biology of the manta ray, *Manta birostris* Walbaum, in the Indo-Pacific. *Proceedings of the 5th Indo-Pacific Fish Conference*. 209–216.

Horrocks, J.A. & Hunte, W. (1986). Sentinel behaviour in vervet monkeys: Who sees whom first? *Animal biology*. **34:** 1566-1567.

Inman, A.J. & Krebs, J. (1987). Predation and group living. *Tree*. Vol 2.

Itani, J & Nishimura, A. (1973). The study of infrahuman culture in Japan. *Precultural primate behaviour*. Menzel. Basel: Karger: 26-50.

IUCN (2007). Marshall, A., Ishihara, H., Dudley, S.F.J., Clark, T.B., Jorgensen, S., Smith, W.D. & Bizzarro, J.J. 2006. *Manta birostris*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species.*

Janik, V.M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncates). Science.* **289:** 1355-1357. Not seen, cited in Lusseau (2003).

Jarman, R.J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*. **48**: 215-267.

Johnson, D.D.P., Kays, R., Blackwell, P.G., Macdonald, D.W. (2002). Does the resource dispersion hypothesis explain group living? *Trends in ecology and evolution*. **17**: 563-570.

Kawai, M. (1965). Newly acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima inlet. *Primates*. **6:** 1–30.

Klimley, A.P. (1985). Schooling in *Sphyrna lewini*, a species with low risk of predation: a non egalitarian state. *Z. Tierpsychol*. **70:** 297-319. Not seen, cited in Wilson (2004).

Klimely, A.P. (1987). The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini. Environmental Biology of Fishes*. **18:** 27-40.

Krause, J. & Ruxton, G.D. (2002). *Living in groups*. Oxford University press.

Kuroda, S. (1980). Social behaviour of the pygmy chimpanzees. *Primates.* **21**: 181-197.

Laland, K.N. & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal behaviour*. **53:** 1161-1169.

Last, P.R., & Stevens, J.D. (1994). *Sharks and rays of Australia*. *CSIRO* Australia. 513pp

Lusseau, D. (2003). The emergent properties of a dolphin social network. *Proceedings of the royal society London*. **270**: 186-188.

Mann, J. & Barnett, H. (1999). Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: Defence and reactions by the mother. *Marine mammal science*. **15:** 568-574.

Marshall, A. Manta and Whale shark research centre. Tofo beach, Mozambique.

McKibben, J.N. & Nelson, D.R. (1986). Patterns of movements and grouping of grey reef sharks, Carcharinus amblyrhynchos, at Enewetak, Marshall Islands. *Bulletin of marine science*, **38:** 89-110.

Meekan, M.G., Bradshaw, C.J.A., Press, M., McLean, C., Richards, A., Quasnichka, S., Taylor, J.G. (2006). Population size and structure of whale sharks *Rhincodon* *typus* at Nigaloo reef, Western Australia. *Marine ecology progress series*. **319**: 275-285.

Michener, C. (1974). *The social behaviour of the bees: A comparative study*. Harvard university press.

Milinski, M.Z. (1977). Do all members of a swarm suffer the same predation? *Tierpsychol*. **45:** 373-88.

Milinski, M & Heller, R. (1978). Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.) *Nature* **275**: 642 - 644

Molvar, E.M. & Bowyer, T.R. (1994). Costs and benefits of group living in a recently social ungulate: The Alaskan moose. *Journal of mammalogy*. **75**: 621-630.

Mooring, M.S. & Hart, B.L. (1992). Animal grouping for protection from parasites: Selfish herd and encounter dilution effects. *Behaviour*. **123**: 173-193.

Morrissey, J.F. & Gruber, S.H. (1993). Habitat selection by juvenile lemon sharks, *Negaprion brevirostris. Environmental biology of fishes*. **38:** 311-319.

Morrissey, J.F. (1991). Home range of juvenile lemon shark. *Discovering sharks*. American littoral society. 85-86.

Moss, S.A. (1977). Feeding mechanisms in sharks. *American zoology*. **17**: 355-364.

Nelson, D.R. (1969). The silent savages. *Oceans*. **1:** 8-22.

Nelson, D.R. (1977). On the field study of shark behaviour. *American zoologist*. **17**: 501-507.

Nicol, C.J. & Pope, S.J. (1993). Food deprivation during observation reduces social learning in hens. *Animal Behaviour*. **45:** 193–196.

Northcutt, R.G. (1977) Elasmobranch central nervous system organization and its possible evolutionary significance. *American* Zoo*logist.* **17:** 411-29.

Norris, K.S. & Schilt, C.R. (1988). Cooperative societies in three-dimensional space: On the origins of aggregations, flocks and schools, with special reference to dolphins and fish. *Ethology and sociobiology*. **9:** 149-179.

Norris, K.S., Wursig, B., Wells, R.S., Wursig, M. (1994). *The Hawaiian spinner dolphin*. University of California press.

Notarbartolo-di-Sciara, G. & Hillyer, E.V. (1989). Mobulid rays off Eastern Venezuela (Chondrichthyes, Mobulidae). *Copia*. 607-614.

Owen, R.E. (1984). Distribution and ecology of the basking shark *Cetorhinus maximus* (Gunnerus, 1765). MSc thesis, University of Road Island. 64 pp. Not seen, cited in Wilson (2004).

Pitcher, T.J. & Parrish, J.K. (1993). Functions of schooling behaviour in teleosts. *Behaviour of teleost fish.* 2nd edition. London. Chapman and Hall.

Pyle, P., Anderson, S.D., Klimley, A.P., Henderson, R.P. (1996). Environmental factors affecting the occurrence and behaviour of white sharks at the Farallon Islands, California. *Great white sharks: the biology of Carcharodon carcharias*. San Diego, CA: Academic press. Not seen, cited in Sims *et al*. (2000).

Ryer, C.H. & Olla, B.L. (1992). Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. *Animal Behaviour.* **44:** 69–74.

Semeniuk, A.D. (2003). Resting behaviour of the Cowtail stingray (*Pastinachus sepen*) in Shark bay, Western Australia. Master's thesis. Simon Fraser University, B.C. Canada. Not seen, cited in Carrier *et al*. (2004).

Sen, P.S., Dasgupta, A., Chatterjee, P.A., Sreeram, G., Mukherjee, G., Manna, S.S. (2003). Small-world properties of the Indian railway network. *Physical review E.* **67:** 036106. Not seen, cited in Croft *et al*. (2008).

Shorrocks, B. & Croft, D.P. (2008). Necks and networks: a preliminary study of population structure in the reticulated giraffe (*Giraffa camelopardalis reticulata* de Winston). *African journal of ecology.*

Sims, D.W. (1999). Threshold foraging behaviour of basking sharks on zooplankton in a small-scale front. *Proceedings of the royal society of London*. **266**: 1437-1443.

Sims, D.W., Southall, E.J., Quayle, V.A., Fox, A.M. (2000). Annual social behaviour of basking sharks associated with coastal front areas. *Proceedings of the Royal Society London B*. **267:** 1897-1904.

Sims, D.W., Nash J.P., Morritt, D. (2001). Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Marine* Bio*logy*. **139:** 1165-1175.

Stevens, G. Maldivian Manta Ray Project (MMRP). Four Seasons resort, Landaa Giravaru, Baa Atoll. Republic of Maldives.

Strasburg, D.W. (1958). The diet and dentition of *Isistius brasiliensis*, with remarks on tooth replacement in other sharks. *Copeia.* 1963: 33-40.

Suboski, M.D., Bain, S., Carty, A.E., McQuoid, L.M., Seelen, M.I., Seifert, M. (1990). Alarm reaction in acquisition and social transmission of simulated predator recognition by zebra danio fish (*Brachydanio rerio*). *Journal of comparitive Psychology.* **104:** 101–112.

Tadic, B. (2001). Dynamics of directed graphs: The World-Wide Web. *Physica A*. **293:** 273-284. Not seen, cited in Croft *et al*. (2008).

Tait, R.V. (1980). *Elements of marine ecology*. London: Butterworths. Not seen, cited in Wilson (2004).

Taylor, L. (1993). *Sharks of Hawaii: their biology and cultural significance*. University of Hawaii press, Honolulu. 126pp. Not seen, cited in Economakis & Lobel (1998).

Taylor, J.G. (1996). Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo reef, Western Australia. *Marine and freshwater research*. **47:** 637-42.

Taylor, J.G., Compagno, LJV., Struhsaker, P.J. (1983). Megamouth, a new species, genus and family of laminid shark (*Megachasma pelagios*, family *Magachasmidae*) from Hawaiian islands. *Proceedings Calif Acadamy of science*. **43**: 87-110.

Thorpe, W.H. (1956). *Learning and Instinct in Animals*. London: Methuen.

Turner, G.F & Pitcher, T.J. (1986). Attack abatement: A model for group protection by combined avoidance and dilution. *American naturalist*. **128:** 228-240.

Uetz, G.W & Hieber, C.S. (1994). Group size and predation risk in colonial web-building spiders: Analysis of attack abatement mechanisms. *Behavioural ecology* **5:** 326-333.

Whitehead, H. & Dufault, S. (1999). Techniques for analysing vertebrate social structure using identified individuals: review and recommendations. *Advances in the study of behaviour*. **28:**

Whitehead, H. (1994). Investigating structure and temporal scale in social organisations using identified individuals. *Behavioural ecology*. **2:** 199-208.

Whitehead, H. (1997). Analysing animal social structure. *Animal behaviour*. **53**: 1053-1067.

Whitehead, H.P & Glass, C. (1985). Orcas (killer whales) attack humpback whales. *Journal of mammalogy*. **66**: 183-185.

Whitehead, H. (1999) Programs for analysing social structure. SOCPROG.

Whitehead, H., Christal, J., Tyack, P.L. (2000). *Cetacean societies, field studies of dolphins and whales*. The university of Chicago press.

Whitehead, H. & Weilgart, L. (2000). *Cetacean societies. Field studies of whales and dolphins*. University of Chicago press.

Whiten, A. (2000). Primate and social learning. *Cognitive science*. **24:** 477-508.

Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behaviour*. **21:** 239–283.

Wilson, E.O. (1975). *Sociobiology: The New Synthesis*. Cambridge, Massachusetts: Belknap Press.

Wilson, A.G. (2004). Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. *Fisheries oceanography*. **13:** 283-286.

Wittemyer, G., Douglas-Hamilton, I., Getz, M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal behaviour*. **69:** 1357–1371

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour*. **75:** 262-292.

Wranghm, R.W. (1982). Mutualism, kinship and social evolution. *Current problems in socio-biology*. Kings college socio-biology group, Cambridge university press.

Xu, T., Chen, R., He, Y., He, D.R. (2004). Complex network properties of Chinese power grid. *International journal of modern physics B*. **18:** 2599-2603. Not seen, cited in Croft *et al*. (2008).

Yano, K., Sato, F., Takahashi, T. (1999). Observations of mating behaviour of the manta ray, *Manta birostris*, at Ogasawara islands, Japan. *Ichthyological society of Japan*.

Appendix 1. Summarising table of the costs and benefits individuals face while living in groups, adapted from Krause & Ruxton (2002).

Benefits	Costs
Anti-predator	**Predation**
Many eyes effect	Increased conspicuonous
Encounter dilution	Confusion during escape

Predator confusion
Predator mobbing
Selfish herd effects
Parasite dilution
Communal defence
Predator learning
Foraging
Group hunting
Learning
Mate choice
Environmental challenges
Reduced heat loss
Reduced desiccation
Transport
Competition
Kleptoparasitism
Aggression between conspecifics
Mates
Socially transmitted disease

Appendix 2.

Strength of correlation as defined by Cohan (1988).

r = .10 - .29 +/-	Small
r = .30 - .49 +/-	Medium
r = .50 - 1.0 +/-	Large

Appendix 3.

Individual I.D's from original network (all years and behaviours) with corresponding node degree and cluster coefficient.

Individual I.D.	Node degree	Node cluster coefficient
M1	79	0.760
M2	41	0.710
M3	107	0.563

M4	1	0.000
M5	15	1.124
M6	29	0.679
M8	84	0.788
M9	99	0.484
M10	2	1.000
M11	108	0.502
M12	25	0.577
M13	2	2.000
M14	86	0.629
M15	23	0.333
M16	5	1.000
M17	5	1.000
M18	6	0.733
M19	14	0.615
M20	49	1.006
M21	30	0.914
M22	12	1.470
M23	51	0.934
M24	78	0.597
M25	162	0.421
M26	65	0.703
M27	55	0.969
M28	99	0.525
M29	25	0.992
M30	165	0.473
M31	78	0.540
M32	68	0.590
M33	137	0.531
M34	4	1.000
M35	4	1.000
M36	6	0.467
M37	33	0.869
M38	6	1.067
M39	6	1.067
M40	6	1.067
M41	7	1.000
M42	6	1.067
M43	7	1.000
M44	35	0.741
M45	12	0.564
M46	8	1.071
M47	16	0.552
M48	8	1.071
M49	8	1.071
M50	8	1.071

M51	8	1.071
M52	10	0.833
M53	50	0.692
M54	36	1.348
M55	22	1.009
M56	32	0.778
M57	58	0.297
M58	121	0.462
M59	105	0.443
M60	33	0.800
M61	12	1.409
M62	126	0.431
M63	59	0.681
M64	41	1.155
M65	41	1.132
M66	118	0.454
M67	88	0.690
M68	115	0.510
M69	104	0.501
M70	48	0.999
M71	183	0.390
M72	36	1.348
M73	52	0.548
M74	36	1.348
M75	91	0.679
M76	42	1.167
M77	17	1.095
M78	46	1.095
M79	58	0.846
M80	20	1.163
M81	92	0.634
M82	101	0.517
M83	108	0.651
M84	36	0.779
M85	36	1.348
M86	35	0.847
M87	90	0.677
M88	45	0.722
M89	22	0.788
M90	128	0.367
M91	42	0.695
M92	20	1.163
M93	20	1.163
M94	47	0.710
M95	41	0.662
M96	20	1.163

M97	79	0.717
M98	76	0.737
M99	44	1.082
M100	118	0.515
M101	93	0.612
M102	164	0.452
M103	100	0.594
M104	145	0.428
M105	187	0.331
M106	94	0.659
M107	3	1.000
M108	3	1.000
M109	3	1.000
M110	3	1.000
M111	3	1.000
M112	17	0.882
M113	11	0.618
M114	9	0.389
M116	9	0.861
M118	97	0.510
M119	1	0.000
M120	52	0.614
M121	43	0.747
M122	6	1.333
M123	61	0.518
M124	60	0.380
M125	21	0.971
M126	59	0.451
M127	84	0.579
M128	127	0.468
M129	36	0.806
M130	31	0.872
M131	27	0.935
M132	60	0.568
M134	52	0.778
M135	16	1.375
M136	60	0.748
M137	35	0.430
M138	16	1.375
M139	16	1.375
M140	20	0.974
M141	31	1.005
M142	2	1.000
M143	40	0.985
M144	1	0.000
M145	85	0.679

M146	62	0.599
M147	8	0.714
M148	20	0.994
M149	7	1.286
M150	18	0.876
M151	30	0.480
M152	7	1.286
M153	34	0.819
M154	19	0.882
M155	32	0.901
M156	34	0.627
M157	21	0.643
M158	1	0.000
M160	43	0.748
M161	20	0.661
M162	33	0.923
M163	2	2.000
M164	30	0.983
M165	60	0.717
M166	66	0.802
M167	13	1.121
M168	13	1.538
M169	37	0.693
M170	23	0.874
M171	12	1.833
M172	6	0.467
M173	99	0.581
M174	74	0.659
M175	63	0.499
M176	69	0.745
M177	33	0.740
M178	26	1.020
M179	22	1.276
M180	4	2.333
M181	51	0.767
M183	54	0.517
M184	20	1.111
M185	24	1.016
M186	2	1.000
M187	2	1.000
M188	2	1.000
M189	100	0.527
M190	19	0.649
M191	5	1.100
M192	5	1.100
M193	37	0.943

M194	12	1.348
M195	29	0.751
M196	12	1.348
M197	13	1.641
M198	33	0.637
M199	9	1.417
M200	8	1.500
M201	17	0.890
M202	22	1.153
M203	7	1.667
M204	92	0.358
M205	45	0.902
M206	2	1.000
M207	3	1.000
M208	3	1.000
M209	3	1.000
M210	3	1.000
M211	78	0.613
M212	5	1.000
M213	5	1.000
M214	5	1.000
M215	14	0.505
M216	5	1.000
M217	39	0.661
M219	14	0.714
M220	10	0.533
M221	6	0.667
M222	3	1.000
M223	3	1.000
M224	8	1.071
M225	10	0.833
M226	8	1.071
M227	12	1.015
M228	12	1.015
M229	41	0.633
M230	20	0.521
M231	12	1.015
M232	24	0.515
M233	12	1.015
M234	25	0.525
M235	27	0.493
M236	77	0.451
M237	12	1.015
M238	12	1.015
M239	37	0.749
M240	83	0.422

M241	8	1.036
M242	8	1.036
M243	8	1.036
M245	8	1.036
M246	8	1.036
M247	15	0.486
M248	33	1.006
M249	59	0.568
M250	25	1.320
M251	25	1.320
M252	53	0.671
M253	25	1.320
M254	9	1.361
M255	9	1.361
M256	20	0.842
M257	9	1.361
M258	54	0.595
M259	15	1.438
M260	15	1.438
M261	50	0.751
M262	11	1.491
M263	17	1.301
M264	16	1.475
M265	37	0.938
M266	16	1.475
M267	17	1.404
M268	25	0.924
M269	19	1.333
M270	9	1.250
M271	37	0.482
M272	47	0.840
M273	19	1.129
M274	12	1.803
M275	13	0.782
M276	13	1.026
M277	13	1.026
M278	17	0.632
M279	13	1.026
M280	22	0.515
M281	13	1.026
M282	13	1.026
M283	13	1.026
M284	13	1.026
M285	13	1.026
M286	51	0.754
M287	89	0.806

M288	1	0.000
M289	1	0.000
M290	7	1.143
M291	8	1.607
M292	8	1.607
M293	15	1.000
M294	15	1.590
M296	1	0.000
M297	7	0.714
M298	38	1.183
M299	7	1.905
M301	5	1.000
M302	5	1.000
M303	5	1.000
M304	5	1.000
M305	5	1.000
M306	5	1.000
M308	3	1.000
M309	3	1.000
M310	6	2.000
M311	4	1.000
M312	4	1.000
M313	4	1.000
M314	4	1.000
M315	4	1.000
M317	20	1.005
M318	26	0.633
M319	1	0.000
M320	22	0.817
M321	1	0.000
M322	3	0.333
M323	2	1.000
M324	2	1.000
M326	1	0.000
M328	22	0.824
M329	13	1.273
M330	15	1.124
M331	21	0.919
M332	15	1.124
M333	15	1.124
M334	19	0.791
M335	15	1.124
M336	15	1.124
M337	18	0.934
M338	1	0.000
M339	21	1.057

M340	59	0.624
M341	32	0.713
M342	21	1.057
M343	21	1.057
M344	28	0.646
M345	21	1.057
M346	22	0.961
M347	21	1.057
M348	97	0.704
M349	21	1.057
M350	21	1.057
M351	21	1.057
M352	2	1.000
M353	2	1.000
M354	2	1.000
M355	5	1.400
M356	5	1.400
M357	20	1.005
M358	51	0.502
M359	20	1.005
M360	20	1.005
M361	20	1.005
M362	20	1.005
M363	21	0.910
M364	96	0.711
M365	20	1.005
M366	20	1.005
M367	20	1.005
M368	20	1.005
M369	20	1.005
M370	31	0.513
M371	20	1.005
M372	20	1.005
M373	35	0.497
M374	20	1.005
M375	20	1.005
M376	28	0.624
M378	2	1.000
M379	2	1.000
M380	2	1.000
M381	6	1.600
M382	1	0.000
M383	17	1.108
M384	7	1.905
M385	6	2.133
M386	8	1.071

M387	8	1.071
M389	4	1.000
M390	4	1.000
M391	4	1.000
M392	4	1.000
M394	15	1.124
M395	15	1.124
M396	15	1.124
M399	7	1.000
M400	7	1.000
M401	14	0.462
M402	7	1.000
M403	7	1.000
M404	7	1.000
M405	7	1.000
M406	1	0.000
M407	5	1.500
M408	5	1.500
M409	59	0.490
M410	2	1.000
M411	2	1.000
M412	6	1.000
M413	6	1.000
M414	96	0.796
M415	6	1.000
M416	6	1.000
M417	111	0.433
M418	100	0.640
M419	8	1.036
M420	8	1.036
M421	8	1.036
M422	10	0.667
M423	8	1.036
M424	1	0.000
M425	1	0.000
M426	2	1.000
M427	4	0.333
M428	2	1.000
M429	6	1.000
M430	6	1.000
M431	6	1.000
M432	6	1.000
M433	6	1.000
M434	6	1.000
M435	6	1.000
M436	84	0.935

M437	8	1.143
M438	22	0.667
M439	29	1.094
M440	29	1.094
M441	67	0.689
M442	67	0.689
M443	110	0.668
M444	143	0.500
M445	38	0.716
M446	5	1.000
M447	121	0.641
M448	5	1.000
M449	24	0.493
M450	5	1.000
M451	29	1.094
M452	105	0.706
M453	29	1.094
M454	29	1.094
M455	29	1.094
M456	29	1.094
M457	71	0.573
M458	181	0.386
M459	81	0.485
M460	67	0.627
M461	29	1.094
M462	29	1.094
M463	67	0.689
M464	154	0.527
M465	33	0.909
M466	95	0.859
M467	15	1.000
M468	15	1.000
M469	15	1.000
M470	15	1.000
M471	15	1.000
M472	15	1.000
M473	15	1.000
M474	15	1.000
M475	15	1.000
M476	15	1.000
M477	15	1.000
M479	9	1.000
M480	1	0.000
M481	44	0.788
M482	1	0.000
M483	166	0.483

M484	2	1.000
M485	2	1.000
M486	39	1.035
M487	1	0.000
M488	29	1.047
M489	6	1.400
M490	57	0.605
M491	6	1.400
M492	6	1.400
M493	7	1.000
M494	7	1.000
M495	7	1.000
M496	7	1.000
M497	7	1.000
M498	7	1.000
M499	7	1.000
M500	7	1.000
M501	1	0.000
M502	39	1.123
M503	5	1.100
M504	5	1.100
M505	2	1.000
M508	10	0.556
M509	20	0.689
M510	1	0.000
M511	5	0.900
M512	1	0.000
M513	1	0.000
M518	38	1.183
M519	4	0.500
M520	1	0.000
M521	1	0.000
M524	2	2.000
M528	2	1.000
M529	2	1.000
M530	1	0.000
M531	1	0.000
M532	1	0.000
M533	1	0.000
M535	7	1.000
M537	7	1.000
M538	7	1.000
M541	39	0.997
M542	1	0.000
M543	38	1.051
M544	38	1.051

M545	219	0.331
M546	38	1.051
M548	38	1.183
M550	38	1.051
M551	38	1.051
M552	38	1.051
M553	152	0.497
M554	41	0.911
M555	67	0.557
M556	38	1.051
M557	38	1.051
M558	38	1.051
M559	38	1.051
M560	76	0.615
M561	38	1.051
M562	38	1.051
M563	52	0.673
M564	38	1.051
M565	38	1.051
M566	38	1.051
M567	190	0.391
M568	38	1.051
M569	40	0.949
M570	45	0.773
M571	38	1.051
M572	38	1.051
M573	38	1.051
M574	38	1.051
M575	8	0.786
M576	1	0.000
M577	42	0.974
M578	45	0.862
M579	7	1.000
M580	7	1.000
M581	7	1.000
M582	7	1.000
M583	7	1.000
M584	7	1.000
M585	1	0.000
M586	1	0.000
M587	2	1.000
M588	2	1.000
M589	4	1.000
M590	4	1.000
M591	4	1.000
M592	3	1.000

M601	9	1.000
M604	76	1.067
M606	76	1.067
M611	6	1.800
M612	1	0.000
M613	1	0.000
M614	1	0.000
M615	5	1.000
M616	2	1.000
M617	40	0.985
M618	1	0.000
M619	2	2.000
M620	3	1.000
M621	3	1.000
M622	3	1.000
M623	49	0.769
M627	1	0.000
M628	1	0.000
M629	18	1.105
M630	7	1.524
M631	4	1.000
M632	4	1.000
M633	17	1.221
M634	17	1.221
M635	17	1.221
M636	17	1.221
M637	13	1.385
M638	10	1.133
M639	11	1.855
M658	4	0.667
M659	3	1.000
M660	3	1.000
M661	4	1.000
M662	4	1.000
M663	4	1.000
M664	13	0.538
M665	4	1.000
M669	76	1.067
M708	9	1.000
M711	7	1.000
M728	1	0.000
M734	114	0.728
M735	14	1.066
M736	38	1.051
M748	29	1.047
M751	7	1.000

M759	87	0.973
M769	7	1.000
M770	7	1.000
M771	55	0.628
M772	7	1.000
M773	7	1.000
M775	9	1.000
M776	38	1.091
M778	14	1.286
M789	5	1.000
M795	67	0.590
M796	38	1.183
M798	14	1.066
M811	7	1.000
M812	4	1.500
M813	1	0.000
M814	1	0.000
M815	5	1.000
M816	38	1.091
M817	38	1.091
M833	116	0.657
M835	76	1.067
M837	49	0.790
M849	76	1.067
M855	76	1.067
M864	1	0.000
M866	76	1.067
M867	38	1.091
M869	38	1.091
M878	92	0.908
M883	11	1.564
M884	87	0.973
M888	14	1.286
M890	38	1.183
M891	5	1.100
M894	152	0.526
M895	81	0.600
M904	76	1.067
M918	5	1.000
M919	29	1.047
M923	28	0.655
M925	128	0.652
M926	5	1.000
M927	5	1.000
M928	5	1.000
M929	1	0.000

M930	1	0.000
M932	2	1.000
M933	2	1.000
M934	2	1.000
M935	5	1.000
M936	5	1.000
M937	5	1.000
M938	5	1.000
M939	5	1.000
M940	9	0.444
M942	2	1.000
M944	1	0.000
M945	4	0.500
M946	5	0.400
M947	128	0.596
M948	14	1.066
M949	104	0.713
M950	14	1.066
M951	43	0.626
M952	19	0.708
M953	14	1.066
M954	90	0.902
M955	90	0.902
M956	14	1.286
M957	90	0.902
M958	76	1.067
M959	7	1.000
M960	83	0.902
M961	7	1.000
M962	7	1.000
M963	3	1.000
M964	3	1.000
M965	76	1.067
M966	81	0.992
M967	76	1.067
M968	76	1.067
M969	76	1.067
M970	152	0.526
M971	76	1.067
M972	76	1.067
M973	76	1.067
M974	76	1.067
M975	76	1.067
M976	76	1.067
M977	76	1.067
M978	76	1.067

M979	105	0.693
M980	76	1.067
M981	76	1.067
M982	105	0.693
M983	76	1.067
M984	114	0.666
M985	76	1.067
M986	114	0.728
M987	76	1.067
M988	76	1.067
M989	76	1.067
M990	76	1.067
M991	76	1.067
M992	114	0.728
M993	76	1.067
M994	76	1.067
M995	76	1.067
M996	76	1.067
M997	76	1.067
M998	76	1.067
M999	76	1.067
M1001	76	1.067
M1002	116	0.657
M1003	40	0.751
M1004	11	1.564
M1005	11	1.564
M1006	39	1.123
M1007	1	0.000
M1008	29	1.047
M1009	38	0.666
M1010	29	1.047
M1011	29	1.047
M1012	29	1.047
M1013	29	1.047
M1014	29	1.047
M1015	29	1.047
M1016	67	0.622
M1017	29	1.047
M1018	29	1.047
M1019	29	1.047
M1020	29	1.047
M1021	29	1.047
M1022	67	0.590
M1023	11	1.018
M1024	20	0.495
M1025	11	1.018

M1026	11	1.018
M1027	11	1.018
M1028	11	1.018
M1029	11	1.018
M1030	49	0.790
M1031	11	1.018
M1032	11	1.018
M1033	5	0.400
M1034	5	1.100
M1035	5	1.100
M1036	5	1.100
M1037	9	1.000
M1038	9	1.000
M1039	47	0.752
M1040	9	1.000
M1041	9	1.000
M1042	9	1.000
M1043	9	1.000
M1044	38	1.091
M1045	38	1.091
M1046	38	1.091
M1047	38	1.091
M1048	76	0.668
M1049	38	1.091
M1050	38	1.091
M1051	38	1.091
M1052	38	1.091
M1053	38	1.091
M1054	38	1.091
M1055	38	1.091
M1056	38	1.091
M1057	41	0.939
M1058	38	1.091
M1059	38	1.091
M1060	38	1.091
M1061	3	1.000
M1062	4	1.000
M1063	4	1.000
M1064	4	1.000
Mean	31.938	