A study of the social interactions of Manta Rays in the Baa Atoll, Maldives.

Love, L., 2013. *Manta alfredi*. [Photograph]

Abstract

Manta rays (*Manta alfredi*) have a K-selected life history, making them vulnerable to the increasing pressures of anthropogenic threats. Manta ecotourism is a growing industry in the Maldives, with many visitors drawn to Baa Atoll to swim with the resident population. With little known about the social behavior of manta rays, anecdotal reports document "friendlier" interactions with mature females. This study investigates the different levels of response between males, females, juveniles, and mature adults to establish if there are behavioral patterns within the population, considering the effect of the location, activity type, and number of snorkelers during interactions. Results show a clear distinction between the reactions of the sexes and age classes; females displaying the lowest level of reaction, with juveniles exhibiting higher levels of disturbance in comparison to the mature adults. Such results could be due to factors related to sexual dimorphism. These differences have implications for the ecotourism industry and must be considered in order to reduce negative impacts on manta populat

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Introduction

Manta rays are the subject of global intrigue. They attract SCUBA divers across their subtropical range (Figure 1) (Marshall *et al.*, 2009) in search of encounters with these "gentle giants", but they have not always been positively perceived. Historically branded "Devilfish" (Marshall *et al.*, 2009) due to their hornlike cephalic fins, gigantic size and unfamiliar behaviour, manta rays earned the persona of fearful sea creatures (Barcott, 2009). There are still many aspects of this solitary species life which remain a mystery. In 2009, official confirmation of two visually distinct species, *M. birostris* (Oceanic manta) *and M. alfredi* (Resident Reef manta), the focus of this study, was documented (Marshall *et al.*, 2009). A potential third, hybrid species *M. sp. cf. birostris* (Atlantic or Caribbean manta) is currently being studied (Marshall *et al.*, 2009).

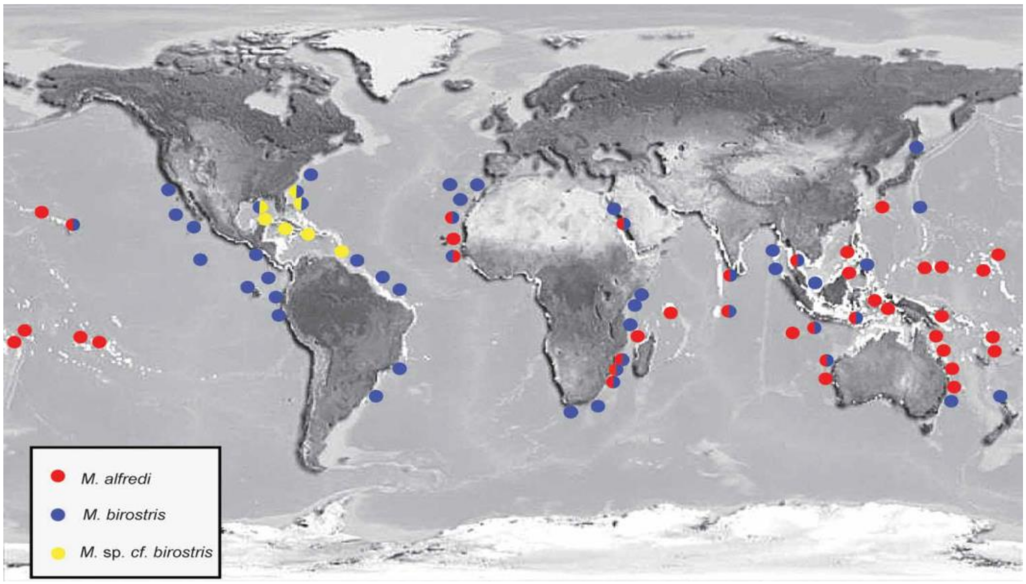


Figure 1: Shows the global distribution of M. alfredi, M. birostris and M. sp. cf. birostris (Taken from Marshall *et al.*, 2009)

The K-selected life history of manta rays leave them vulnerable to anthropogenic threats (Holden, 1974); slow-growing, with low fecundity and late maturation (Jacoby *et al*., 2012), populations are susceptible to rapid depletion and slow recovery (Hoenig & Gruber, 1990). Ovoviviparous elasmobranches, mantas are thought to produce single pups only every two to three years (Deakos, Baker & Bejder, 2011), in some cases every five years (Stevens, pers. comm. 2013). With a gestation period lasting one to three years (Compagno & Last, 1999; Homma *et al.*, 1997), this increases the strain on population regrowth. Such characteristics make manta rays particularly vulnerable to the multiple anthropogenic threats including targeted fisheries and bycatch.

Conservation

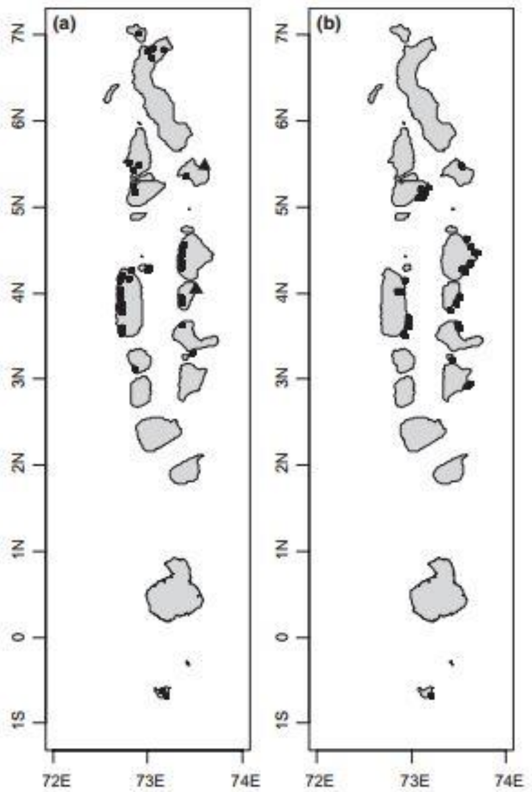
The increase in manta ecotourism has publicised their vulnerability and the need for further research and conservation (Anderson *et al.*, 2011b). In 2011, the Convention of Migratory Species of Wild Animals (CMS) added *M. birostris* under Appendix I and II, meaning the 116 nations party to the convention must implement protection for both the species and key habitats (CMS, 2013). An increase in consumptive threats and public awareness influenced a review of the 2006 International Union for the Conservation of Nature (IUCN) listing for *M. birostris*. Following Marshall's 2009 re-description, both species were included on the IUCN Red List of Threatened Species in 2011 (IUCN, 2013). Further progress was made in March 2013, with manta rays included on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), recognised by 178 world nations (CITES, 2013).

Ecotourism: In recent years marine ecotourism has proved lucrative, especially when centred on charismatic megafauna (O'Malley *et al.* 2013). Globally, it is estimated that manta tourism generates nearly US$140 million direct economic impact and US$70 million direct revenue per year, far exceeding the US$5 million profit made by specialised fisheries (O'Malley *et al.* 2013). The reliable nature of large plankton driven aggregations (Last & Stevens, 2009, Homma *et al.* 1999) means that tourist operators worldwide now offer "swim-with" experiences (Pravin, 2000). The popularity of such programs therefore proves that manta rays are worth more economically alive than dead. Anderson *et al.* (2011b) estimated that each manta in the Maldives was worth US$100,000 over a 20-year period, while O'Malley *et al.* (2013) estimate that individuals in the Yap population are worth approximately US$1.9 million over a 25-year period.

Similar "swim-with" and "watching" programs are offered worldwide, involving various megafauna including whales, turtles, manta rays, and sharks (O'Malley *et al.*, 2013). Such programs educate tourists on the welfare and conservation of these species, therefore assigning financial worth to projects (Clua *et al.* 2010). Unfortunately, mismanagement of this non-consumptive resource use can cause disturbances including behavioural, physiological, and reproductive changes amongst communities. Martin's (2007) study documented whale sharks (*Rhincodon typus*) partially retracting their eyes in response to the constant flashing of cameras, with Quiros (2007) recording 'banking' behaviour when sharks felt threatened by swimmers. A study of bottlenose dolphins (*Tursiops truncatus*) in Florida documents a habitual shift in dolphin behaviour due to increased human presence, with individuals spending 77% of observed time around people (Samuels & Bejder, 1998). This reduced natural foraging behaviour, causing increased reliance on humans for food and in some cases caused an increase in aggressive behaviour towards swimmers (Frohoff & Packard, 1995).

Although there are inherent negative impacts of ecotourism, there is also potential for huge ecological benefits; by placing a strong emphasis on education and awareness, ecotourism can support conservation efforts on a larger scale (O'Malley *et al.,* 2013). Pressure from both tourists and dive operators, in addition to the economic value of manta related dive tourism helped influence policy makers to pass regulation for the protection of manta rays in various regions, including Yap, Indonesia and the Maldives (O'Malley *et al.*, 2013). Similar legislation was enforced in Baa Atoll, Maldives, following studies into the impact of ecotourism on the manta population carried out by the Maldivian Manta Rays Project (MMRP).

Mantas of the Maldives: The Maldives has the largest number of identified individuals in the world, with sightings recorded throughout most of the 26 atolls (Stevens, pers. comm., 2013). The archipelago itself is characterised by two monsoons, with reversing oceanic currents driven by the seasonal retreating winds (Anderson *et al.*, 2011a). The Boreal or southwest (SW) monsoon occurs from May to October, with the boreal winter monsoon or northeast (NE) monsoon predominantly from December to March. Oceanic water dominates the upstream region of the archipelago, while rich nutrients are washed to the surface waters as monsoon currents pass over the Maldives ridge (Anderson *et al.*, 2011a). Increased chlorophyll levels encourage zooplankton blooms in the downstream waters of the archipelago, providing a rich food supply for planktivores, including whale sharks and manta rays (Anderson *et al*., 2011a). This explains the seasonality of manta sightings across the archipelago (Figure 2), having implications for manta ecotourism across atolls. During the NW monsoon mantas are typically sighted on the western side of atolls, with increased sightings in eastern waters during the SW monsoon (Kitchen-Wheeler, 2010).



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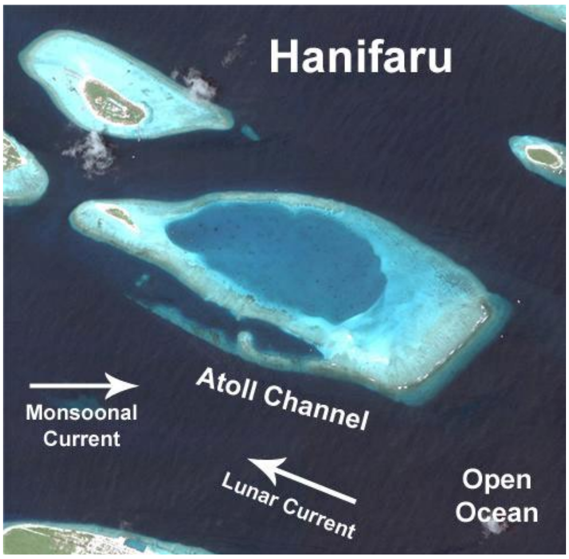
Baa Atoll boasts the highly productive aggregation site, Hanifaru Bay (Figure 3), drawing large numbers of tourists to the region every year. During the SW monsoon lunar tides collide with the opposing monsoonal currents, producing a back-eddy leading into the body of the bay, funnelling plankton into these confined waters (Brooks & Stevens, 2010). With the plankton concentration come large aggregations of manta rays and whale sharks, with the highest recorded sightings exceeding 200 individuals on one day's feeding (Brooks & Stevens, 2010). Recognised as a vital aggregation site, Hanifaru Bay was designated a marine protected area (MPA) in 2009, but studies performed by the MMRP highlighted the need for stringent on-site management to protect the bay, the manta population, and tourists themselves. Brooks and Stevens (2010) documented the breaching of regulations during the 2010 manta season; rules were broken by tourist operators on 36 of the 121 survey days (Brooks & Stevens, 2010). The report also documented the impact on manta behaviour; individuals were observed stopping feeding in reaction to diver exhausts, as well as the restriction caused by divers immediately below and snorkelers above mantas, limiting movement and efficiency of feeding (Brooks, 2010). Following the report and proposed mitigation plans, Hanifaru Bay was closed to SCUBA diving in 2011 and entrance restrictions were applied. Today a maximum of five boats are allowed in the bay at once and tourist numbers are limited to 80 (Brooks & Stevens, 2010), with access to the bay split between resorts and safari boats using a timetable of alternative days.



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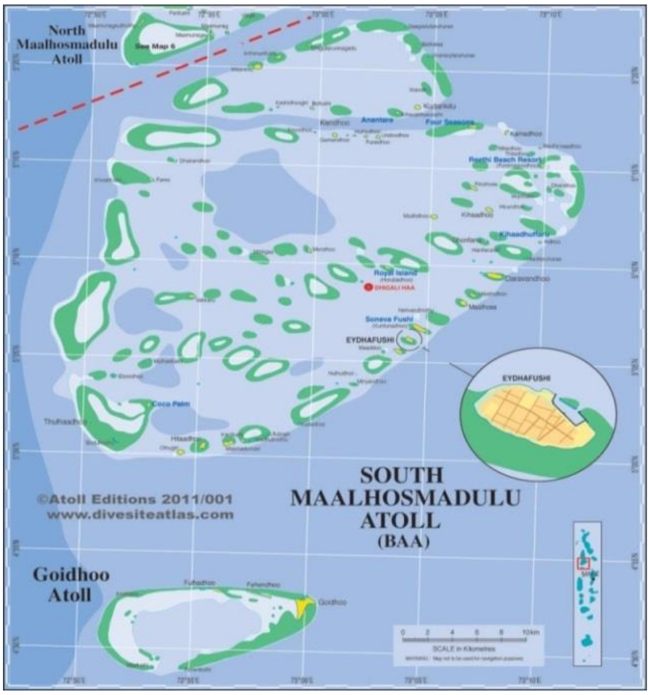
Conservation of the resident population is vital for the continued economic benefits enjoyed by local resorts. Anderson *et al*. (2011b) reported that in 2010 manta ecotourism generated US$ 8.1 million, with Hanifaru Bay generating an estimated US$ 243,262 in August alone (Brooks & Stevens, 2010). The more stringent regulations offer greater conservation and protection for the manta population, whilst enabling tourists to experience more intimate and safer interactions (pers. obs., 2013).

Social behaviour: One aspect of manta research which requires extensive study is the social behaviour of populations. Little is known about the community hierarchy and behaviour of mantas, making it difficult to fully understand and predict both their mating and feeding patterns, thus further complicating the conservation of the species. Studies on other marine animals provide insights into community behaviour. Dunbar and Shultz (2007) discuss the elevated occurrence of hierarchal governance and complex social bonds, shown through displays of symbiotic reliance within many other elasmobranch communities. With high brain to body mass ratio, elasmobranchs are capable of forming complex social bonds (Northcutt, 1977) and with the highest ratio of all ray species (Chen *et al*., 2011), mantas can be assumed to have similar social capabilities. With little interspecies interaction and limited studies, the social formalities of mantas are yet to be documented, but anecdotal observations commonly describe “friendlier” interactions between mature females and humans (Stevens, pers. comm. 2013). Whether this “friendliness” is affected by external variables including aggregation size, type of activity or physiological features of females is still unknown. One argument is that these “friendly” encounters occur in areas of high human traffic, such as Baa Atoll, thus creating a familiarity with humans, increasing the animal’s tolerance during interactions (Stevens, pers. comm. 2013). With the increasing popularity of manta ecotourism, it is vital that this differing behaviour within populations is considered in order to avoid isolating and limiting individuals.

Aim: This study will analyse the behaviour exhibited by reef manta rays during human encounters in order to establish if there is any significant difference in the reaction and perceived “friendliness” between males, females, juveniles, and mature adults.

Methods

Study sight: Baa Atoll (Figure 4), located north-west of Male, was named a UNESCO World Biosphere Reserve in 2011. Sites regularly visited by the Manta Trust research vessel were used for data collection; Hurai Faru, Hanifaru Bay, Reethi Beach and Veyofushi (Table 8). The topography of the sites varied, which was considered in analysis as a response variable. Hanifaru Bay is an enclosed shallow bay, while other study sites are more geographically exposed, shallow reef systems. The study focused on just one aspect of manta behaviour, feeding, by recording individuals actively seeking or involved in feeding activity. Data was collected whilst snorkelling, over an eight-week period during July and August.



In-water: Interactions between manta rays and humans were recorded using a Go Pro Hero 2 video

camera and aspects of behaviour were later analysed.

Atoll (Source: h oll-Map)

s were identified by examining the unique spot-pattern on the ventral surface (Figure 5); matching this pattern with photographs in the regional branchial database, which contains photographs of individuals, as well as data on the sex, age and condition of individuals (noticeable injuries, tail length).

Figure 5: Shows the unique spot-pattern on the ventral surface. (Love, L., 2013. *Manta alfredi*. [Photograph])

Mantas were sexed; males have visible claspers, which are absent in females (Figure 6). This was verified when videos were analysed.

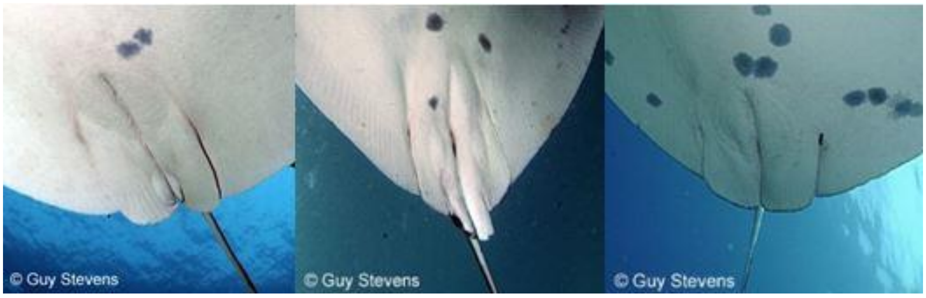


Figure 6: Shows the anatomical differences between juvenile males, mature males and females (Stevens, G., 2013. *Manta Birostris.* [Photograph])

Individuals were aged according to their size. Reef mantas mature at 10 – 15 years; females maturing on reaching 3 metres and males 2.7m (Stevens, pers. comm., 2013). This was gauged during observations but was verified by referring to the regional branchial database. Interactions where the sex could not be determined were excluded from analysis.

Using the video timer, the time mantas spent <5m and >5-20m from humans was recorded and the human behaviour was noted, i.e. passive interaction, diving under, or accidental obstruction. The reaction of the animal was logged using a pre-designed reaction scale. The scale of 1-4 measured the severity of the reaction (Table 1).

Table 1: Shows the scale of reaction used to grade manta reactions during interactions.

1	**No reaction**	**Individual continues with current behaviour**
2	**Slight reaction**	Minor direction change to move away from obstruction
3	**Direction change**	Distinct direction change to avoid obstruction
4	**Avoidance**	Complete alteration of behaviour to avoid obstruction

Manta rays display a large variety of behavioural traits and for the purpose of this study any reaction which was deemed to be positive, including circling and curiosity in humans was classified as a "no reaction".

Boat data: Interactions were analysed using the above criteria for encounters observed from the boat in situations where in-water recording would not be possible. This was appropriate for interactions in larger, non-sheltered areas where following the snorkeler and manta in order to document the interaction may alter the behaviour and response of the subjects. If the reaction could not be clearly viewed from the boat, snorkelers described animal behaviour. Data was collected on a dive slate. Information on sex and age were collected from snorkelers immediately following the interaction and ID images collected were later analysed to verify identification. Interactions where the sex could not be determined were excluded from analysis.

Data analysis: In-water and boat data were combined.

The mean response of reactions exhibited by males, females, juveniles, and matures were calculated by working out an overall average for each category. A Mann-Whitney U test was used to test for significance in the difference of reactions for mantas of different sexes and ages.

Additional response variables were analysed in direct relation to the sex of individuals, in order to establish whether external factors proved influential in the responses. This was then repeated for mantas of different ages (Table 2).

Table 2: Shows the response variables and description of categories.

Response variable	Categories
Activity type	• Group feeding (interactions involving more than one individual per 5m) • Individual activity
Number of Snorkelers (including videographer)	• 1 • 2-4 • 5+
Location	• Hanifaru Bay • Hurai Faru • Veyofushi • Reethi Beach

The mean response for manta reactions was calculated within each of the variable categories. In order to test for significance groupings were created, for example the response of juveniles involved in group feeding vs. juveniles during individual activity. A Mann-Whitney U test was used to test for significance.

All statistical tests were carried out and significant results were reported. A False Discovery Rate (FDR) correction was used to account for repetitive testing, resulting in a reduced alpha value, decreasing the risk of Type I errors.

Results

A total of 400 interactions were recorded over the study period; 277 filmed interactions and 123 out-of-water observations. The study population involved a substantially larger number of mature females (Table 3). The overall mean response for the study population resulted in a reaction of 1.64 (Table 4).

Table 3: Shows a breakdown of the study population.

	Juvenile	Mature
Male	76	74
Female	42	199

Table 4: Shows a review of the responses displayed by the study population and the overall mean response.

	Response			
	1	**2**	**3**	**4**
Male	69	43	28	11
Female	164	47	33	5
Juvenile	51	34	23	10
Mature	178	53	37	5
Mean Response				**1.64**
Standard deviation				**0.08**

Sex: The mean response for females was calculated at 1.49, with male interactions averaging 1.86 (Figure 7). Results from the Mann-Whitney U test proved statistically significant, with a p-value of 0.001 (Table 5), confirming that males exhibit a stronger response during human interactions.

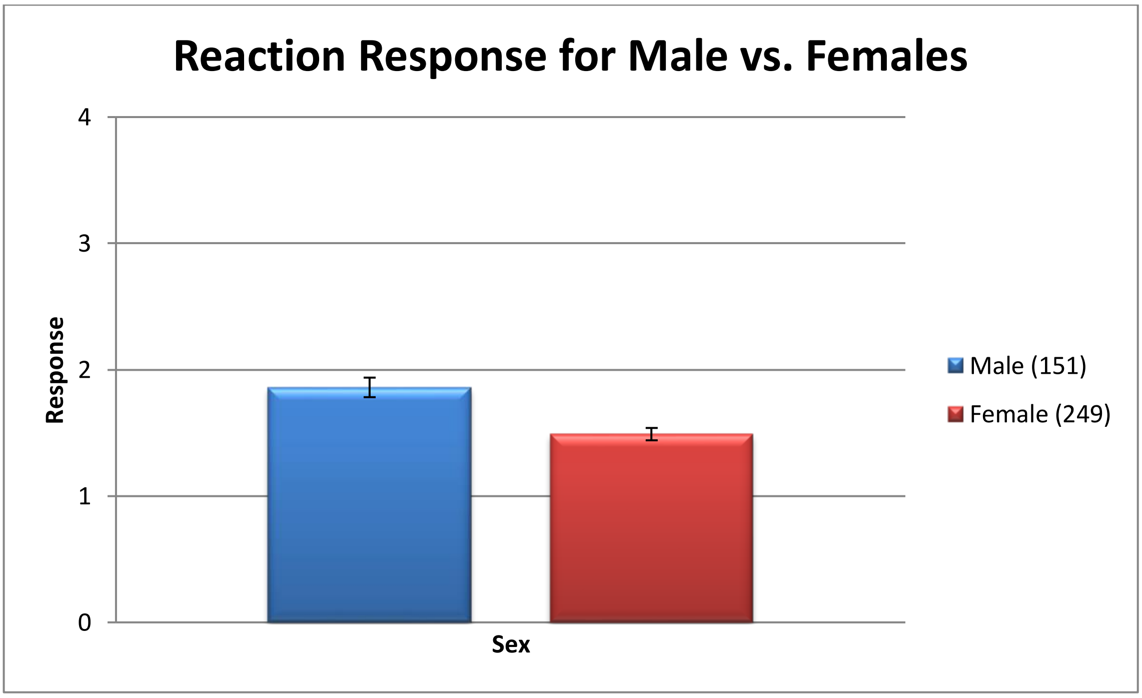


Figure 7: The reaction response (1: No response, 2: Slight reaction, 3: Direction change, 4: Avoidance) for male (n = 151) and female (n = 249) individuals.

Table 5: Shows the mean response and result from Mann-Whitney U test for male and female manta rays.

Sex	Response
Male (151)	1.86
Female (249)	1.49
n	400
p-value	0.001

Age: The mean response for juvenile interactions was calculated at 1.89, while mature individuals exhibited a mean response of 1.52 (Figure 8). This was proven statistically significant with a p-value less than 0.001 (Table 6) showing juveniles demonstrate a stronger reaction during human interactions.

Table 6: Shows the mean response and result from Mann-Whitney U test for juvenile and mature manta rays.

Age	Response
Juvenile (118)	1.89
Mature (273)	1.52
n	400
p-value	<0.001

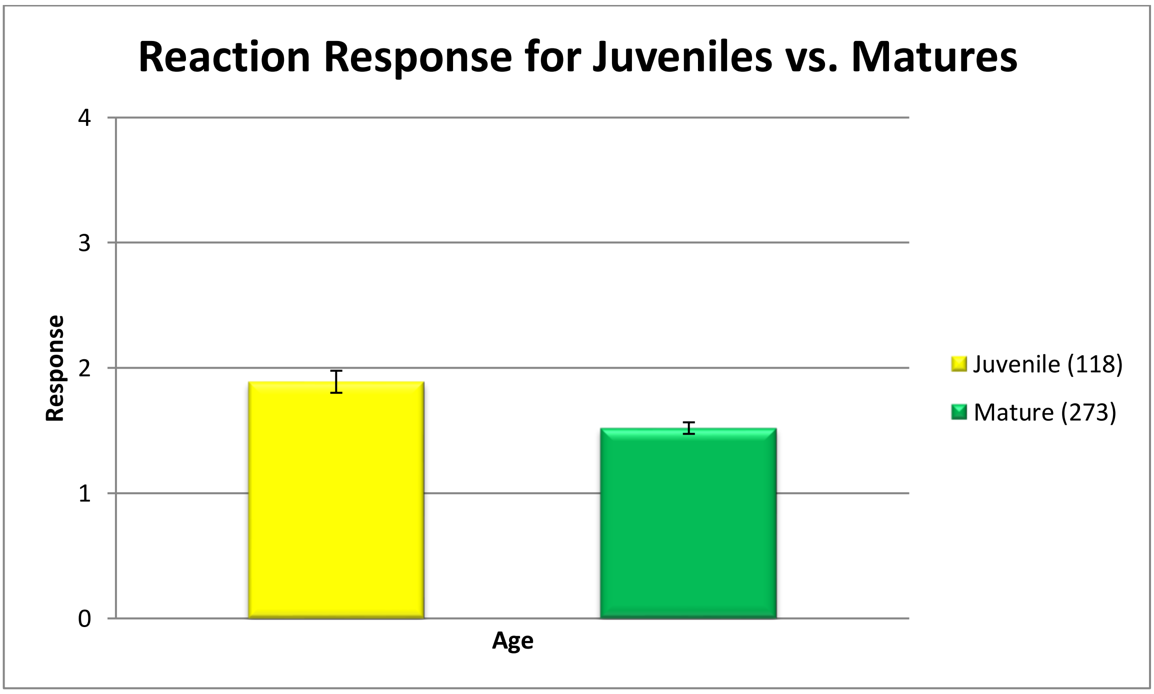


Figure 8: Shows the reaction response (1: No response, 2: Slight reaction, 3: Direction change, 4: Avoidance) for juvenile (n = 118) and mature (n = 273) individuals.

Sex vs. age: Juveniles showed the greatest reaction across both males and females, with a mean response of 2.01 and 1.72 respectively (Figure 9). Mature females showed a mean response of 1.44 and the difference between juvenile and mature females proved significant with a p-value of 0.002. Mature males displayed a mean response of 1.70 and juveniles 2.01, which proved non-significant with a p-value of 0.156 (Table 9).

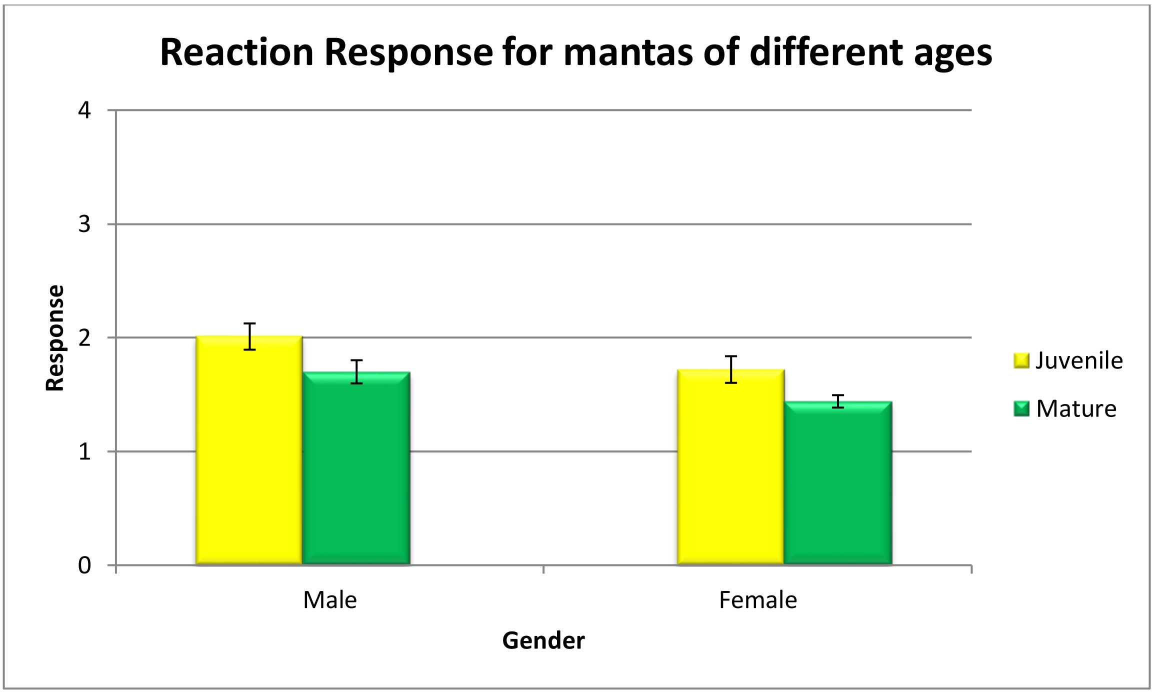


Figure 9: The reaction response (1: No response, 2: Slight reaction, 3: Direction change, 4: Avoidance) for the sexes. Males: juvenile (n = 76) and mature (n = 74). Females: juvenile (n = 42) and mature (n = 199).

Activity: The greatest reactions were recorded during individual activity. Males and juveniles exhibited the greatest response; males demonstrating mean responses of 2.12 and 1.59 during individual activity and group feeding respectively, with juveniles recording mean responses of 2.04 and 1.58 respectively (Figure 10). Statistical results show that the male response is significantly greater than female during individual activity, with a p-value of <0.001, and juvenile reactions proved significantly greater than matures, with a p-value of 0.006 (Table 9). The reaction of mantas involved in individual activity between Hanifaru Bay (least exposed reef) and Reethi Beach (most exposed reef) proved significant, with a p-value of <0.001. The response of mantas involved in group feeding was lower, with no significant results for the age, activity type and location categories.

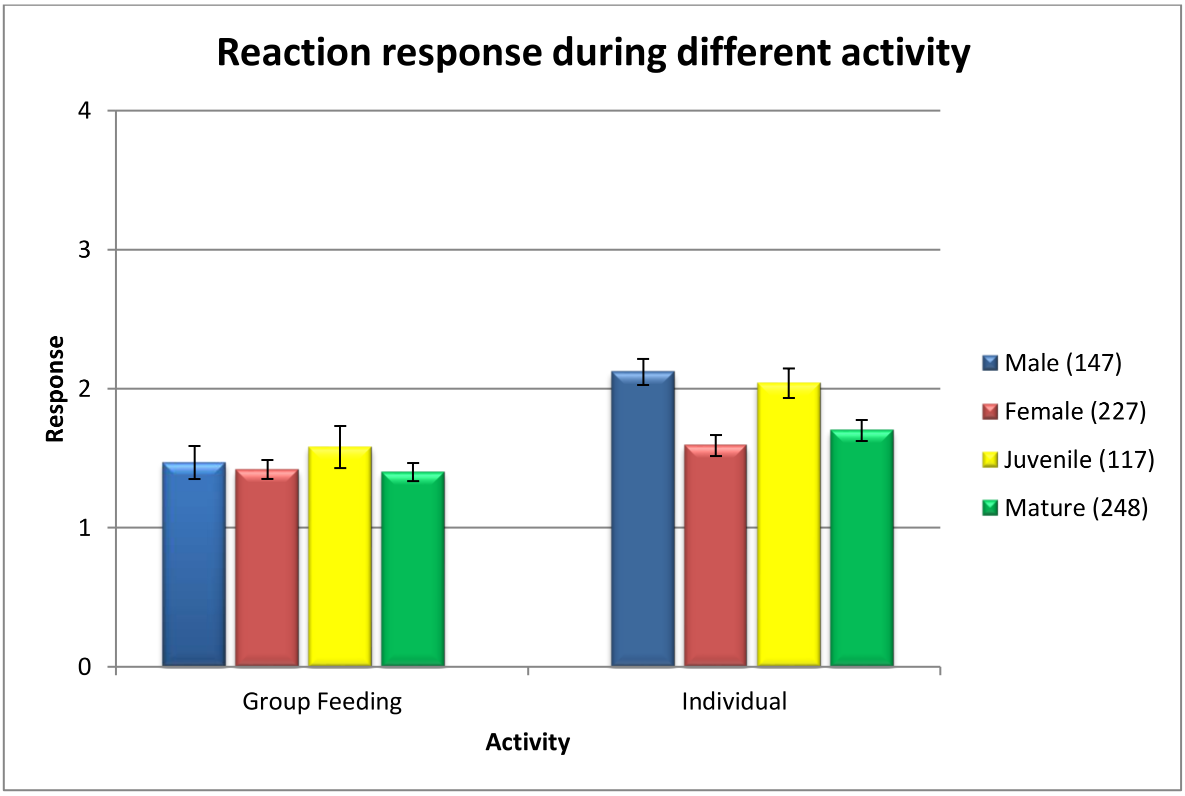


Figure 10: The reaction response (1: No response, 2: Slight reaction, 3: Direction change, 4: Avoidance) for types of activity: Group Feeding (GF), Individual Activity (IA). Male: (GF) n = 53, (IA) n = 94. Female: (GF) n = 115, (IA) n = 112. Juvenile: (GF) n = 35, (IA) n = 82. Mature: (GF) n = 127, (IA) n = 121.

Number of Snorkelers: There was little variation in the mean responses of mantas between the different group sizes. The strongest response was again exhibited by the male and juvenile individuals. Males recorded a mean response of 2.10 (1), 1.68 (2-4) and 2.02 (5+) and females 1.44 (1), 1.44 (2-4) and 1.62 (5+) (Figure 11). Juveniles recorded mean responses of 2.04 (1), 1.74 (2-4) and 2.03 (5+), in contrast to mature responses of 1.53 (1), 1.46 (2-4) and 1.64 (5+).

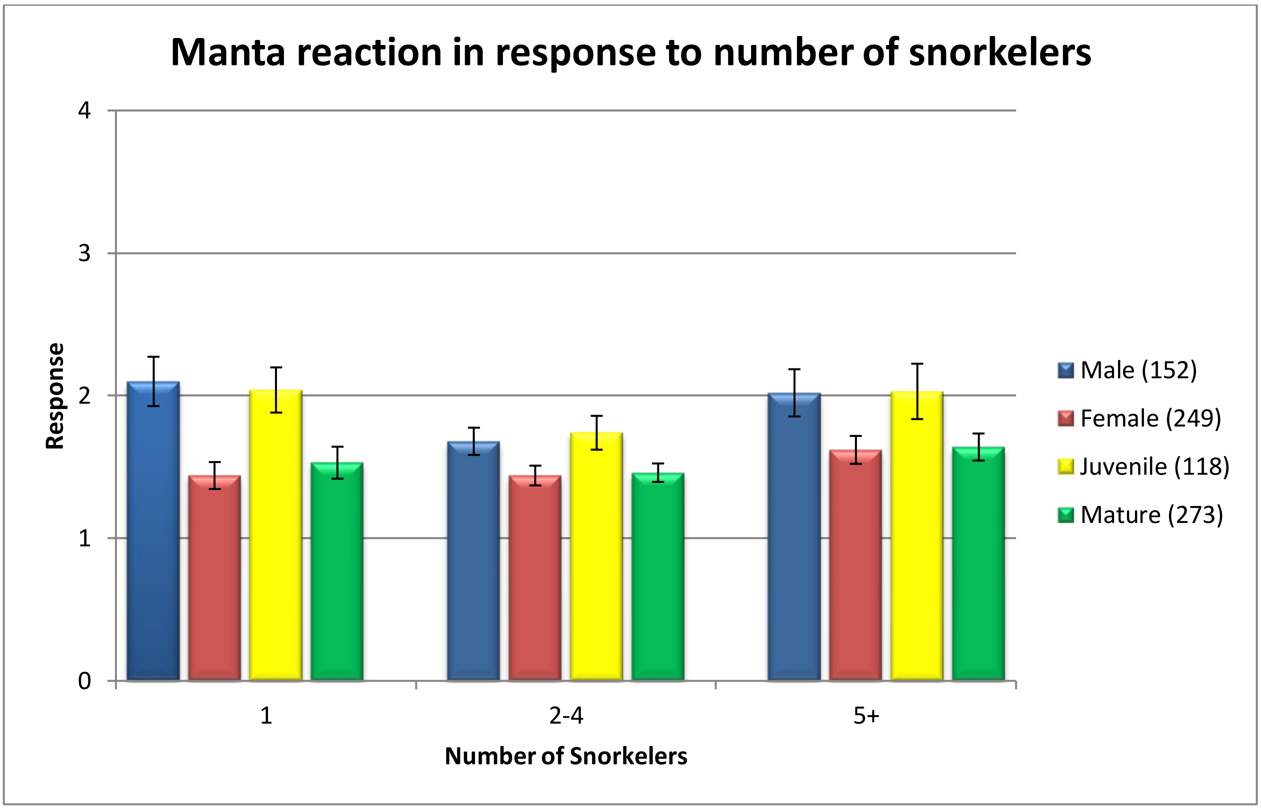


Figure 11: Displays the reaction response (1: No response, 2: Slight reaction, 3: Direction change, 4: Avoidance) for groups of snorkelers: 1, 2-4, 5+. Male: (1) n = 32, (2-4) n = 79, (5+) n = 41. Female: (1) n = 57, (2-4) n = 118, (5+) n = 74. Juvenile: (1) n = 29, (2-4) n = 55, (5+) n = 34. Mature (1) n = 57, (2-4) n =138, (5+) n = 78.

Location: Mantas displayed the least response during interactions at Hanifaru Bay in three of the four categories, with only juveniles exhibiting the least mean response of 1.50 at Hurai Faru (Figure 12). Results from the Mann-Whitney U test show that juveniles have significantly more of a reaction at Hanifaru Bay, compared to mature adults with a p-value of 0.00 (Table 9). There was no significant difference in responses between the sexes for interactions recorded at Hanifaru Bay and Reethi Beach, but looking individually at male and female reactions at these two sites, there was a significant difference in response levels, with both reacting more at Reethi Beach (Table 9).

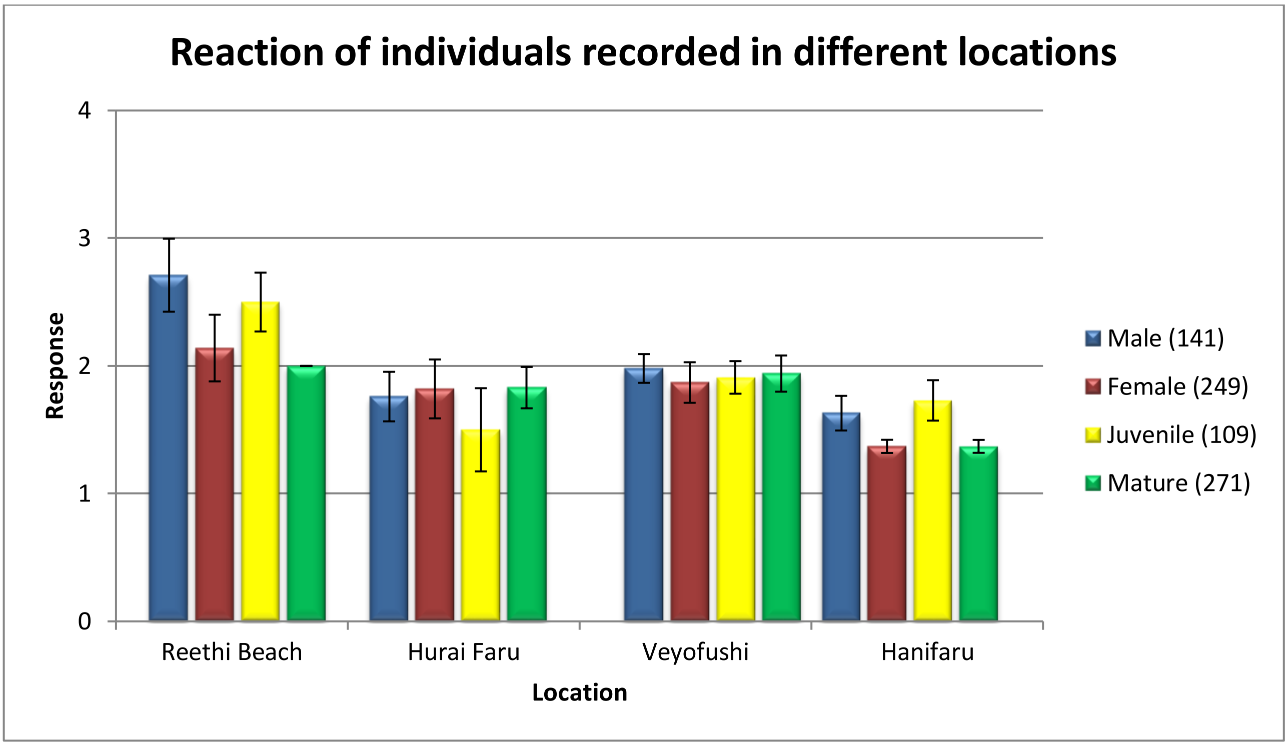


Figure 12: Displays the reaction response (1: No response, 2: Slight reaction, 3: Direction change, 4: Avoidance) for categories at different study sites: Reethi Beach (RB), Hurai Faru (HF), Veyofushi (VF), Hanifaru (HA). Male: (RB) n = 7, (HF) n = 25, (VF) n = 53, (HA) n = 56. Female: (RB) n = 7, (HF) n = 17, (VF) n = 31, (HA) n = 194. Juvenile: (RB) n = 12, (HF) n = 6, (VF) n = 46, (HA) n = 45. Mature: (RB) n = 2, (HF) n = 36, (VF) n = 35, (HA) n = 198.

The activity type produced differences in response at Hanifaru Bay, with individual activity resulting in a higher response 1.55 (Figure 13) compared to group activity, with a p-value of 0.045 (Table 7). Following endpoint adjustment this p-value was above the alpha value of 0.025 therefore proves non-significant yet represents variation between responses during these activities. Additional analysis of results recorded at Hanifaru Bay show that 80% of individuals were actively feeding, with 53% involved in group feeding and 37% in individual activity.

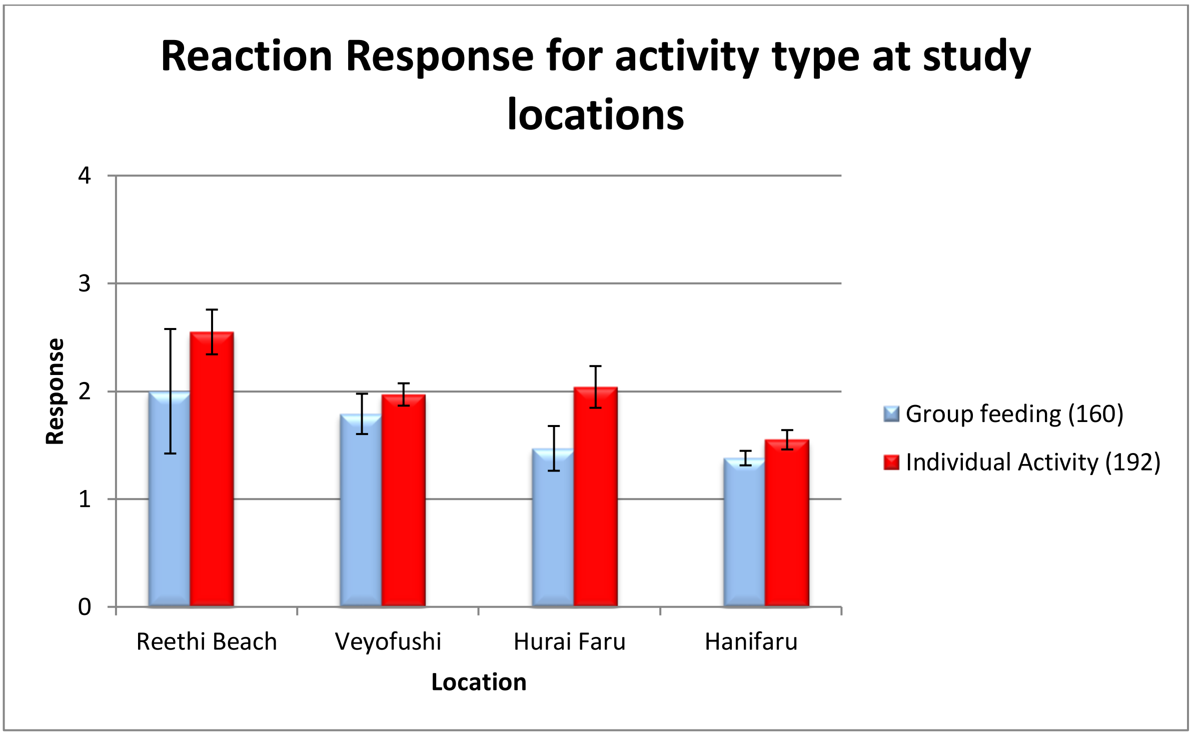


Figure 13: Displays the reaction response (1: No response, 2: Slight reaction, 3: Direction change, 4: Avoidance) for different activity, Group Feeding (GF) and Individual Activity (IA) at study sites. Reethi Beach: (GF) n = 3, (IA) n = 11, Veyofushi: (GF) n = 14, (IA) n = 70, Hurai Faru: (GF) n = 19, (IA) n = 23, Hanifaru: (GF) n = 124, (IA) n = 88.

Table 7: Shows the mean response for individuals during group feeding and individual activity on the four study sites.

Location	Group feeding	Individual activity
Reethi Beach	2.00	2.55
Veyofushi	1.79	1.97
Hurai Faru	1.47	2.04
Hanifaru	1.38	1.55

Table 8: Shows the four study sites, from the most geographically exposed, Reethi Beach to the least exposed, Hanifaru Bay, with the mean response of individuals recorded at the site. (Image provided by Manta Trust).

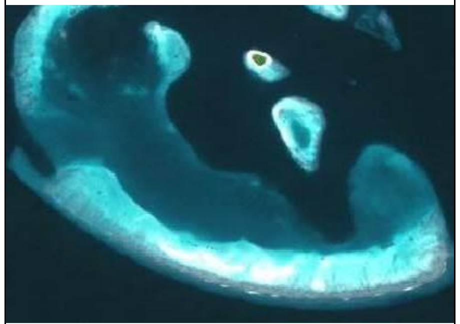
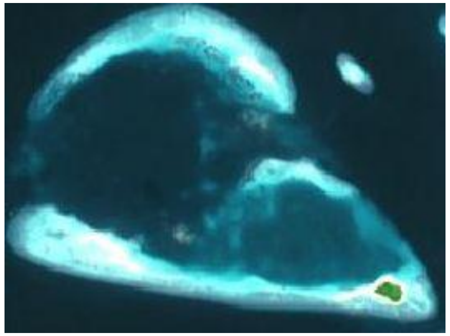
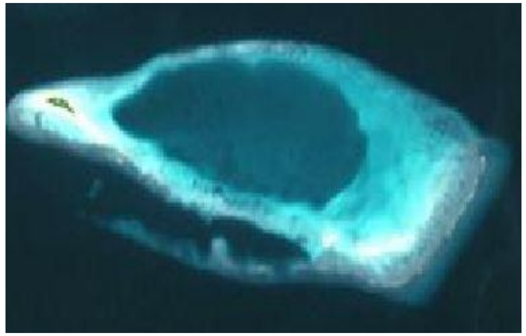
Reethi Beach	**Hurai Faru**	**Veyofushi**	**Hanifaru**
			
Located on the edge of Baa Atoll, a shallow reef extending along the border with deeper ocean.	Extended shallow reef system surrounding a protected, enclosed bay which is inaccessible by boat. Small hooked bay at the northern end of the reef.	Extended shallow reef located between Veyofushi Island and the adjacent sandbank.	Protected, enclosed, shallow bay. Colliding lunar and monsoonal currents funnel and entrap shoals of plankton and attracting large aggregations of planktivores.
2.43 (± 0.20 SE)	**1.79 (±0.15 SE)**	**1.94 (±0.09 SE)**	**1.43 (±0.05 SE)**

Table 9: Shows p-values for the different study categories resulting from Mann-Whitney U tests across the various categories (* denotes a significant result after FDR end-point adjustment giving an alpha value of 0.025).

	Female	**Male**	**Juvenile**	**Mature**	**Group Feeding**	**Individual**	**Hanifaru Bay**	**Reethi Beach**
Female **Male**			Z = -0.934 p = 0.350	Z = -3.249 p = 0.001*	Z = -0.182 p = 0.855	Z = -4.244 p = <0.001*	Z = -1.681 p = 0.93	Z = -1.330 p = 0.184
Juvenile **Mature**	Z = -3.035 p = 0.002*	Z = -1.419 p = 0.156			Z = -1.366 p = 0.172	Z = -2.753 p = 0.006*	Z = -2.838 p = 0.005*	Z = -1.000 p = 0.317
Group Feeding **Individual**	Z = -1.625 p = 0.104	Z = -4.538 p = <0.001*	Z = -2.563 p = 0.010*	Z = -3.418 p = 0.001*			Z = -2.003 p = 0.045	Z = -.0938 p = 0.348
Hanifaru Bay **Reethi Beach**	Z = -3.135 p = 0.002*	Z = -2.919 p = 0.004*	Z = -2.321 p = 0.020*	Z = -2.017 p = 0.044	Z = -1.541 p = 0.123	Z = -3.727 p = <0.001*		

Discussion

Close analysis of the data reveals interesting behavioural contrasts between the different age and sex classes, supporting the anecdotal hypothesis that the level of response exhibited by individuals varies due to numerous factors.

Gender: Results for the reactions between the different sexes reveal a significant variance in the severity of responses, with females consistently recording a lower degree of reaction in each category. Firstly, the type of activity showed a strong influence on behaviour; data shows a non-significant variation in reactions between males (1.47) and females (1.42) during group feeding, which can be explained by the sheer nature of the activity. Aggregation sites such as Hanifaru Bay attract large numbers of mantas consumed by the task of feeding, therefore are less likely to react to external factors such as humans. Manta rays form similar aggregations as other batoid species; Silliman and Gruber (1999) document large aggregations of spotted eagle rays (*Aetobatus narinari*), where between five and 50 individuals congregate and interact in numerous patterns often associated with feeding. During feeding events, manta rays use each other to optimise food consumption by either forming long feeding chains or move in pairs, with the smaller males swimming directly above females (Manta Trust, 2013).

A significant variation in mean responses between males and females is demonstrated during individual activity, with males again demonstrating a higher degree of reaction. Elevated responses among males could be attributed to factors related to sexual dimorphism; Deakos (2010) found that on average females were significantly larger than males, with the largest female of the study sample being 18% larger than the biggest male. Sims (2003, 2005) hypothesised that the differences in the behavioural traits in certain elasmobranchs of different sexes could be due to the reproductive needs and success of individuals. Hight and Lowe (2007) go on to suggest that females prioritise their time to find suitable gestation and birthing refuges, while males are more driven to find a mate. Such differing priorities could influence behavioural traits.

The influence of location shows that environmental conditions contribute to disturbance levels during interactions. The lowest response was recorded within Hanifaru Bay for each class except juveniles, which can again be related to the nature of the activity; feeding. With 80% of interactions recorded at Hanifaru involving active feeding behaviour and 53% of these in aggregations such an outcome was foreseeable.

Females exhibit little variation in the degree of response as the number of snorkelers increases, whereas male's record elevated reactions throughout snorkeler categories, once again logging the highest response. Such results suggest that males exhibit the least “friendly” behaviour during interactions and suggest they find such encounters more stressful.

Age: Juveniles consistently recorded a higher degree of disturbance during interactions throughout the study period. Analysis of data reveals the significant impact which activity has on the behaviour of juveniles, who recorded an average response of 2.04 when performing individual activity in comparison to a response of 1.58 during group feeding. The juvenile stage of development leaves elasmobranchs vulnerable to predation, therefore many species form aggregations to increase the chance of survival (Morrissey & Gruber, 1993; Economakis & Lobel, 1998). Safety in numbers could explain the reduced reaction displayed by juveniles during group feeding, as discussed by Heupel and Simpfendorfer (2005) who documented aggregation of sharks. The study concluded that such behaviour increases protection but also improves the efficiency of feeding activity (Heupel & Simpfendorfer, 2005). This hypothesis can be applied to juvenile mantas, which periodically aggregate on protected, inshore reefs to feed. The lower mean response of juveniles at Hanifaru Bay, recorded at an average of 1.73 demonstrates a reduced level of disturbance. The significant difference in juvenile reaction between Hanifaru Bay and Reethi Beach could be related to the topography and nature of the site: protected and commonly visited by large aggregations, thus representing a less vulnerable location.

The number of snorkelers present appears to make the least impact on the reaction of juveniles, which consistently record elevated scores. These results mirror those logged for male individuals, suggesting that juveniles experience higher levels of stress during interactions therefore altering their behaviour. In order to definitively explain this difference, further studies are needed.

Location and activity type: The location of interaction appears to highly impact the response exhibited during both types of behaviour. Reethi Beach logged the highest mean response for both group feeding (2.00) and individual activity (2.55). This area is the most exposed; located on the edge of Baa Atoll it has little protection and lacks the topography to attract and hold large plankton blooms. This means that of all the study sites, it is the least likely to attract large feeding aggregations. Hanifaru Bay however is characterised by large feeding aggregations, therefore individuals recorded here were more commonly involved in group feeding, therefore less prone to disturbance. There was shown to be no significant difference in the response of animals during group feeding between these two sites, supporting previous findings of a lower response during group activity. Another explanation could be the potential conditioning of individuals in specific locations. Due to the nature of the bay, Hanifaru attracts large groups of snorkelers. Although this factor appears to have little impact on the reaction of mantas, most interactions involving five or more snorkelers were recorded at Hanifaru Bay. It could be possible that individuals experience lower stress levels within this protected, aggregation site which is commonly revisited by members of the population. As multiple sightings of individuals have been recorded within the area, it is likely that animals are returning to the site to both clean and feed (Homma *et al.* 1997). This should be a consideration of ecotourism operators, as individuals are more vulnerable to disturbance on the more exposed reefs, therefore the possible reduction in the size of snorkel groups on these reefs could impose less disturbance on animals.

The significant variations in response exhibited by mantas in this study suggest that behavioural traits are highly correlated with sexual dimorphism and age. With the growing marine ecotourism industry such behaviour demonstrates the impact which human encounters are having on populations.

Ecotourism and management: Worldwide interest in Hanifaru Bay initiated a surge of visitors, with manta ecotourism generating US$8.1 million in 2010 and Hanifaru Bay US$603,284 from July to November the same year (Brooks & Stevens, 2010). With global interest in manta rays being sustained and recent conservation advances following the CITES convention (CITES, 2013), the region is set to maintain high levels of manta ecotourism. Observations made in this study indicate the varying level of negative responses displayed across the resident population. These observations should be noted and considered by ecotourism operators, who in turn need to alter procedures suitably in order to mitigate causing elevated levels of disturbance of the manta's natural behaviour.

The first step to effective management of a resident population is through educational programs for both the tourist and local community. By educating people on the ecological traits of mantas, they have a clearer grasp of what impact their behaviour may have on these animals, whilst providing people with a better understanding of the threats which affect the species (O'Malley *et al.*, 2013). Anderson *et al.* (2011) notably identified a lack of education in manta ecotourism in the Maldives, therefore highlighting the need for a structured program to be introduced across the archipelago. Programs such as the MMRP provide informative briefings prior to interactions as well as offering tourists the opportunity to learn more about mantas during weekly presentations and excursions on the research vessel (pers. obs., 2013). More of these programs would increase the level of awareness on both a local and international scale, therefore increasing support for conservation measures (O'Malley *et al.* 2013).

Ultimately studies of the social behaviour of mantas should be used to create a comprehensive code of conduct for in-water interactions. With increasing marine ecotourism, it is vital that detrimental behaviour is limited and controlled by tour operators; pre-encounter informative briefings on safe and appropriate behaviour, along with close in-water monitoring would contribute to this. Quiros (2007) qualifies the benefits of codes of conduct, which highlight the human behaviour which most impacts animals, thus allowing operators to limit such behaviour during interactions. Without 100 percent compliance detrimental impacts cannot be fully mitigated (Quiros, 2007), therefore educational programs in conjuncture with codes of conduct are critical.

Limitations: Observations for this study were collected over an eight-week period but in order to produce conclusive results a long-term study would be effective. Data was collected during the months of July and August, which are considered peak months for manta encounters in the Maldives. In order to include data on mating behaviour research would need to be carried out throughout the months of October, November, March, and April, during the transition between monsoonal seasons (Manta Trust, 2013). Long-term studies would also allow examination of the behaviour of individual's, aiming to create a clearer image of the social structure of populations.

This study solely considered negative responses during interactions but from anecdotal reports and personal experience, manta rays commonly exhibit positive reactions, often displayed through curiosity towards humans. This behaviour constitutes as a clear reaction therefore demonstrating that human presence is having an impact on their natural behaviour. For a more conclusive understanding of manta behaviour future studies should examine these positive reactions in conjuncture with negative responses documented in this study, making a clear comparison of both the frequency and severity of reactions.

As this study was carried out on a wild population, one must consider the lack of control over the number and regularity of sightings, which impacts the quantity of interactions considered.

Future studies: In order to reduce the stress impacted on individuals during human interactions further studies should concentrate on a wider range of manta behaviour. This study initially recorded limited interactions with rays cleaning and no encounters were recorded on SCUBA, therefore these behaviours were excluded from analysis. As the cleaning ritual is critical for the health of individuals (Losey, 1972), recording responses during interactions would clarify the level of disturbance experienced. As many cleaning stations are located on deeper reefs (Kitchen-Wheeler, 2013), it is more common to encounter cleaning individuals whilst on SCUBA. The popularity of SCUBA in the Maldives and other regions populated by manta rays is high (O'Malley *et al.*, 2013). It often has a negative impact on the reef ecosystem (Barker & Roberts, 2004), therefore the impact of SCUBA could be analysed in conjuncture to the response of cleaning individuals. Another vital activity omitted from this study is mating behaviour. Analysing encounters with mating trains, during which a single female is tracked by a train of males (Deakos *et al.*, 2011) would document different behavioural traits exhibited by the sexes during mating activity, a subject which remains unclear (Marshall & Bennett, 2010).

Throughout the study the behaviour of humans was noted; further studies could consider what impact this has on the level of response. Future studies should examine which response variable has the most impact on the reaction of individuals; this analysis was omitted from the study due to the small sample sizes.

Conclusion

This study shows that there are significant differences in the behaviour and responses of manta rays between males, females, juveniles, and mature adults, supporting anecdotal observations of positive reactions exhibited by mature females. It offers a valuable insight into manta behaviour; a subject which has been little documented in previous studies and which should be considered at this vital time for the species. As manta ecotourism grows in global popularity and anthropogenic threats remain present, it is vital that these populations are protected from further detrimental impact which excessive human presence may inflict. This study provides a platform for future research to establish the influence of factors such as sexual dimorphism on manta behaviour in order to further the conservation of this charismatic species.

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Bibliography

Alava, M. N. R., Dolumbaló, E. R. Z., Yaptinchay, A. A., & Trono, R. B. (2002, July). Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997* (pp. 132-148). By: IUCN, Gland, Switzerland and Cambridge, UK.

Anderson, R. C., Adam, M. S., & Goes, J. I. (2011a). From monsoons to mantas: seasonal distribution of Manta alfredi in the Maldives. *Fisheries Oceanography*, *20*(2), 104-113.

Anderson, R. C., Adam, M. S., Kitchen-Wheeler, A. M., & Stevens, G. (2011b). Extent and economic value of manta ray watching in Maldives. *Tourism in Marine Environments*, *7*(1), 15-27.

Barcott, B. (2009). Feeding Frenzy. *National Geographic*, July 2009. [Online].
Available at: http://ngm.nationalgeographic.com/2009/07/manta-rays/barcott-text
Accessed 28th August 2013.

Barker, N. H., & Roberts, C. M. (2004). Scuba diver behaviour and the management of diving impacts on coral reefs.

Bigelow, H.B. & Schroeder, W.C. (1953) Sawfish, guitarfish, skates, and rays. *In:* Tee-Van et al. (Eds), *Fishes of the Western North Atlantic, Part 2.* Sears Foundation for Marine Research, Yale University, New Haven, pp. 508–514.

Brooks. K. (2010) *Investigating tourism at Hanifaru Bay marine protected area, Maldives.* MSc Thesis for University of York. Unpublished data.

Brooks, K. & Stevens, G. (2010) *Developing Tourism at Hanifaru Bay Marine Protected Area (MPA). A short report for the Ministry of Environment, Maldives; EPA and AEC Project.* Manta Trust literature.

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

Chen, Z., Um, T. I., & Bart-Smith, H. (2011, March). Ionic polymer-metal composite enabled robotic manta ray. In *SPIE Smart Structures and Materials+ Non-destructive Evaluation and Health Monitoring* (pp. 797637-797637). International Society for Optics and Photonics.

Convention on International Trade in Endangered Species of Wild Fauna and Fauna (CITES) (2013) [Online].
Available at: http://www.cites.org/eng/app/appendices.php Accessed 5th September 2013.

Convention of Migratory Species of Wild Animals (CMS) (2011) [Online]
Available at:
http://www.cms.int/bodies/COP/cop10/appendices_proposals/1_5_manta_birostris_e.pdf
Accessed 8th September 2013.

Clua, E., Buray, N., Legendre, P., Mourier, J., & Planes, S. (2010). Behavioural response of sicklefin lemon sharks Negaprion acutidens to underwater feeding for ecotourism purposes. *Marine Ecology Progress Series*, *414*, 257-266.

Compagno, L.J.V., Last, P.R., 1999. Mobulidae. In: Carpenter, K.E., Niem, V.H. (Eds.), FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central

Pacific. Vol. 3. Batoid Fishes, Chimaeras and Bony Fishes. Part 1 (Elopidae to Linophyrnidae). FAO, Rome,
pp. 1524–1529.

Deakos, M. H. (2010). Paired-laser photogrammetry as a simple and accurate system for measuring the body size of free-ranging manta rays Manta alfredi. *Aquatic Biology*, *10*(1), 1-10.

Deakos, M. H., Baker, J. D., & Bejder, L. (2011). Characteristics of a manta ray Manta alfredi population off Maui, Hawaii, and implications for management. *Marine Ecology Progress Series*, *420*, 245-260.
Dewar, H. (2002). Preliminary report: Manta harvest in Lamakera. *Report from the Pfleger Institute of Environmental Research and the Nature Conservancy*, 3.

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*(2), 121-133.

Dunbar, R. I., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*(5843), 1344-1347.

Economakis, A. E., & Lobel, P. S. (1998). Aggregation behavior of the grey reef shark, Carcharhinus amblyrhynchos, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes*, *51*(2), 129-139.

Emerton, L., Baig, S., & Saleem, M. (2009). Valuing Biodiversity The economic case for biodiversity conservation in the Maldives. *AEC Project, Ministry of Housing, Transport and Environment, Maldives*.

Ford, E. (1921). A contribution to our knowledge of the life histories of the dogfishes landed at Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, *12*(3), 468-505.

Frohoff, T. G., & Packard, J. M. (1995). Human interactions with free-ranging and captive bottlenose dolphins. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, *8*(1), 44-53.

Hammitt, W. E., & Cole, D. N. (1998). *Wildland recreation: ecology and management*. John Wiley & Sons.

Heinrichs. S., O'Malley. M., Medd. H., Hilton. P. (2011). *Manta Ray of Hope. 2011 Report. The Global Threat to Manta and Mobula rays*. [Online].
Available at:
https://www.sharksavers.org/files/9013/3184/4869/The_Global_Threat_to_Manta_and_Mobule_Rays.pdf [Accessed 10th September 2013.

Heupel, M. R., & Simpfendorfer, C. A. (2005). Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology*, *147*(5), 1239-1249.

Hight, B. V., & Lowe, C. G. (2007). Elevated body temperatures of adult female leopard sharks,< i> Triakis semifasciata</i>, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? *Journal of Experimental Marine Biology and Ecology*, *352*(1), 114-128.

Hoenig, J. M., & Gruber, S. H. (1990). Life-history patterns in the elasmobranchs: implications for fisheries management. *NOAA Technical Report NMFS*, *90*(1), 16.

Holden, M. J. (1974). Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *Sea Fisheries Research. John Wiley & Sons, New York.[Links]*.

Homma, K., Maruyama, T., Itoh, T., Ishihara, H., & Uchida, S. (1997, November). Biology of the manta ray, Manta birostris Walbaum, in the Indo-Pacific. In *Indo-Pacific fish biology: Proc 5th Int Conf Indo-Pacific Fishes, Noumea* (pp. 209-216).

Hulbert, L. B., Aires-da-Silva, A. M., Gallucci, V. F., & Rice, J. S. (2005). Seasonal foraging movements and migratory patterns of female Lamna ditropis tagged in Prince William Sound, Alaska. *Journal of Fish Biology*, *67*(2), 490-509.

IUCN (2013). The IUCN Red List of Threatened Species. [Online].
Available at: http://www.iucnredlist.org/details/198921/0 [Accessed 5th September 2013]

Jacoby, D. M., Croft, D. P., & Sims, D. W. (2012). Social behaviour in sharks and rays: analysis, patterns, and implications for conservation. *Fish and Fisheries*, *13*(4), 399-417.

Kitchen-Wheeler, A. M. (2010). Visual identification of individual manta ray (Manta alfredi) in the Maldives Islands, Western Indian Ocean. *Marine Biology Research*, *6* (4), 351-363.

Last, P. R., & Stevens, J. D. (2009). Sharks and rays of Australia.

Losey Jr, G. S. (1972). The ecological importance of cleaning symbiosis. *Copeia*, 820-833.

Love, L. (2013) [Photograph]

Manta Trust (2013). Gill Plate Trade. [Online].
Available at: http://www.mantatrust.org/ [Accessed 28th August 2013].

Marshall, A. D., Compagno, L. J., & Bennett, M. B. (2009). Redescription of the genus Manta with resurrection of Manta alfredi (Krefft, 1868)(Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa*, *2301*, 1-28.

Marshall, A. D., & Bennett, M. B. (2010). Reproductive ecology of the reef manta ray Manta alfredi in southern Mozambique. *Journal of Fish Biology*,*77*(1), 169-190.

Martin, R. A. (2007). A review of behavioural ecology of whale sharks (< i> Rhincodon typus</i>). *Fisheries Research*, *84*(1), 10-16.

Morrissey, J. F., & Gruber, S. H. (1993). Habitat selection by juvenile lemon sharks, Negaprion brevirostris. *Environmental Biology of Fishes*, *38*(4), 311-319.

Müllner, A., Eduard Linsenmair, K., & Wikelski, M. (2004). Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (< i> Opisthocomus hoazin</i>). *Biological Conservation*, *118*(4), 549-558.

Munn, C. A. (1992). Macaw biology and ecotourism, or when a bird in the bush is worth two in the hand. *New world parrots in crisis: solutions from conservation biology*, 47-72.

Northcutt, R. G. (1977). Elasmobranch central nervous system organization and its possible evolutionary significance. *American Zoologist*, *17*(2), 411-429.

O'Malley, M. P., Lee-Brooks, K., & Medd, H. B. (2013). The Global Economic Impact of Manta Ray Watching Tourism. *PloS one*, *8*(5), e65051.

O'Shea, O. R., Kingsford, M. J., & Seymour, J. (2010). Tide-related periodicity of manta rays and sharks to cleaning stations on a coral reef. *Marine and Freshwater Research*, *61*(1), 65-73.

Pravin, P. (2000). Whale shark in the Indian coast-need for conservation.*Current science*, *79*(3), 310-315.

Quiros, A. L. (2007). Tourist compliance to a Code of Conduct and the resulting effects on whale shark (< i> Rhincodon typus</i>) behavior in Donsol, Philippines. *Fisheries Research*, *84*(1), 102-108.

Samuels, A., & Bejder, L. (1998). A pilot study of habitual interactions between humans and wild bottlenose dolphins near Panama City Beach, Florida. A Report to the Marine Mammal Commission, Bethesda, Maryland, USA (unpublished). 13pp.

Semeniuk, C. A., & Dill, L. M. (2006). Anti-Predator Benefits of Mixed-Species Groups of Cowtail Stingrays (Pastinachus sephen) and Whiprays (Himantura uarnak) at Rest. *Ethology*, *112*(1), 33-43.

Silliman, W., & Gruber, S. H. (1999). Behavioral biology of the spotted eagle ray, Aetobatus narinari. *Bahamas Journal of Science*, *7*(1), 13-20.

Sims, D. W. (2003). Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. *Journal of Fish Biology*, *63*(s1), 53-73.

Sims, D. W. (2005). Differences in habitat selection and reproductive strategies of male and female sharks. *Sexual segregation in vertebrates: ecology of the two sexes*, 127-147.

Sorice, M. G., Shafer, C. S., & Scott, D. (2003). Managing endangered species within the use/preservation paradox: understanding and defining harassment of the West Indian manatee (Trichechus manatus). *Coastal Management*, *31*(4), 319-338.

Stevens, G. Founder of Manta Trust. (Personal communication, 1st August 2013).

Stevens, G. (2013) [Photograph – Online]
Available at: http://www.mantatrust.org/about-mantas/sexual-selection/ [Accessed 9th September 2013].

White, W. T., Giles, J., & Potter, I. C. (2006). Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. *Fisheries Research*, *82*(1), 65-73.

Würsig, B. (1978). Occurrence and group organization of Atlantic bottlenose porpoises (Tursiops truncatus) in an Argentine bay. *Biological Bulletin*, *154*(2), 348-359.

Yano, K., Sato, F., & Takahashi, T. (1999). Observations of mating behavior of the manta ray, Manta birostris, at the Ogasawara Islands, Japan. *Ichthyological Research*, *46*(3), 289-296.