

The reproductive ecology of resident manta rays (*Manta alfredi*) off Maui, Hawaii, with an emphasis on body size

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Received: 22 December 2010 / Accepted: 27 October 2011
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Abstract In resident manta rays (*Manta alfredi*) off Maui, sexual maturity appears delayed until growth exceeds 90% of maximum size, an indicator that large body size provides a reproductive advantage at the expense of a shorter reproductive time period. In this study, 286 surveys were conducted between 2005 and 2010 using photo-identification and photogrammetry to study the reproductive ecology of a resident population of manta rays off Maui, Hawaii, and investigate the reproductive benefits of large body size in each sex. Although reproductive activities occurred year-round, mating trains and late-term pregnant females were significantly more likely to be observed during the winter months. Some females were pursued by males during both winter and summer of the same year, suggesting multiple ovulations may be possible in a single year. Males likely detect a female's reproductive state by positioning directly behind her, or passing through her bodily excretions. The mean pregnancy rate was estimated at 0.56 pregnancies/adult female/year with

larger females pregnant more often, and more likely in consecutive years. The operational sex ratio was heavily skewed with 2.68 adult males per reproductively available female. Although males appear to compete with one another for females within a mating train, no direct physical competition was ever observed between males. Evidence of highly dynamic mating trains lasting more than one day suggests endurance rivalry may be the primary mating strategy among males, during which larger males may benefit from greater energy reserves. The study area appears to be an important staging area for mating individuals in this population.

Keywords Manta ray · *Manta alfredi* · Reproductive ecology · Body size · Mating strategies · Operational sex ratio

Introduction

In many species, larger body size provides a reproductive advantage for males and females (Ralls and Mesnick 2002). For females, larger size generally equates to greater physiological resources for reproduction, and often results in the production of larger, healthier, or more frequent offspring. For males that compete physically with one another for access to mates, larger males generally win out over smaller males.

The proportion of maximum growth reached at sexual maturity can be an indicator of the importance of large body size for reproductive success and can

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also be an indicator of the availability and predictability of food resources (Shine 1988). This study examines the reproductive ecology of a resident manta ray (*Manta alfredi*) population off Maui, Hawaii, and the relationship of body size and reproductive activities.

Two species of manta ray are currently recognized (Marshall et al. 2009): *Manta birostris*, herein referred to as oceanic manta rays, and *Manta alfredi*, herein referred to as resident manta rays (Deakos 2010). The oceanic manta ray is the larger of the two species with a maximum disc width (DW; measured from wing tip to wing tip) reported at 6.7 m (Bigelow and Schroeder 1953) and is widely distributed, occurring in tropical, sub-tropical and temperate waters around the globe. Members of this species spend the majority of their time in deep waters but are commonly sighted along productive coastlines with regular upwellings, oceanic island groups, and near offshore pinnacles, seamounts, and submarine ridge systems (Compagno and Last 1999; Rubin 2002; Marshall et al. 2009). Resident manta rays average smaller than oceanics, with a maximum recorded DW of 5.5 m (Marshall et al. 2009). This species is found in tropical and subtropical regions of the Pacific, Atlantic, and Indian oceans within 30° of latitude to the north and south of the equator where they occur primarily along shallow coastal areas that are often associated with coral reef habitats within a few kilometers of land (Homma et al. 1999; Marshall 2009).

Most female resident manta rays become pregnant on average every 2–3 years, though some are capable of becoming pregnant in consecutive years (Homma et al. 1999; Marshall and Bennett 2010). Pupping has never been reported in free-ranging manta rays and sites of parturition are unknown. The only documented pupping event occurred at the Okinawa Churaumi Aquarium in Japan, where a resident female produced a single, precocial pup, following what was determined to be a twelve-month gestation period (Uchida et al. 2008). Parturition was immediate and the mother was seen mating again within hours. Three additional births have been reported, with the last pup measuring 1.8 m DW and weighing 66 kg (Okinawa Churaumi 2010). The smallest free-swimming manta ray of either species has been reported to be between 1 and 1.5 m DW (Bigelow and Schroeder 1953; Homma et al. 1999; Marshall et al. 2009). Parental care is absent beyond gestation and no information exists about pup development or survival.

Pre-copulatory behavior of manta rays involves multiple escorting males pursuing a single, fast-swimming female in what is known as a “mating train” (Yano et al. 1999). Rapid swimming is interrupted by periods of quick turns and somersaults initiated by the female and often mimicked by the pursuing males (Marshall and Bennett 2010). When copulation occurs, a male directly behind the female moves over her while biting her pectoral fin, almost always on the left side, and twists his body so that his ventral side is against hers and a clasper is inserted into her cloaca for insemination. Although mating trains are commonly observed, reports of actual copulation in free-ranging manta rays are rare (Yano et al. 1999; Marshall and Bennett 2010).

Resident manta rays are sexually dimorphic with females as much as 16% larger than males (Deakos 2010; Marshall and Bennett 2010). This size difference make it unlikely that males are able to force an unwilling female to mate. Also given that females carry the majority of parental investment during the 12 month gestation period, they are likely the choosier sex (Trivers 1972) and should select males that are the most fit (Fisher 1930). Mating trains are likely a way for reproductively available females to evaluate potential mates. By moving rapidly through an area while advertising her willingness to mate, a female may recruit male escorts in an attempt to find the best suitor. These “female recruitment runs” have been observed in other species. For example, female bison (*Bison bison*) seek to replace a lower-ranking, tending male by running away from him and towards higher-ranking males, usually resulting in her tending male being replaced by one of higher rank (Wolff 1998). Humpback whales (*Megaptera novaeangliae*) also engage in similar behavior, in which two or more males (sometimes 20 or more), compete physically for the primary escort position closest to the female (Tyack and Whitehead 1982; Baker and Herman 1984; Herman et al. 2007). In humpback whales, the primary escort is typically the largest male in the group (Spitz et al. 2002).

Our limited understanding of elasmobranch reproduction is in large part due to the difficulty in studying them in the wild. Their wide distribution in an aquatic environment poses many challenges. However, two characteristics of resident manta rays facilitate our ability to study their life history. First, each individual manta ray is born with a unique

pattern of spots on its ventral surface (Marshall et al. 2008), which appear to remain unchanged over its lifetime and can be reliably identified (Homma et al. 1999; Yano et al. 1999; Clark 2001; Marshall 2009; Kitchen-Wheeler 2010). Second, though the home range of individuals in this population is broad and extends throughout Maui County waters, an area comprising over 3210 km² (Deakos et al. 2011), resident manta rays are known to congregate at specific locations on the reef known as cleaning stations. Cleaning stations are where individuals solicit host cleaner fish to remove parasitic copepods from their body's surface (Losey 1972; Coté 2000). Strong site fidelity to these cleaning stations allows for reliable encounters (e.g., Homma et al. 1999), making these aggregation areas ideal for studying resident manta rays (Homma et al. 1999; Clark 2001; Dewar et al. 2008; Marshall 2009; Deakos et al. 2011).

This paper focuses on the reproductive cycles and the role of body size in the reproductive ecology of a resident manta ray population off Maui, Hawaii. Several aspects of their reproductive ecology were investigated.

Reproductive cycles

Most viviparous elasmobranchs follow annual reproductive cycles with somewhat synchronous mating, gestation, and parturition (for review see Hamlett and Koob 1999). Seasonal reproduction generally occurs if it maximizes a female's chance to successfully produce offspring. This is often influenced by the seasonal availability of food so that young are developing during a time of year when food is more plentiful. A reduction in predation and improved weather conditions could also influence the occurrence of seasonal breeding.

Reproductive seasonality in the Maui population of resident manta rays was investigated. Females observed in mating trains were assumed to be ovulating. The hypothesis tested was that a reproductive advantage to seasonal breeding should reveal mating trains and late-term pregnancies (based on a 12 month gestation period) to occur more often during certain times of the year.

Role of body size

The role of body size in the Maui population of resident manta rays was investigated by examining the relationship between body size and reproductive

activity. Based on data collected by Deakos (2010), the estimated size of the largest female and male in this population using paired-laser photogrammetry was 3.62 m DW and 3.05 m DW respectively. The minimum size at sexual maturity was estimated at 3.37 m DW for females, and 2.80 m DW for males. Assuming these maximum sizes are representative of maximum growth, sexual maturity in both sexes appears delayed until growth reaches greater than 90% of maximum size. This suggests that the reproductive advantage of larger size must strongly outweigh the cost of a reduced reproductive time period. Given that larger body size should provide a reproductive advantage to both males and females in this population, several hypotheses were tested:

- 1) Larger females should have higher pregnancy rates and more consecutive year pregnancies than smaller females. Larger females, being more fecund, should attract a greater number of escorts to her mating train than do smaller females (cf. Pack et al. 2009).
- 2) Larger males should be more likely to hold the position closest to the female in a mating train (cf. Spitz et al. 2002). These males should be larger, on average, than all other males in the train, primarily those that have never been observed as the closest to the female. Larger males should also be more likely to choose larger females and therefore should be associated with larger females (cf. Pack et al. 2009).

These hypotheses are based on the assumptions: a) males physically compete with other males for access to limited females, and b) that an operational sex ratio (OSR), defined as the average ratio of fertilizable females to sexually active males at any given time (Emlen 1976; Emlen and Oring 1977), that is skewed towards males, should favor male competition for limiting females.

The minimum OSR for the Maui resident manta population, assuming all adult females were fertilizable each year, was approximately two adult males for every adult female (Deakos et al. 2011). Generally the sex with the lower parental investment will be the sex towards which OSR is biased (Trivers 1972). The level of bias in the OSR will determine how intense the sex that is in excess will compete for access to the other. The sex in shortage may afford to be selective if there are many potential mates to choose among (e.g.,

Berglund 1994) or they may be unselective and simply mate with fitter mates as an outcome of contest competition (Cox and Le Boeuf 1977).

Methods

Data collection

Surveys of resident manta rays were conducted with SCUBA at an aggregation area off the west coast of the island of Maui over a 6-year period from 2005 through 2010. A description of the study area and detailed methodology is described in Deakos et al. (2011). A survey consisted of a rectangular search pattern originating from the same location covering an area approximately 200 m × 150 m. When manta rays were encountered, attempts were made to collect the following information on each individual: (1) photo-identification, (2) sex, (3) age class, (4) female pregnancy status, (5) DW measurements, and (6) behavioral role when in a mating train.

Ventral markings of each individual were photographed for identification using either a Canon Powershot S70 still camera in an underwater housing, or a Sony HDR-HC1 high definition camcorder housed in a Sea & Sea VX-HC1 underwater housing. Sex was determined by the presence (males) or absence (females) of claspers. Calcification of claspers occurs rapidly over a relatively narrow range of growth with the majority of calcification occurring once the claspers have extended beyond the length of the pelvic fins (White et al. 2006; Marshall and Bennett 2010). Since the onset of clasper calcification in elasmobranchs coincides with a rapid rate of clasper growth and gonadal maturation (e.g., Marshall et al. 2007), claspers extending well beyond the margins of the pelvic fins were used as a reliable indicator of sexual maturity in males. Females were considered mature if they were obviously pregnant based on the extreme distention of her abdomen (Marshall and Bennett 2010), or measured larger than 3.37 m DW, the largest measured pregnant female in this population (Deakos 2010). The distention of the abdomen does not become apparent until at least 6.5 months into a female's pregnancy (Marshall and Bennett 2010). A female that was never measured and that was never observed pregnant was given an age class status of "unknown." DW measurements (measured between each pectoral fin tip) were obtained

using paired-laser photogrammetry as described in Deakos (2010). A mating train consisted of a single female being pursued by at least two adult males. On rare occasions a female leading a mating train was seen to follow a second female for a brief period; this second female was not considered part of the mating train. The female considered part of the mating train was given the behavioral role of "nuclear female" (NF). The male directly behind the NF was referred to as the "nuclear primary escort" (N1E). The male directly behind the N1E was referred to as the "nuclear secondary escort" (N2E). All additional males in the train were referred to as "nuclear escorts" (NE). Since the position of males often changed while observing a mating train, males could receive multiple behavioral roles as part of any given train. Mating train events were recorded using the high-definition, underwater, video camera.

Data analysis

Photo-identification images of each individual from a survey were matched against a catalog of all identified individuals from the study area to determine if that individual had been previously seen (a resight) or was a first sighting. Size measurements were processed as described in Deakos (2010).

For a given time period, the number of surveys in which trains were observed was divided by the total number of surveys to obtain a proportion of mating trains observed. Proportions were calculated for each month and for each season. Seasons were categorized as "winter" (November through April) and "summer" (May through October) encompassing the coldest and wettest months and the warmest and driest months of the year, respectively. The proportion of sightings an individual was observed in a particular behavioral role was calculated for each individual, and for each behavioral role. If an individual was observed in more than one behavioral role during a sighting, a proportion was calculated for each.

Reproductive cycles

Chi-square analyses were used to compare the proportion of surveys containing mating trains, and the proportion of surveys containing a pregnant female (PF), by month and by season. Mean train sizes were calculated by month and season and

analyzed for significant differences using a Kruskal–Wallis Test, and a Mann–Whitney *U*-Test respectively.

Pregnancy rates were estimated by dividing the number of years in which a female was determined to be visibly pregnant by the total number of years seen. Years with insufficient sightings to determine if a female was pregnant during that year were omitted. The overall mean pregnancy rate for the population was an average of all individual pregnancy rates. A successful consecutive year pregnancy was scored if a female was observed pregnant during two consecutive years, with a minimum of 7 months occurring between the two pregnancies. Since females are likely only visibly pregnant during a 5–6 month period (Marshall and Bennett 2010) this minimum time period would ensure that the same pregnancy was not counted in both years. A failed consecutive year pregnancy was scored if a female was not observed pregnant the year following a pregnancy. The rate of consecutive year pregnancies for a female was calculated by dividing successful scores by the sum of successful and failed scores. Only years with enough sightings to determine whether or not a female was pregnant during that year, were used in the analysis.

OSR was determined by calculating the total number of males prepared to mate divided by the total number of females prepared to mate. Since it was not possible to determine which adult males and adult females were seeking out mates, it was assumed that all adult males and adult females were available for mating.

Role of body size

Minimum, maximum, and mean DWs, and standard deviations (SD) were quantified for NFs, PFs, N1Es, N2Es, and NEs. The mean DW of NFs was compared to the mean DW of PFs using a Mann–Whitney *U*-Test. Linear regression was used to determine if larger PFs were correlated with higher pregnancy rates, and more consecutive year pregnancies. Linear regression was also used to determine if larger NFs were positively correlated with more males in her train. A Kruskal–Wallis Test was used to compare mean sizes between all adult males, NEs, N1Es, N2Es, and NEs that have never been observed as a N1E. Linear regression was used to determine if larger N1Es were positively correlated with larger NFs. A Mann–Whitney *U*-Test was used to compare the mean DW of all N1Es to the mean DW of all NEs that had never

been observed as an N1E. All linear regression tests were directional (one-tailed) since the hypothesis was that larger predictor variables would correlate positively with larger body size. Significance was determined at a 0.05 probability level. Statistical analyses were performed using SPSS version 17.0 (SPSS, Inc. 2007).

Results

Of the 309 different manta rays identified, 159 (51%) were males and 150 (49%) were females. Based on clasper length alone (Deakos 2010), 112 (70%) males were considered adults and 57 (30%) were considered juveniles. Based on the estimated size at sexual maturity for males and females in this population (Deakos 2010), of the 85 measured males, 51 (60%) were of adult size and 34 (40%) were of juvenile size, and of the 78 measured females, 37 (47%) were of adult size and 41 (53%) were of juvenile size. Applying the adult male (60%) and adult female (47%) percentages to the total number of males and females in the population, 95 adult males and 71 adult females are estimated to be available for mating. This equates to an OSR of 1.34 adult males per adult female.

A total of 286 surveys were conducted between 4 February 2005 and 14 July 2010 (Table 1). Even though it was somewhat common to see a single male in pursuit of a female, the interaction was generally brief lasting only a few seconds before the male abandoned the female and therefore was not considered a mating train. Mating trains were observed on 32 (11%) surveys and ranged in size from 3 to 18 individuals. Generally, only one mating train was seen on a survey. Mating trains were observed each year and in all months of the year except May and August.

Reproductive cycles

The proportion of surveys containing a mating train varied significantly by month (Chi-Square Test: $\chi^2=27.255$, $df=11$, $n=286$, $p=0.004$) and by season (Chi-Square Test: $\chi^2=11.932$, $df=1$, $n=286$, $p=0.001$). Mating trains were three times more likely to be observed during the winter months (Table 1). The mean mating train size was 7.22 animals (SD=4.10) with the smallest containing a female and two males (by definition) and the largest containing a female and

Table 1 Summary of surveys conducted by month and season showing the total number and proportion of surveys observed with mating trains and pregnant females. The proportions of

surveys with trains and pregnant females were significantly higher during the winter season

	Month	No. Surveys	No. Surveys with Trains	Proportion with Trains	Mean Train Size	Surveys with PFs	Proportion with PFs
Winter	NOV	22	1	0.05	6.00	5	0.23
	DEC	24	7	0.29	8.29	6	0.25
	JAN	16	3	0.19	6.33	1	0.06
	FEB	15	5	0.33	6.20	4	0.27
	MAR	16	3	0.19	4.67	5	0.31
	APR	31	4	0.13	8.25	5	0.16
<i>Winter Subtotal</i>		124	23	0.19 ^a	6.62	26	0.21 ^b
Summer	MAY	25	0	0.00	–	1	0.04
	JUN	19	2	0.11	9.00	3	0.16
	JUL	30	4	0.13	5.00	0	0.00
	AUG	23	0	0.00	–	1	0.04
	SEP	34	2	0.06	14.50	4	0.12
	OCT	31	1	0.03	4.00	6	0.19
<i>Summer Subtotal</i>		162	9	0.06 ^a	8.13	15	0.09 ^b
<i>Grand Total</i>		286	32	0.11	7.22	41	0.14

^{a,b} Significantly different, $p < 0.05$

17 males. The most common train size was 2 males (25%); 9 trains (28%) had 10 or more males. Train size did not vary significantly by month (Kruskal-Wallis Test: $\chi^2=9.220$, $df=9$, $n=32$, $p=0.417$) or by season (Mann-Whitney U -Test: $Z=-0.407$, $n=32$, $p=0.705$). Of the 28 trains observed, 21 different NFs were identified (Table 2). On average, these females were seen in the NF role on 21% of their sightings (4–50%). Most were seen only once as a NF ($n=16$) and one was seen four times as a NF. Five NFs (24%) were pregnant while leading the mating train.

The mean proportion of sightings containing a pregnant female varied significantly by month (Chi-Square Test: $\chi^2=19.917$, $df=11$, $n=286$, $p=0.046$) and by season (Chi-Square Test: $\chi^2=7.841$, $df=1$, $n=286$, $p=0.006$). Pregnant females were more than twice as likely (21%) to be observed during the winter compared to the summer (9%). During 51 (18%) surveys, at least one pregnant female was observed (Table 1). A total of 20 individual females were observed pregnant (Table 3). On average these females were observed pregnant on 25% of the surveys (3–100%).

One notable female (ID# 5003) was observed as a NF on 4 occasions over an eight-month period (Fig. 1). On 22 Apr 2008, she was an NF with 6 males, periodically

following a larger pregnant female (ID#5013), who was not considered part of the mating train. On 23 Apr 2008 she was being pursued briefly by a single male (ID#8002) that had not been present the day before, and again periodically following a larger, pregnant female (ID#5008), one different from the day before. On 24 Apr 2008, she was observed on her own. The same male (ID#8002) was pursuing her two days later on 26 Apr 2008. On 15 May 2008, she was observed on her own with other mating trains in the vicinity. On 12 Jun 2008 she was leading a train of 7 males. On 24 Jun 2008 she was on her own and was not seen again until 10 Dec 2008, when she was leading a train of 9 males. On 8 Feb 2009 she was observed on her own, and on 21 Mar 2009 she was observed on her own while a separate eight animal train passed through the area. During both of these latter sightings, she did not appear pregnant, but on 24 Aug 2009, she was visually confirmed to be pregnant.

Role of body size

The mean, minimum, and maximum body size of all females, NFs, PFs, all males, juvenile males, transition males, adult males, all escorting males, N1Es,

Table 2 The resight history of 21 nuclear females (NF) observed between years 2005 and 2010 with their respective DW (m). Numbers below years indicate the month in which

they were observed as a NF during that year with train size shown in brackets. Bolded IDs indicate females observed in a train during a summer month

Nuclear Female ID	DW (m)	2005	2006	2007	2008	2009	2010	Total Sightings
1021	n/a		4(18)					2
1029	n/a				2(9)			5
1062	n/a					1(10)		4
2002	n/a				12(7)		1(3)	5
3011	n/a	9(16)						4
3041	n/a					3(8)		4
3056	n/a					2(4)		2
5023	n/a				12(8)			5
5029	n/a					4(5)		3
13005	3.30	9(13)			12(10)	7(5)		15
7006	3.37			7(11)				25
3003	3.39				10(4)		3(3)	14
3019	3.39					1(6)		19
12010	3.41				2(9)			9
5001	3.42					1(10)		9
5003	3.44	7(3)			4(6), 6(7), 12(10)			21
7002	3.45				12(3)			13
8008	3.48				2(3)			15
6011	3.48				12(10)			7
3060	3.52					2(4)		4
3030	3.62						3(3)	10
mean	3.44							

N2Es, and NEs that have never been seen as an N1E are shown in (Fig. 2).

The average female DW was 3.18 m (SD=0.31). A total of 21 NFs and 20 pregnant females were observed. NFs averaged 16% larger than all males measured in mating trains, but NF DWs did not significantly differ from PF DWs (Mann–Whitney *U* Test: $Z=-1.196$, $n=29$, $p=0.232$). Larger PFs had significantly higher pregnancy rates than smaller PFs (Linear Regression: $R^2=0.520$, $df=8$, $F=8.684$, $p=0.009$), and were significantly more likely to be observed pregnant in consecutive years (Linear Regression: $R^2=0.882$, $df=5$, $F=37.470$, $p=0.001$). Mating trains with larger females did not contain significantly more males (Linear Regression: $R^2=0.277$, $df=11$, $F=3.841$, $p=0.078$).

Most pregnant females were observed to be pregnant only once during the 6 years of the study ($n=15$). Two were observed pregnant in two separate

years, and three were observed pregnant in three separate years. The latter three were among the nine largest females of the 77 measured. Three females were confirmed pregnant in two consecutive years. One female, confirmed pregnant in three consecutive years, was the second largest female measured in the population. Based on 11 females observed pregnant at least once, with sufficient sightings to determine pregnancy status for at least 3 separate years, the estimated mean pregnancy rate was 0.56 pups per year (0.20–1.0; Table 3). If this biennial pregnancy rate is representative of nearly half the females not making themselves available for mating, this would inflate the OSR to 2.68 adult males per reproductively available female. The most likely months for giving birth based on the earliest confirmation that a pregnant female was no longer pregnant were November through April. One half of the PFs were confirmed with mating scars; spot scarring and

Table 3 The resight history and disc width (DW), if available, of 20 pregnant females during the years 2005 through 2010. P indicates she was observed pregnant and her pregnancy was new for that year; N indicates she was observed enough times during that year to determine she was unlikely pregnant; U indicates she was observed during that year but not sufficiently often to determine if she was visibly pregnant; and a dash (–) indicates she was not sighted during that entire year. Bolded IDs indicate females observed pregnant during a summer month. Estimated Pregnancy Rates (EPR) based on a minimum of 3 years with sufficient data, and Estimated Consecutive Pregnancy Rates (ECPR) based on a minimum of 2 consecutive yrs with sufficient data are shown

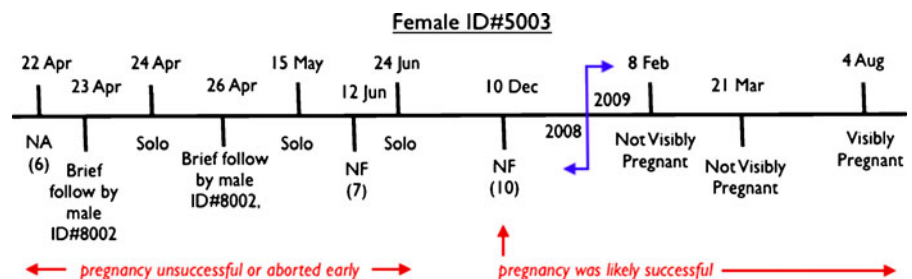
Pregnant Female ID	DW (m)	2005	2006	2007	2008	2009	2010	EPR	ECPR	Total Sightings
2036	n/a	–	–	P	–	–	–	–	–	1
3041	n/a	–	–	U	N	P	P	0.67	1.00	4
3056	n/a	–	–	–	U	P	–	–	–	2
12009	3.35	–	–	–	P	–	–	–	–	6
12011	3.39	–	–	–	P	–	–	–	–	4
3003	3.39	P	–	N	P	N	U	0.50	0.00	14
3019	3.39	–	N	P	N	N	–	0.25	0.00	19
5013	3.41	–	–	–	P	N	–	–	0.00	21
5008	3.44	–	U	–	P	–	–	–	–	6
5003	3.44	N	N	U	N	P	–	0.25	–	21
10002	3.45	N	N	P	N	–	N	0.20	0.00	31
8008	3.48	N	U	U	P	–	–	0.50	–	15
3001	3.51	U	P	U	N	N	–	0.33	–	6
10000	3.52	U	–	–	P	–	–	–	–	7
3060	3.52	–	–	–	U	P	–	–	–	4
7000	3.53	P	P	–	P	N	–	0.75	0.50	6
3008	3.55	P	U	U	U	P	P	1.00	1.00	17
12005	3.58	–	–	P	U	N	–	–	–	5
1007	3.59	U	U	U	P	P	P	1.00	1.00	15
3030	3.62	–	P	–	U	N	P	0.66	–	10
mean	3.48							0.56		

abrasions on the pectoral fins caused by males during mating attempts (Yano et al. 1999; Marshall and Bennett 2010). At least two PFs were confirmed without mating scars. Of the 41 females observed with mating scars, all had scars on the dorsal side of their left wing tip, and two (5%) females had visible mating scars on the dorsal surface of both the left and

right wing tip. No males were observed with mating scars.

The average male DW was 2.83 m (SD=0.14). A total of 22 different males were identified occupying the N1E position in a mating train (Table 4). On average these males were observed as the N1E on 14% of the surveys (2–40%), and the majority (73%)

Fig. 1 The sighting history of a notable female (ID#5003) observed multiple times as a NF. Numbers in brackets indicate the number of animals in the mating train



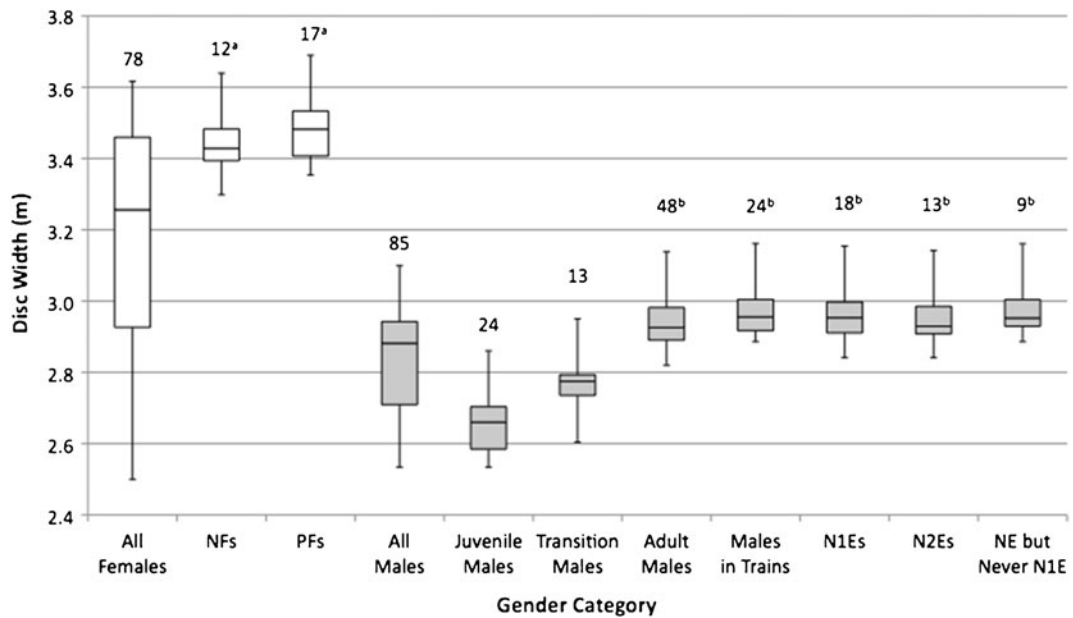


Fig. 2 Distribution of manta ray disc widths. Heavy black lines = means, box boundaries = 25th and 75th percentiles, whiskers = smallest and largest observed values, numbers = sample sizes. ^anot significant, $p=0.232$ ^bnot significant, $p=0.363$

were only seen once as the N1E during the 6 years. A total of 19 different N2Es were observed. On average these males were observed as N2E's 17% of the time (7%–50%). A total of 40 different NEs were observed. On average these males were observed as NEs on 22% of the surveys (4%–100%). No significant differences were found between the mean sizes of all adult males, NEs, N1Es, N2Es, and NEs never seen as N1Es (Kruskal-Wallis Test: $\chi^2=4.328$, $df=4$, $n=112$, $p=0.363$). Larger N1Es were not significantly correlated with larger NFs (Linear Regression: $R^2=0.001$, $df=14$, $F=0.011$, $p=0.918$).

Adult males were frequently observed following females briefly from behind, or occasionally turning abruptly in order to pass through an area where a female recently defecated. One notable male (ID#13007) was the most frequently sighted individual in the study. He was observed on 45 occasions over six years, and during seven of these sightings he was observed pursuing a female (Fig. 3). Except for encounters on 22 Apr 2008 and 24 Apr 2008, in which the female was the same, all other females were different. On 20 Jan 2009, one of the few occasions when more than one mating train was in the area, he was observed switching back and forth between the two NFs. His behavioral role within the train varied frequently as did others but he often moved

to the N1E position with what appeared to be little effort and without any conflict from those males already in the primary position, even if the current N1E was larger.

Discussion

Reproductive cycles

Mating trains and late-term pregnant manta rays from this Maui population were significantly more likely to be observed during the winter season, indicating a reproductive advantage during this time of year. One advantage may be to help concentrate adult males at certain times of the year, thereby increasing a female's access to more or better mate choices. Deakos et al. (2011) documented significantly more manta rays present and greater numbers of new individuals appearing during the winter months, but the percentage of males did not differ significantly during this time of year. Females seeking mates during the summer may have less competition with other females but may also have fewer mate choices and possibly fewer quality males. Another advantage of seasonal breeding may be improved food resources available to pups or reduced predation on them. Without knowing

Table 4 The resight history and disc width (DW), if available, of 22 individual nuclear primary escorts (N1Es) during the years 2005 through 2010. N1E indicates he was the primary escort in a mating train, and the bracketed numbers represent the month followed by the train size. S indicates the male was

sighted but not as a N1E during that year. A dash (–) signifies he was not sighted during any surveys for that entire year. Bolded and underlined IDs indicate a male observed escorting in a train during the summer

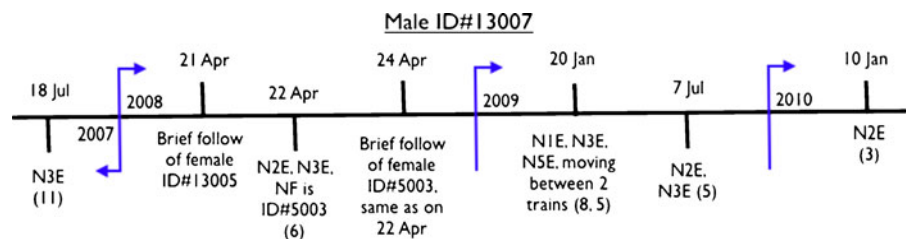
N1E ID#	DW (m)	2005	2006	2007	2008	2009	2010	Total Sightings
1033	n/a	–	–	S	S	N1E(3:8)	–	4
2014	n/a	S	N1E (4:18)	–	N1E (12:10)	–	S	5
3017	n/a	–	S	S	N1E (12:10)	S	–	14
3055	n/a	–	–	–	N1E (6:7)	–	–	5
6023	n/a	–	–	–	S	–	N1E(3:3)	3
8017	2.84	S	S	–	N1E (6:7,6:11)	S	S	32
2005	2.89	N1E (7:3)	S	S	S	S	S	16
1001	2.90	S	S	–	S	S	N1E(1:3)	12
3064	2.90	–	–	–	S	N1E(1:6)	–	4
2039	2.91	–	–	–	S	S	N1E(3:3)	8
4000	2.92	S	S	S	N1E (2:9)	N1E(1:10,2:4)	–	27
7010	2.92	–	–	–	N1E (12:10)	–	–	5
3007	2.94	S	–	N1E (7:11)	S	S	–	12
13007	2.94	S	S	S	S	N1E(1:10,2:4)	S	45
5019	2.96	–	–	–	N1E(4:6)	S	–	12
8012	2.98	–	S	–	S	N1E(1:10)	–	10
3033	2.98	–	–	S	S	S	N1E(3:3)	6
8002	2.99	N1E (9:16)	S	N1E (7:11)	N1E(10:4)	N1E(7:3)	–	34
2037	3.00	S	–	–	N1E(2:9,12:7)	S	–	8
1003	3.02	S	S	–	S	N1E(2:4)	–	10
3023	3.02	–	S	S	S	N1E(4:5)	S	21
8009	3.03	S	S	S	N1E(12:3)	N1E(1:10)	–	31
mean	2.95							

the location of pupping areas, the resources pups use during their initial years of development, and pup predation rates, it is difficult to identify the benefits that may exist for individuals born during the winter months.

Females that are unsuccessful in getting pregnant during the winter months may mate again during the summer, a less favorable time of year. Among the five females observed in summer mating trains, two were

also observed in trains during the preceding winter. Additionally, a female observed in a mating train 14 and 16 months prior to being visibly pregnant, further suggests that not all mating events are successful and that multiple ovulations may occur in the same year, an attribute not yet documented in mobulids. Although the presence of a mating train does not confirm a NF is ovulating or that mating will take

Fig. 3 The sighting history of a notable male (ID#13007) with a DW of 2.94 m, observed pursuing a female on seven occasions. The behavioral role(s) observed are indicated for each sighting as well as the train size in brackets



place, adult males in pursuit of a NF generally ignored other adult females in the area, other than occasional brief investigations by positioning directly behind her. These brief investigations were likely attempts by adult males to sense a female's reproductive state through her bodily excretions since it was also common to see adult males make abrupt turns in order to pass directly through a female's defecation. Close follows by males pursuing a lead female has been reported in other elasmobranch fishes (e.g., Tricas 1980), with suggestions that it may be olfaction-mediated behavior (Johnson and Nelson 1978).

Elasmobranchs are known to have a very good sense of olfaction and taste (Hodgson and Mathewson 1978; Kleerekoper 1978) and can use these senses to detect biochemical products released by other organisms, including females trying to attract potential mates (Johnson and Nelson 1978; Gordon 1993). Ari and Correia (2008) reported an acute sense of smell from a captive oceanic manta ray. The observations in this study of adult males pursuing select females while ignoring other adult females in the area, suggest males are able to detect a female's reproductive state, adding further support that NF's are likely ovulating.

Asynchronous ovulations could have the benefit of reduced competition between females allowing all reproductively available females an opportunity to mate with higher-ranking males. Staggered ovulation would also make it possible for a select subset of higher-ranking males to dominate paternity, at least within a localized area. Asynchronous reproductive cycles have been reported in some viviparous chondrichthyans (e.g., Braccini et al. 2006). The rarity of seeing two mating trains occurring during the same survey could be an indication that ovulations may be staggered. However, since the study area represents only a small portion of the estimated home range of this population, other mating trains may have been occurring in synchrony beyond the area being observed.

A female's lifetime reproductive success is dependent on her ability to raise offspring to the age of independence (Clutton-Brock et al. 1982), and the habitat she chooses is often a trade-off between an area rich in food resources and the needs and security of her offspring. Females that are preparing to give birth may choose a habitat that is near sufficient food resources and cleaning stations, but also near a desired pupping area. Aggregation sites in close proximity to pupping areas may have a greater

abundance of pregnant females, while non-pregnant females and others in the population take advantage of locations with better food resources that may be distant from pupping areas. Females seeking out mates may choose aggregation areas where adult males are concentrated, or vice versa, and reproductively unavailable females may choose areas with few adult males.

The OSR of an aggregation area may reflect these habitat choices by males, females, and different age classes in the population, and could vary by season. This is reflected in the sex ratio differences between the Maui aggregation site, where females comprise 47% of individuals, and an aggregation site off Mozambique, in which females comprise 75% of individuals (Marshall and Bennett 2010). Age class segregation is also supported with small manta rays being absent or very rare at both of these aggregation sites (Deakos 2010; Marshall and Bennett 2010).

The rate at which females give birth among many elasmobranchs is commonly biennial, most likely to allow for post-partum recovery, a period of time to rebuild reproductive reserves before mating again (Pratt and Carrier 2001). The mean pregnancy rate of 0.56 pregnancies per adult female per year is consistent with biennial pupping, and with a biennial pregnancy rate reported in resident manta rays off Mozambique (Marshall and Bennett 2010). This mean pregnancy rate however, should be used with caution due to small sample sizes and the possibility that females classified as non-pregnant in earlier years of the study could have been immature at that time. Additionally, if some pregnant females had less distended abdomens during late-term pregnancy, they could have also been recorded as non-pregnant females.

Role of body size

Larger females had significantly higher pregnancy rates and were significantly more likely to become pregnant in consecutive years, consistent with larger females benefiting from greater reproductive success. Larger females did not have a greater number of male escorts, contrary to what was expected if males were exhibiting mate choice and choosing larger, more fecund females. However, given that mating trains could last several hours and possibly several days, the number of males observed during the survey may consist of only a fraction of the total.

Males holding the N1E position in a mating train were not significantly larger than any other adult male, contrary to what was expected if males were competing physically for mating access to the NF (cf. Spitz et al. 2002). There was also no evidence that larger males were choosing larger females to escort. Occasionally males that were not part of the mating train inserted themselves into the primary position for very brief periods. When this occurred, the N1E at the time simply retreated to the N2E position without any confrontation. It is possible that dominance had already been established among these males and risking injury by fighting a more dominant male was not advantageous. The absence of male combats suggests that this is not a preferred strategy of males or perhaps other mating opportunities are available that reduce the need to engage in fighting for potential mates.

A variable OSR across seasons can strongly influence the success of male tactics and the predominant mating system for that season (Madsen and Shine 1993). When OSR is low (female bias), body size seems to show little advantage in reproductive success since many females are available, few combats occur, and smaller males receive mating opportunities. Factors that may affect OSR include biased adult sex ratios, differences between the sexes in age at maturity, reproductive longevity, migration schedules, spatial distribution, mortality during the reproductive season (for review see Clutton-Brock and Vincent 1991), or momentary differences in the distribution of the sexes (e.g., Höglund et al. 1993).

Although the overall number of males and females in this population were nearly equal, the sex ratio of adults was estimated at 1.34 males per female. Biennial mating would reduce the number of reproductively available females by half, giving an OSR of 2.68 mating males for every mating female in this population. This male bias should favor more intense competition between males but the absence of male combats in mating trains indicates such competition may not be directly physical.

Some studies have found that in the absence of intense physical competition between males, male reproductive success is influenced more by social factors than by morphological traits associated with size (Bercovitch 1989). In whitetip reef sharks (*Triaenodon obesus*), group courtship has been observed where multiple males at the same time bite,

mount, and attempt to copulate with a single female (Whitney 2004). Cooperation between males has also been suggested in order to achieve successful mating with a female (Carrier et al. 1994).

Sperm competition may be an alternative mating strategy by males, in which the male's sperm compete for fertilization of the eggs during a single fertile period (Parker 1970). Observations of some female sharks copulating with multiple males during a mating bout suggest sperm competition may be occurring in some elasmobranch species (Carrier et al. 1994; Pratt and Carrier 2001). Yano et al. (1999) reported two male oceanic manta rays mating in succession with the same female, although this is the only report of a female manta mating with more than one male in the same day (Marshall and Bennett 2010).

Among mammals, relative testes size is a good indicator of whether or not sperm competition exists (Gomendio et al. 1998). Right whales (*Eubalaena australis*) for example, which have multiple males mating almost in unison with a single female, have testes weighing over one ton each, more than 1% of their total body weight, while those of sperm whales and humpback whales, which are known to fight aggressively for mates, have testes weighing less than 0.5% of their total body weight (Brownell and Balls 1986). The relative weight of manta ray testes in mature males is undocumented and should be further examined to determine the likelihood of sperm competition as a male mating strategy. In birds and mammals, where the frequency of copulation is high, testes tend to be large, and where it is low, testes tend to be small (e.g., Harvey and Harcourt 1984; Birkhead et al. 1993). The rarity of observed copulation acts and the evasiveness of the female towards pursuing males, suggests sperm competition is unlikely a predominant male mating strategy in resident manta rays.

Endurance rivalry, which can be defined as the ability to remain reproductively active during a large part of the mating season (Andersson 1994), can favor larger males for reasons of energetics (Andersson and Iwasa 1996). Large adult male manta rays may be more able to endure a long lasting mating-train, consisting of rapid swimming, abrupt turns, and somersaulting, especially if their ability to feed, while in pursuit, is forfeited or severely inhibited. With NF's at the head of the train dictating its direction and pace, they are more likely able to continue feeding.

Deakos et al. (2011) tracked a NF equipped with an acoustic transmitter, and documented her still leading a mating train after 24 h, providing support that mating trains can persist multiple days. Females selecting males based on endurance would likely select those fit enough to remain with the train over long periods, and not simply from their proximity to her within the train. Unfortunately, the absence of observed copulations makes it difficult to know which males mate most often. Future work with genetic sampling would be beneficial in deciphering paternity, and could help to identify which traits may be contributing to male reproductive success.

Conclusion

A winter breeding and pupping season exists in a resident population of manta rays off Maui, Hawaii. Maturation in females occurring after 90% of maximum growth, suggests that food resources are likely readily available and predictable and that large body size is advantageous. Females, primarily larger females, have the ability to give birth in consecutive years, but the energy requirements are likely so great that most females will rest for one or more years between pregnancies. Late maturation by males for larger body size also suggests a reproductive advantage in males, possibly providing greater resources for endurance during long lasting mating trains. The Maui aggregation area appears to be an important breeding area due to the recurrence of the same reproductively active individuals across years. Future work should include long-term field studies combined with genetic sampling to identify paternity and reproductive success among males.

Acknowledgments J. Whitney, A. Ligon, R. Deakos, and E. Lyman provided valuable support with ongoing data collection. I wish to thank R. Deakos, S. Spitz, and B. Brainstetter for their assistance with paired-laser photogrammetry calibrations. L. Herman, S. Yin, S. Spitz, A. Pack, J. Mobley, K. Minke, and P. Couvillon provided valuable feedback on earlier versions of this manuscript. My sincere gratitude goes to G.S. Mills for his guidance and support aboard the Oscar Elton Sette. For assistance with animal care permit issuance, I wish to thank J. Mobley. Research was conducted under the University of Hawaii Animal Care & Use Committee, Protocol No. 08-591-2, and Assurance number A3423-01.

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