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First observation of mating behavior in three species of pelagic myliobatiform rays in the wild

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Abstract Information on elasmobranch mating behavior is limited. For batoids, observations of mating behavior in the wild are available only for a few species. We present video documentation of new cases of mating behavior for three species of myliobatiform rays. On July 20, 2013, a group of six cownose rays (*Rhinoptera bonasus*) were observed mating in shallow coastal waters off New Jersey. On August 19, 2014, two whitespotted eagle rays (*Aetobatus narinari*) were observed mating in Harrington Sound, Bermuda. In both cases, all stages of the mating sequence described in the

literature were observed: 1) close following, 2) pre-copulatory biting, 3) copulation/insertion, 4) resting, and 5) separation. This is consistent with observations of mating behavior for whitespotted eagle rays and Javanese cownose rays (*Rhinoptera javanica*) in captivity. This is the first time a complete mating sequence has been documented in the wild for either species. Additionally, on May 18, 2015, a group of four bentfin devil rays (*Mobula thurstoni*) were observed engaging in pre-mating behaviors at the Archipelago of Saint Peter and Saint Paul, Brazil and is the first documented account of mating behavior for this species. In all three cases, we noted that the female was considerably darker in color than the males, which may be evidence of a visual pre-copulation cue, as seen in other marine fishes. The similarity of the behaviors presented here and those observed in other species (e.g., *M. birostris*, *Hypanus americanus*, and *Taeniurops meyeri*) suggests mating behavior may be highly conserved among batoids.

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Introduction

Worldwide, populations of sharks and rays are declining as a result of over exploitation from fishing, habitat destruction, and pollution (Dulvy et al. 2014). Successful management and conservation rely on a complete understanding of the life histories of these animals, in particular their reproductive biology. While the overall

reproductive biology of elasmobranchs is fairly well understood (see Carrier et al. 2004), there is limited understanding of reproductive behavior (i.e. courtship and mating) (see review by Pratt and Carrier 2001). In their review, Pratt and Carrier (2001) note that current knowledge of elasmobranch reproductive behavior has been inferred from examining the reproductive structures of specimens and from observations of animals held in captivity. The overall paucity of observations of mating behavior in the wild can likely be attributed to the inherent difficulty of observing free-living elasmobranchs (Duffy and Tindale 2018).

Mating behavior in the wild has only been documented for 12 of the 600+ species of batoids (rays and skates). Courtship or pre-mating behaviors have been observed for six species and copulation has been observed in six species (Table 1). The first complete description of the batoid mating sequence was based on observations from the wild of the mating behavior of the giant manta ray, *Mobula birostris* (Walbaum 1792) (Yano et al. 1999). Yano et al. (1999) specifically described five steps in the mating sequence, including chasing, biting, copulating, post-copulating, and separation. Chapman et al. (2003) described the complete mating sequence for the southern stingray, *Hypanus americanus* (Hildebrand and Schroeder 1928), observing a similar sequence of behaviors as those described by Yano et al. (1999). The similarity in mating behaviors

between both species led Chapman et al. (2003) to suggest that mating behavior might be conserved among the batoids. Based on these accounts, a general template for ray mating behavior can be characterized as follows: 1) close following – one or more males following a female for an extended period of time; 2) pre-copulatory biting – the male ray bites onto one of the female's pectoral fins; 3) copulation/insertion – male inserts clasper into the female's cloaca and rapidly flaps his pectorals; 4) resting – copulation is complete but male remains attached to female, and 5) separation – male releases grasp of female (Yano et al. 1999; Chapman et al. 2003).

The order Myliobatiformes (Chondrichthyes: Batoidea) is a monophyletic group of stingrays (Dunn et al. 2003) represented by 160+ species (Compagno 1999) and includes pelagic rays of the families Aetobatidae, Mobulidae, and Rhinopteridae. The whitespotted eagle ray, *Aetobatus narinari* (Euphrasen, 1790), is a large bodied aetobatid ray found in tropical and warm-temperate waters of the western Atlantic Ocean (Bigelow and Schroeder 1953). The cownose ray, *Rhinoptera bonasus* (Mitchill, 1815), is a medium-sized rhinopterid ray found in the coastal and estuarine waters of the western Atlantic and Gulf of Mexico (Bigelow and Schroeder 1953; McEachran and Séret 1990). The bentfin devil ray, *Mobula thurstoni* (Lloyd 1908), is a large pelagic mobulid ray found in the tropical and sub-tropical waters of the Atlantic, Pacific, and Indian Oceans (Couturier et al. 2012). All three species are listed as near threatened on the IUCN Red List, and are highly susceptible to exploitation and overfishing (Barker 2006; Kyne et al. 2006; Walls et al. 2016); however, little is known about the reproductive and mating behavior of these species. Tricas (1980) reported two instances of courtship and mating-related behaviors for *A. narinari*, and Uchida et al. (1990) documented successful mating attempts for eagle rays in captivity. Both of these accounts are from the Indo-West Pacific; however, recent taxonomic revisions (White and Last 2012; White 2014) suggest the observed species in each case was likely an ocellated eagle ray, *Aetobatus ocellatus* (Kuhl, 1823). Pre-mating behavior has also been observed for *R. bonasus* (Poulakis 2013); however, copulation was not observed. To our knowledge, there has been no documentation of any mating behavior for *M. thurstoni*.

Here we present video documentation of mating behavior in the wild for three species of myliobatiform

Table 1 List of batoid species with documented observations of mating behavior in the wild

Species	Reference
<i>Aetobatus</i> cf. <i>narinari</i>	Tricas 1980
<i>Hypanus americanus</i>	Brockman, 1975; Deloach 1999; Chapman et al. 2003*
<i>Mobula alfredi</i>	Marshall and Bennett 2010*; Deakos 2012
<i>Mobula birostris</i>	Yano et al. 1999*
<i>Mobula mobular</i>	Duffy and Tindale 2018
<i>Mobula tarapacana</i>	Sobral 2013
<i>Myliobatis californica</i>	Feder et al. 1974; Tricas 1980
<i>Rhinoptera bonasus</i>	Poulakis 2013
<i>Taeniurops meyeri</i>	Arnés-Urgellés et al. 2018*
<i>Urobatis concentricus</i>	McCourt and Kerstitch 1980
<i>Urobatis halleri</i>	Nordell 1994*
<i>Urobatis jamaicensis</i>	Young 1993*

*Denotes accounts where copulation was observed

rays. In the first two cases, we provide the first fully detailed description of the complete mating sequence for the whitespotted eagle ray (*A. narinari*) and the cownose ray (*R. bonasus*). The third case describes the first documented account of courtship and pre-mating behavior of the bentfin devil ray (*M. thurstoni*).

Methods

The detailed accounts of mating behaviors for *A. narinari*, *R. bonasus*, and *M. thurstoni* described below were obtained from opportunistic videos of individuals recorded in the wild. The behaviors of *A. narinari* and *R. bonasus* were recorded by laypersons and the original video files were provided to the authors for review and analysis. Video of *A. narinari* mating was recorded using a DJI Phantom 2 Vision+ Quadcopter (SZ DJI Technology Co., Ltd.). The drone was able to follow and record the rays for approximately 486 s. Video of *R. bonasus* mating behavior was recorded using a GoPro action sports camera (GoPro, Inc.). Nine sequential video clips ranging from 11 s – 119 s were recorded. Upon receiving the raw video files, the individual clips were combined to create one complete video file using GoPro Studio (GoPro, Inc., version 2.5) and the Protune filter was applied to reduce glare on the surface of the water. Video footage of *M. thurstoni* mating was recorded by co-author Ramón Bonfil using a Phantom 2 Vision+ Quadcopter and captured 95 s of video.

Video footage was reviewed and analyzed for each species, and detailed descriptions of mating behaviors and the time at which they occurred (mm:ss; elapsed time) were recorded. All videos were viewed using VLC media player (VideoLAN Organization, version 3.0.7.1). Still photos of key mating behaviors were obtained from the raw videos using the VLC snapshot tool and used for the in-text figures. Full length videos for each account are provided as additional Online Resources.

Observations

Aetobatus narinari

The mating behavior of *A. narinari* was recorded on August 19, 2014 in Harrington Sound, Bermuda (32°

20.0562 N 64° 44.1065 W). In the video (Online Resource 1), two individual rays, a lightly colored male and a darker colored female of similar sizes, were observed swimming near the surface along the south-western shoreline of the sound (Fig. 1a). Both rays were swimming at a moderate pace, with the male swimming behind and slightly offshore of the female. The male closely followed the female and made multiple sharp turns towards the female (Fig. 1b), appearing to prevent the female from moving into deeper waters and continued for ~ 97 s. At 01:39 min the male made a sharp turn towards the female, pushing her closer to the shoreline (Fig. 1c). The female slowed her swimming speed and appeared to pause momentarily as the male stopped swimming and began to glide towards her. At 02:02 min the male made a quick burst of speed and attempted to bite onto the right pelvic fin of the female. During this attempt, the two rays thrashed at the surface as the female tried to escape from the male's grasp (Fig. 1d). After biting onto the female's pelvic fin, the two rays slowly swam along the surface for ~ 27 s. From 02:11–02:38 min the male continued to bite the female while moving along the posterior edge of the right pectoral fin until the male was positioned at the tip (Fig. 1e). After grasping the tip of the female's pectoral fin the male moved beneath the female and inverted dorsoventrally, and positioned in a ventral to ventral orientation with the female (Fig. 1f). At 02:37 min the male then appeared to attempt to insert one clasper into the female's cloaca and began to rapidly oscillate its pectoral fins (Fig. 1g). This behavior lasted ~ 25 s, during which the rays spun in a clockwise direction while slowly sinking to the seafloor (Fig. 1h). The rays settled onto the seafloor with the female remaining on top of the male and appeared to rest motionless for 1–2 s. At 02:57, the male released its grasp from the female and the two rays separated (Fig. 1i).

After separating, the female started to swim away and the male immediately began to follow, exhibiting the same close-following behavior that was observed at the beginning of the mating sequence (Fig. 1j). This continued for ~ 148 s post-mating, until the male eventually swam away from the female at 05:37 min. After the male left, the female continued to swim slowly along the shoreline until recording ended. The entire sequence of mating events, including the post-copulatory following, lasted ~ 324 s.



Fig. 1 Mating sequence of whitespotted eagle ray (*Aetobatus narinari*) observed August 19, 2014 in Harrington Sound, Bermuda. The male can be identified throughout the sequence by the lighter dorsal color and the female is identified by the darker dorsal color. **a** “Close following”: Male positioned slightly posterior and offshore of female. **b** Male makes sharp turns, flashing ventral surface, appearing to corral the female close to shore during the close following phase. **c** Male turns and swims towards the female as the female retreats closer to the shoreline. **d** “Pre-copulatory biting”: Male rapidly swims towards female, bites the right pelvic fin, and the two rays thrash at the surface as the female attempts to escape. **e** While biting the female, the

male moves along the posterior edge of female’s right pectoral until positioned along the tip of the female’s pectoral. **f** Male rotates under female and positions abdomen to abdomen with the female. **g** “Insertion/copulation”: Male inserts clasper into the female’s cloaca and begins to rapidly flap pectoral wings. **h** Male and female ray sink to the seafloor, spinning in a tight clockwise rotation. **i** “Resting & Separation”: Male comes to rest with dorsal surface on the seafloor with the female on top, and the two rays separate after ~ 1–2 s. **j** “Post-mating following”: Male continues to follow the female after separating, performing similar behaviors as during phase 1 “close following”

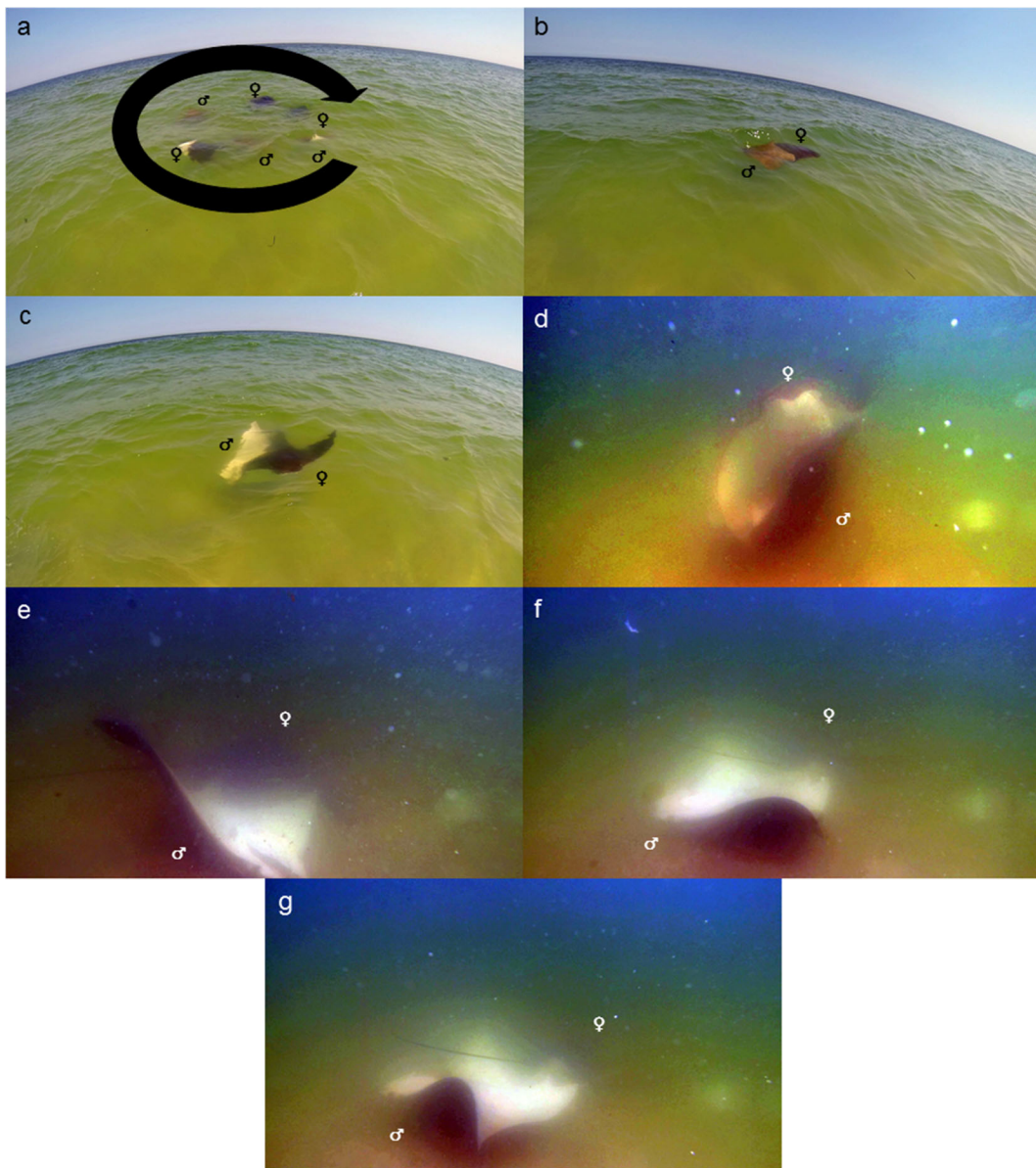


Fig. 2 Mating sequence of cownose ray (*Rhinopterus bonasus*) observed July 20, 2014 off New Jersey, USA. Males can be identified throughout the sequence by lighter dorsal color and are denoted by male symbol, females are darker in color and denoted by female symbol. **a** “Close following”: Group of six cownose rays (3 male, 3 female) swimming in clockwise pattern. **b** Male closely following a female ray while positioned slightly behind and above the female's right pectoral wing. **c** “Pre-copulatory

biting”: Male biting onto the tip of the right pectoral fin of the female and begins to rotate underneath. **d** “Insertion/copulation”: Male positioned under the female in abdomen to abdomen position and inserts clasper into female's cloaca as the two rays sink to the seafloor. **e** While resting on the bottom with clasper inserted in the female, the male begins rotating 180°. **f** Male and female ray rotated 180° during copulation. **g** Male rapidly undulating his pectoral wings with clasper inserted into female's cloaca

Rhinoptera bonasus

The mating behavior of *R. bonasus* was documented on July 20, 2013 off the coast of New Jersey, USA

and occurred in shallow water adjacent to the surf zone. Recorded video (Online Resource 2) shows a group of 6 cownose rays, comprising three lighter colored males and three darker colored females,

swimming parallel to shore just below the surface. At 00:21 min the group of rays began to swim in a clockwise pattern (Fig. 2a). This behavior lasted ~ 26 s, at which point the rays broke formation and swam parallel to the beach as a group. At 02:38 min the group again began to swim in a circular pattern, now moving in a counter-clockwise rotation, and were joined by three more rays at 02:47 min. This behavior continued for approximately 76 s as the group moved in and out from the shoreline. During this time, there was an overall increase in activity with the group of rays seen making rapid, tight turns, often with their pectoral fin tips breaking the surface of the water. At 04:13 min two rays, one light and one dark, split from the group and swam rapidly down the shoreline with the darker colored ray chased by the lighter colored ray. The remaining group of rays continued to swim along shore in the opposite direction and was followed for another 160 s, during which time they are again seen swimming in a clockwise rotation.

At 06:53 min the video joins two rays that are observed swimming parallel to the beach. One light colored ray (male) is seen closely following a darker colored ray (female). The male was swimming just behind and slightly offshore of the female, and appeared to be corralling the female towards the shallower water near the shoreline. At 07:36 min, the male was positioned just above and posterior to the female's right pectoral fin (Fig. 2b) and at 07:38 min the male bites the female's right pectoral fin tip. After grasping the female, the male rotated underneath the female (Fig. 2c), positioned into a ventral to ventral orientation (Fig. 2d), and began rapid pectoral fin oscillations. During this process, the two rays slowly sank to the seafloor and came to rest on the bottom with the male below and the female on top (Fig. 2e). While resting on the bottom, the male appears to insert a clasper into the female's cloaca and rotates 180° (07:51–08:15 min; Fig. 2f, g) while continuously oscillating the pectoral fins. At 08:16 min the rays separate and swim away as the video ends. The total mating sequence lasted approximately 83 s.

Mobula thurstoni

The courtship behavior of *M. thurstoni* was documented on May 18, 2015 during a two-week expedition to the

Archipelago of Saint Peter and Saint Paul (ASPSP)-Brazil by a team of researchers from the Department of Fisheries and Aquaculture of the Rural Federal University of Pernambuco (UFRPE) in Brazil. At 09:15 h, a group of *M. thurstoni* was observed passing by the research vessel while anchored ~ 0.5 km southeast of the main inlet. A DJI Phantom 2 Vision+ quadcopter was launched and visually located the devil rays at ~ 09:22 h., approximately 3.2 km east-southeast of the research vessel (0° 54.983 N 29° 20.8 W). The drone followed and recorded (Online Resource 3) the group of rays for 95 s until the group dove to depth and the low battery level required the drone to return to the vessel.

The group of devil rays consisted of three smaller, lighter colored males following a larger, darker female. The group swam just below the surface (00:32 min) with the female in front of the pursuing males, all in a single line formation (Fig. 3a). Shortly after observations began, the female dove below the surface followed by the males (00:48 min), and the rays performed a complete upside-down loop (Fig. 3b). At 00:52 min, the rays surfaced with the female swimming quickly away and the males in pursuit (Fig. 3c). The female would often flap its pectoral fins upward in an exaggerated manner that appeared to provide no speed advantage, but rather seemed to serve more as a way not to be restrained by the males. After swimming for a few more meters the female distinctly stopped swimming and floated motionlessly on the surface. At 01:04 min, one male went directly underneath the cloacal region of the female and then tried to bite the female's left pectoral fin, but it was quickly retracted (Fig. 3d). Meanwhile, a second male swam underneath and positioned himself in front of and deeper than the female, while the first male turned and blocked its movement by positioning himself in front of the female's head at the surface (01:07 min). The third male remained behind the female during these maneuvers (Fig. 3e). After the unsuccessful attempt, the first two males circled back and positioned themselves behind the female, which had remained floating at the surface (Fig. 3f). After a few seconds, the female began swimming and the mating train resumed. Soon after (01:33 min), the female slowed its swimming speed again and the same sequence of events occurred. The female remained floating at the surface, and one male attempted to bite its left pectoral fin tip while the other two males blocked the female's escape (Fig. 3g). The group of rays again dove below the surface, at which time observations were aborted due to the low battery level of the drone.



Fig. 3 Pre-mating sequence of *M. thurstoni* observed May 18, 2015 off the Archipelago of Saint Peter and Saint Paul, Brazil. Sequence includes both “close following” and attempted “pre-copulatory biting” phases. **a** A “mating train” consisting of 3 males closely following a single female. Note: all three males are lighter in color than the female. **b** Male and female rays making a diving loop beneath the surface. **c** Rays surface with female ray quickly

swimming away from pursuing males. **d** Female ray pauses at the surface, while one male attempts to bite onto her left pectoral wing. **e** The other two males attempt to block the female’s escape and force her to remain near the surface. **f** Males circle back behind female in clockwise pattern and rejoin pursuit of female. **g** The female slows near the surface and a male makes a second attempt to bite onto the left pectoral wing of the female

Discussion

The mating behavior we describe for *A. narinari* and *R. bonasus* follows the general mating sequence previously described by Yano et al. (1999) and Chapman et al. (2003), with all five stages of the mating sequence

documented. In both cases presented here, a male was observed closely following a female prior to biting the pectoral fin. The male then rotated under the female, inserted a clasper, and rapidly oscillated both pectoral fins while the pair slowly sank and came to rest on the seafloor before separating. These observations are also

consistent with observations of captive mating made by Uchida et al. (1990) for *A. narinari* (likely *A. ocellatus*, see White 2014) and *R. javanica*, a sister species to *R. bonasus*. In particular, both species use the ventral to ventral posture during copulation (Figs. 1f–h and 2d, e), with *R. bonasus* rotating 180° on the axis of the clasper (Fig. 2f–h) as described by Uchida et al. (1990). It should be noted, however, that while we were able to provide a complete description of the mating sequence for both species, we are unable to determine if either mating event was successful. In their observations, Uchida et al. (1990) suggested that captive mating events were successful based on the presence of a cloud of semen leaking from the female's cloaca after the male removed his clasper. However, given the nature of the video and photographs presented here, such observations were not possible.

Our observations of the courtship behavior of *M. thurstoni* are consistent with courtship behavior previously described for *M. alfredi* Krefft 1868 (Marshall and Bennett 2010; Deakos 2012), *M. birostris* (Yano et al. 1999), *M. mobular* (Duffy and Tindale 2018), and *M. tarapacana* (Sobral 2013). We observed all of the common behavioral components of courtship: mating trains with multiple male participants, rapid bursts of speed, female avoidance, veering and looping behavior, and males nudging the ventral surface of the female (Marshall and Bennett 2010; Duffy and Tindale 2018). Although copulation was not observed, there were two unsuccessful attempts made by the males to bite onto the female's left pectoral fin tip, suggesting male team behavior, as well as a relative degree of cooperation by the female. During these attempts, the female drastically slowed its swimming speed and appeared to stop moving while allowing the males to approach. At this point two of the males were positioned along escape routes of the female, approaching from below and forcing the female toward the surface and making a sharp turn in front of the female to prevent her from swimming forward. The other male then approached from slightly behind and below the female in an attempt to bite the tip of female's left pectoral fin. The approaches from below by the males are consistent with observations by Duffy and Tindale (2018) of male *M. mobular* attempting to grasp the pectoral of females, which they suggested was likely due to the female's tendency to swim close to the surface. Such behavior could limit the males' ability to grasp the female's pectoral fin. Indeed, both unsuccessful attempts that we observed for

M. thurstoni occurred at the surface with the wingtips of the rays often breaking the surface of the water, which could explain why these attempts were unsuccessful. Unfortunately, because the drone had to return to the boat due to a low battery warning, we were unable to remain with the rays and do not know if the courtship behavior continued or resulted in an eventual successful copulation.

Although the general mating behaviors of batoids follow the same sequence of events originally described by Yano et al. (1999), there are some variations among species. Such variations are most notable during the close following/courtship phase of the mating sequence. While describing the reproductive ecology of *M. alfredi*, Marshall and Bennett (2010) suggested that courtship could be subdivided into different stages based on different observed behaviors during this phase. In the three cases presented here, we also observed a variety of behaviors during courtship with differences in behaviors among the three species. For *A. narinari*, courtship (and the entire mating sequence) involved a single male following a female, making multiple sharp turns before swimming rapidly toward the female and biting its pectoral fin. No other rays were seen during the entirety of the observed mating sequence; however, it is possible the two rays were only observed after they had split from a larger group. In the case of *M. thurstoni*, multiple males pursued a single female in a mating train, mimicking the looping and diving behavior of the female until it appeared to slow down enough to allow males to approach. For *R. bonasus*, multiple males and multiple females were observed swimming in a clockwise pattern (Fig. 2a), similar to the tight circular swimming formation of *M. tarapacana* observed by Notarbartolo-Di-Sciara and Hillyer (1989). Although they did not speculate its significance, considering that this behavior immediately preceded copulation in our observations of *R. bonasus*, it is possible the circular swimming pattern may be a variation of the mating train behavior observed in *M. thurstoni* and other *Mobula* species (see Deakos 2012; Sobral 2013; Duffy and Tindale 2018). Despite these variations among species, courtship/close-following behavior appears to be an important step in the mating sequence. Specifically, it has been suggested that close following allows males to assess the reproductive state of the females using olfactory cues. Kajiura et al. (2000) hypothesized that organic molecules originating from the cloaca of female rays

may act as pheromones, and both Uchida et al. (1990) and Chapman et al. (2003) observed males attempting to mate with females almost immediately after parturition. Similarly, Deakos (2012) and Duffy and Tindale (2018) both observed mature males actively pursuing visibly pregnant females during mating, while ignoring other non-pregnant females that were present in the area.

An interesting observation shared among all three cases presented here was the noticeably lighter dorsal coloration of the males compared to the darker dorsal coloration of the females. The difference in color between males and females, in addition to the olfactory cues mentioned above, could serve as a possible visual cue for identifying potential mates. This could be particularly useful for schooling species, such as mobulids, which form large, seasonal aggregations for the purposes of mating (Deakos 2012). While there are no previous accounts of elasmobranchs exhibiting different colorations during the mating season, unique spawning coloration/patterns have been seen in some marine teleosts that form large spawning aggregations, such as groupers (Colin 1992; Gilmore and Jones 1992; Domeier and Colin 1997). The difference in dorsal coloration also suggests that rays might exhibit sexual dimorphism in color between males and females. Kajiura and Tricas (1996) found that dental sexual dimorphism in Atlantic stingrays (*H. sabinus* Lesueur, 1824) was seasonal, with mature males developing cusp like teeth during the mating season presumably to aid in grasping onto the female during copulation. Unfortunately, color expression in elasmobranchs, particularly batoids, is relatively unstudied. Ari (2014) documented rapid and intense color change in the white markings seen on the dorsal surface of the reef manta (*M. alfredi*) but did not speculate on the cause of this change. Gunn (2018) concluded that the ability of the yellow stingray, *Urobatis jamaicensis* (Cuvier, 1816), to change color with respect to its environment was a physiological response. However, the exact mechanism of this response is not certain, despite evidence that physiological color change has a hormonal component (Visconti et al. 1999; Gelsleichter 2004). Although our observations are limited to individual occurrences for each species, the fact that this phenomenon was seen in all three species during mating events suggests a conserved cue to elicit copulation or identify possible mates.

Conclusion

The highly mobile nature of elasmobranchs and their aquatic habitat makes it inherently difficult to observe and document mating behavior (Duffy and Tindale 2018). For batoids in particular, detailed accounts of mating behavior from the wild have been greatly limited. However, with development of inexpensive waterproof action cameras and easily operable aerial drones, it is becoming increasingly easier to observe animal behavior non-intrusively in the wild. The observations presented here provide the first complete descriptions of mating behavior in the wild for both *A. narinari* and *R. bonasus*, as well as the first documented account of courtship behavior in the wild for *M. thurstoni*. While there were some variations among the three species, the overall similarity of the mating behaviors presented here and previous descriptions of batoid mating behavior supports the assertion by both Yano et al. (1999) and Chapman et al. (2003) that these behaviors are likely conserved among batoids.

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Compliance with ethical standards

Ethics statement There are no potential conflicts of interest for any of the contributing authors. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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