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Mating scars among sharks: evidence of coercive mating?

Erich K. Ritter[1,2] · **Raid W. Amin**[1]

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Abstract
On rare occasions, during mating season among sharks, 'mating scars' appear on female sharks' bodies caused by the males holding onto them. The low frequency of sharks bearing such scars indicates that those markers are not part of regular mating efforts. These scars are mostly deeper cuts and punctures, indicating a more forceful motivation such as coercive mating from the male's side. We discuss scenarios based on mating scars from three Carcharhinid species, describe and explain the arrangement of these bite scars, and consider plausible mating strategies used by males, including coercive mating.

Keywords Coercive mating · Behavior · Gill · Scars · Shark

Introduction

Coercive mating, a male's forceful attempt to mate, occurs in many animal groups and is triggered by a variety of factors (e.g., Palmer 1989; Braun and Harper 1993; Neff et al. 2008). The only vertebrate class where coercive copulations have not yet been described are the cartilaginous fishes—the sharks, rays, and chimaeras. However, there is no reason why this type of copulation should not exist among them as well. One potential indicator that it does is the presence of so called 'mating scars' on female sharks, which are sometimes observed during their respective mating seasons (e.g., Stevens 1984; Jensen et al. 2002). In addition to being potential outcomes of actual matings, these marks could also be caused by 'precopulatory biting' (Pratt and Carrier 2001) and were noticed early on in shark research (e.g., Springer 1960, 1967). However, thus far, these scars and wounds have not yet been examined in the context of possible coercive matings.

During mating in most shark species, a male shark uses his jaws to grab the female in or around her gill or pectoral fin area to hold her in position and enable copulation (e.g., Tricas and LeFeuvre 1985; Pratt and Carrier 2001; McCauley et al. 2010) which is identical among rays (e.g., Luer and Gilbert 1985; Ritter and Vargas, 2015). During this act, the male either pins the female down (e.g., Carrier et al. 1994) or clings to her in order to align one of his two claspers with her cloaca (Tricas and LeFeuvre 1985). It appears that while the male shark holds onto a female in this way, it sometimes creates wounds known as mating scars (Fig. 1). These wounds reflect at least subcutaneous skin penetrations, but can be more severe, and can even result in permanent body damage, such as sliced pectoral fin edges (Fig. 2). As a potential consequence of such wounds, female blue sharks (e.g., Nakano and Stevens 2008) or lesser-spotted catsharks may have developed thickened skin (e.g., Crooks et al. 2013).

An injury during copulation, whether temporary or permanent, can result in short-term or indefinite fitness reduction for the female shark. From an evolutionary viewpoint, it is not advantageous for a male to transfer sperm into a female whose survival might be jeopardized, in particular considering that a male shark will not watch over the female during her healing process. Thus, the question arises as to why on rare occasions males use such force during mating bouts that females can be left with damaging wounds. The most likely explanation is that the female was not willing to mate, and the damage occurred in an attempt at coercive copulation by the male.

Here, we present and discuss pictorial evidence that at least some of the mating scars could reflect coercive copulations rather than scars due to regular mating attempts.

✉ Erich K. Ritter
eritter@uwf.edu

1 Department of Mathematics and Statistics, University of West Florida, 11000 University Parkway, Bldg. 4, Pensacola, FL 32514, USA

2 Shark Research Institute, Princeton, NJ 08540, USA

Materials and methods

Fresh teeth marks on female Caribbean reef sharks, *Carcharhinus perezi*, lemon sharks, *Negaprion brevirostris*,

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Fig. 1 Female Caribbean reef shark with several mating scars caused by a male's upper and lower teeth

from different sites in the Northern Bahamas, and blue sharks, *Prionace glauca*, from one site in the Azores, Portugal, were photographed between 2011 and 2014 during their respective spring and summer mating seasons. Despite the rather long data collection period and often daily diving with the respective species, the numbers of females carrying mating wounds remained very low, even when the majority of sharks at the site were females. Since mating sites for these three species are unknown, chances are that the dive sites did not overlap with the respective mating sites, or that these species do not possess defined mating sites.

Half of the sharks could be photographed from both sides. Half of those had no bites on the other side, thus using the average from both sides to compare with the sharks where only one side could be photographed was rejected, and the side with more bites tallied.

Although we used 3D shark models with overlaid grids in previous studies to pinpoint exact locations on a sharks' body (Amin et al. 2016), due to the dissimilar body proportions of the three species in this study, we reduced our approach to larger and comparable body areas (Fig. 3). Since the main target areas for males during mating attempts are the gill and pectoral fin regions of a female (e.g., Tricas and LeFeuvre 1985; McCauley et al. 2010), these two locations were purposely chosen (regions 2 and 3), while the remaining areas were categorized based on comparable body areas (Fig. 3).

Fig. 2 Frazzled pectoral fin edges of a female Caribbean reef shark during mating season

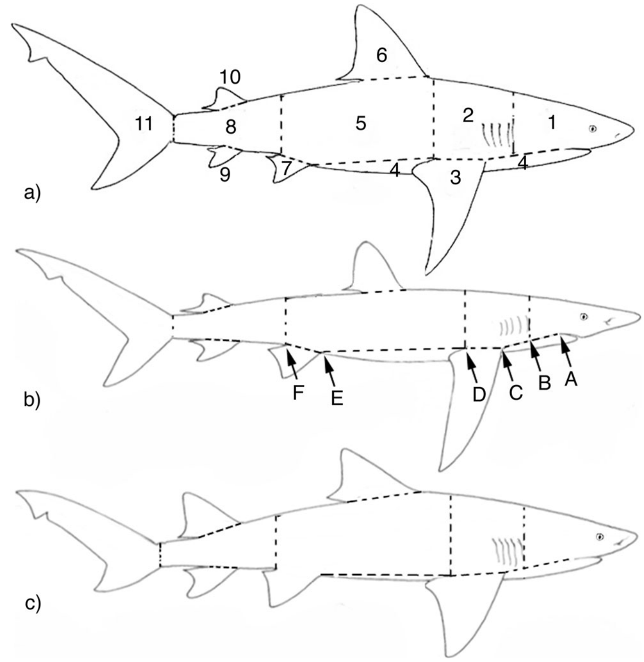

Fig. 3 Bite wound regions (1, 2...11) defined by reference points and transverse planes on an **a** Caribbean reef shark, **b** blue shark, **c** lemon shark. Transverse planes: a = gill plane, in front of the first gill slit; b = pectoral plane, at the insertion of the pectoral fin; c = pelvic plane, at the insertion of the pelvic fin; d = caudal plane, at the origin of the caudal fin. Reference points: A = mouth corner; B = intersection between line AC and gill plane; C = pectoral fin origin; D = pectoral fin insertion; E = pelvic fin origin, F = pelvic fin insertion. Region: 1 = snout, anterior to gill plane and above line AB; 2 = gills, between pectoral plane and gill plane above the pectoral fin base and line BC; 3 = pectoral fin; 4 = belly, below line DE and line AC; 5 = flank, between pectoral and pelvic plane above line DE and below pectoral fin base; 6 = first dorsal fin; 7 = pelvic fin; 8 = peduncle, between pelvic plane, caudal plane and the bases of the second dorsal and anal fin; 9 = anal fin; 10 = second dorsal fin; 11 = caudal fin

Estimation of female size would have benefited the project but the rather quick appearance and disappearance of the targeted females made it impossible to measure their sizes.

It is understood that males of some species such as the small-spotted catshark, *Scyliorhinus canicula*, wrap themselves around the female's body in the cloacal area for the purpose of mating (e.g., Houziaux and Voss 1997). This is not the case for carcharhinid species, which align themselves along their longitudinal axis (e.g., Tricas and LeFeuvre 1985; McCauley et al. 2010).

Potential coercive mating definition

A wound related to potential coercive mating was defined as any bite to a female's body during the mating seasons that caused at least subcutaneous tissue damage. Common scratches in the gill and pectoral fin area were ignored, they could have stemmed from, e.g., competitive bouts (see next paragraph).

Fig. 4 Gill wound as a result of a likely predatory bout. **a** Female Caribbean reef shark, photographed outside her mating season; **b** male lemon shark, claspers were seen in the video clip from which this single frame was taken

Table 1 Number of bites per body side for all examined sharks. For those sharks where both sides were photographed, the side with more bites was chosen and marked with an asterisk (*). L1… L4 = numbered lemon sharks; C1… C10 = numbered Caribbean reef sharks; B1, B2 = blue sharks. Numbers 1 to 11 reflect the areas defined in Fig. 3

Shark	1	2	3	4	5	6	7	8–11
L1	0	0	0	1	2	0	2	0
L2*	0	0	0	1	4	0	0	0
L3*	0	4	0	2	3	0	1	0
L4*	0	2	1	2	6	0	3	0
C1*	0	0	0	2	9	0	0	0
C2*	0	0	0	1	4	0	0	0
C3	0	0	0	2	0	0	0	0
C4*	0	1	0	3	3	0	1	0
C5*	0	1	0	2	6	0	1	0
C6*	0	6	0	1	5	0	0	0
C7	0	1	0	3	2	3	0	0
C8	0	2	2	2	7	2	0	0
C9	0	1	0	1	8	0	0	0
C10	0	2	0	2	8	0	0	0
B1	1	4	1	2	5	0	0	0
B2	0	2	0	2	3	0	0	0

Non-mating-related wounds during mating seasons

Competitive and predatory bouts can also create wounds in the gill area. Competitive bouts among sharks result in rather superficial scratches and never affect subcutaneous layers, as noted during a study on competition between two Carcharhinid species (Ritter 2001). Superficial scratches were thus not considered actual mating scars even if seen during the respective mating season of the three species. On the other hand, predatory bouts leave wounds with an actual tissue loss and are seen year-round (Fig. 4). Overall, it is rather rare to find sharks with severe predatory wounds, since these animals are prone to get killed should they not be able to defend themselves. Gill wounds (as seen in Fig. 4) have not yet been observed during mating seasons of the three examined species.

Statistics used

A ratio between scarred and non-scarred female sharks was not determined due to the very rare appearance of the former, as well as the unknown number of female sharks that showed up repeatedly at the respective sites throughout the data collecting period. Depending on the site, each area showed between 10 and 20 animals/dive for lemon and Caribbean reef sharks and 5 to 10 sharks/dive for the blue sharks. The seven bite areas (Fig. 3) were split into two groups, 'gill bites' (areas 2–3), and 'body bites' (areas 4–7). The single bite in the head area (area 1) of shark B1 (Table 1) was excluded in the evaluation, due to its oddity. To detect potential differences between the two shark groups, aside from the 'gill bites', the number of 'body bites' were compared. Due to the small sample size, a Mann-Whitney-Wilcoxon (MWW) rank sum test with exact one-tailed p values was used, with the proc npar1way procedure of SAS. The exact test was the most appropriate, because a large-sample normal approximation might not have been adequate. To further differentiate bite locations, the 'gill bites', consisted of bites to the gills and pectoral fins, were evaluated with another MWW test.

Results

Sixteen sharks with mating scars were photographed during the data collecting phase. Half of these individuals were photographed from both sides (see below). The average number of bites per shark and side was 9.2 (SE = 0.92; $N = 16$). Comparing the amount of 'body bites' between the two shark groups revealed a significantly greater bite count ($p = 0.0062$) among those sharks that also showed 'gill bites'. When a location within 'gill bites' was chosen, either gill area or pectoral fin, a significant preference for the former was seen ($p = 0.0068$).

Five of the 16 sharks had pelvic fin wounds but none showed wounds in the peduncle area, on the anal fin, secondary dorsal fin, or on the caudal fin (Table 1).

Of the eight specimens that were recorded from both sides, four sharks had wounds on both sides, but only one shark carried wounds in the gill area on both sides.

Discussion

Our results suggest that coercive mating in sharks needs to be considered when it comes to the origin of mating scars. Attributable to the rather low number of observed incidents—despite the almost daily diving throughout the respective mating seasons—it seems that coercive mating events, at least for the three included species, are indeed either rather rare events, or the dive sites did not overlap with mating sites (e.g., Hazin et al. 1994; Feldheim et al. 2002). Due to the further uncertainty whether mating sites even exist for some species, the following discussion does not focus on the actual number of mating events but rather on the possible existence of coercive copulations in sharks and how the scar patterns on the females possibly came about.

Based on this novel interpretation of copulation among sharks, comparable results do not exist; thus, teleosts were used for potential comparisons (e.g., Evans et al. 2002; Plath et al. 2003; Godin and Auld 2013). It is understood that such a comparison can only be used in a tangential manner, but still offers ideas that may be relevant to potential coercive mating among sharks. Although male mate choice (e.g., Dosen and Montgomerie 2004a; Guevara-Fiore et al. 2009; Guevara-Fiore 2012), courtship display, sperm competition, and female mate choice, to name a few, reflect potential causes of coercive mating (e.g., Ryan and Causey 1989; Dosen and Montgomerie 2004b; Godin et al. 2005), the following discussion relies more on aspects directly or indirectly related to the interpretation of the initial picture of the shark wounds.

Potential coercive mating attempts

More than 30% of the sharks did not have bites in the gill and pectoral fin area. Assuming that the males need to hold on the gill and pectoral fin area, as others do within the same family (e.g., Tricas and LeFeuvre 1985; McCauley et al. 2010), a lack of bite injuries in those areas could reflect that mating attempts were not successful and that the female was able to free herself before the males grab her at gill or pectoral fin locations. This could suggest that female choice is of importance, where she only considers males that surpass a certain strength level, or that the females are visually drawn to comparatively larger males within the pool of milling male sharks at the mating site. Females may thus demonstrate a size-selective response where non-desirable males would be fought off. These attempted copulations could also reflect a form of harassment as an expression of coercive behavior (e.g., Clutton-Brock and Parker 1995) and not actual attempts of coercive mating. The lack of gill and/or pectoral fin wounds could also mean, in contrast to nurse sharks, *Ginglymostoma cirratum* (Castro 2000), a polyandrous species, that once a female of one of the examined species has been impregnated, she rejects further copulation attempts. Having no scars or wounds in the gill and/or pectoral fin area after a successful copulation would imply that males do not have to clamp down that hard with their jaws once a copulation occurs willingly; thus, no wounds would be left.

It is known that some shark species do not reproduce on an annual basis (e.g., Driggers et al. 2004; Farrell et al. 2010). It is plausible that such females will not release mating pheromones but still mingle with generally receptive females at potential mating sites. If this is the case, it remains to be seen if male sharks can differentiate between receptive and non-receptive females, as shown for some teleost species (e.g., Guevara-Fiore et al. 2009), and are likewise able to detect the more fecund females (e.g., Jones et al. 2001). However, this could also mean that ready-to-mate males completely disregard the release (or not) of such pheromones indicating receptive females, but instead try to copulate simply based on opportunity.

Targeted body areas

Although pectoral fins are generally used as a target region for male sharks to hold on to a female during mating (e.g., Tricas and LeFeuvre 1985; Carrier et al. 1994), they were hardly damaged among the observed sharks, compared to their gill areas. Nevertheless, females with frazzled pectoral fin edges have been observed in Caribbean reef sharks (Fig. 2). Beside the potential gill preference, the results also indicate a predilection for one-sided approach patterns. This would support the observation that only one functional clasper exists during mating season (e.g., Klimley, 1980; Tricas and LeFeuvre 1985; Pratt and Carrier 2001). From an evolutionary viewpoint, such a suggestion seems unlikely, however since it would limit a male's approach strategy to only one side. The suggestion that both claspers are fully functional during mating season is shown by 'clasper flaring' in whitetip reef sharks, *Triaenodon obesus* (Ritter and Compagno 2013), where both claspers were seen to be independently moved and turned forward.

In this study, the number of bites to the pectoral and gill areas was lower than to the rest of the body should a female carry both. This could indicate that a potential suitor would primarily approach a female's body region from the side or behind and initially just grab her in any body area to slow her down. During this process, the male then would work himself forward until reaching the final desired position at the gill and/

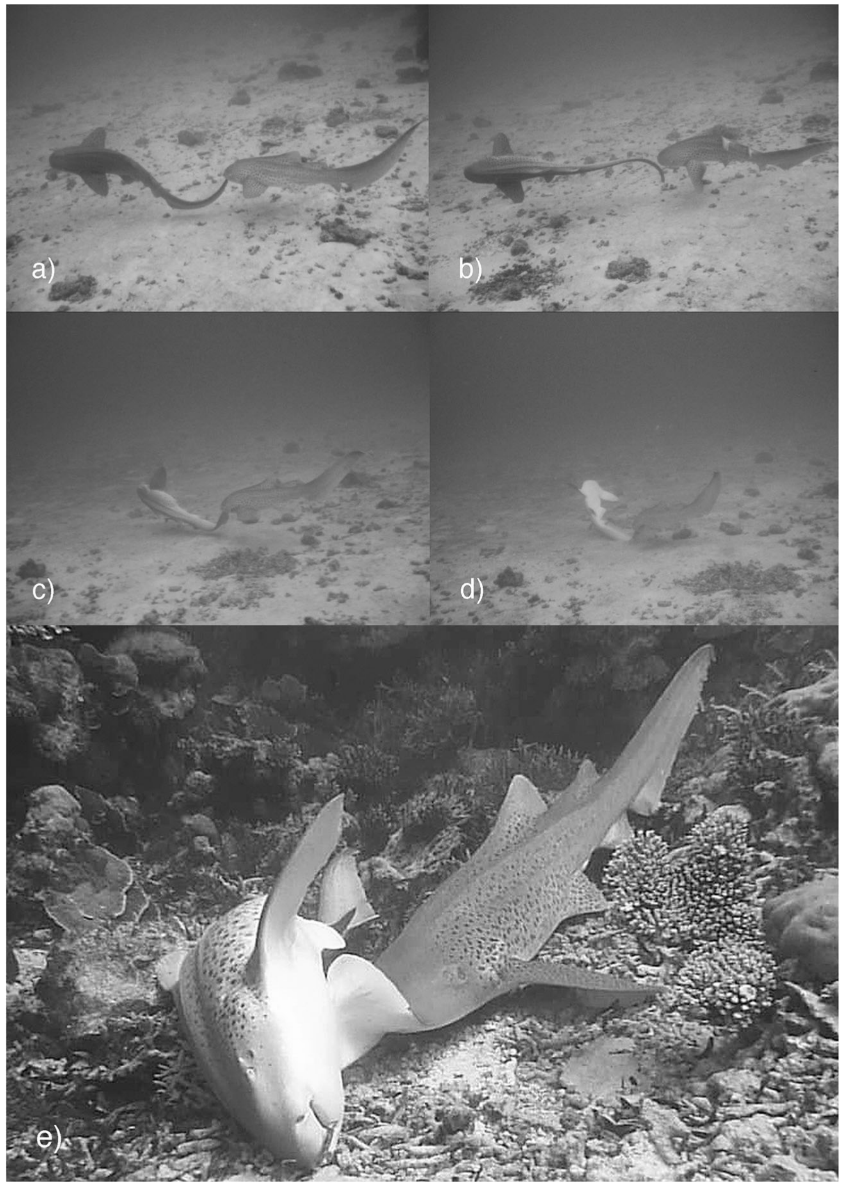

Fig. 5 Putative premating behavior in zebra sharks. **a**–**d** Male approaching female from behind, touching and grabbing her upper tail tip to turn her onto her back; **e** male holding on to the female's pectoral fin prior to mating

or pectoral fin area with its jaws. Meanwhile, the female would try to fight off unsuitable males until she gives in, or is overpowered, especially when the male reached the gill and pectoral fin area. So, a more persistent male would likely keep trying until he reached his copulation position where his jaws could hold on to a female. Such a male would then also likely create more bites in the female's body area while moving forward along her body until he then reaches his copulation position. Such a possible scenario could explain why significantly more body bites in those female sharks occurred that also showed bites in their gill/pectoral fin region. This could also explain why half of the sharks photographed from both sides showed wounds on one side only. Letting go of one side, for whatever reason, and shifting to the other side, would give a non-receptive female an opportunity to escape, or at least temporarily shake the unwanted male off.

It appears that when a male shark has the choice to hold on to either a female's gill area or along a pectoral fin as the final position to enable copulation, the former is favored. Biting the female shark's gill area causes a likely rotation along the male's main body axis which in turn would bring a male's claspers closer towards her cloaca.

Some males targeted the pelvic fin area with their bites. This is also true among rays (Tricas 1980; Ritter and Vargas 2015), the closest relatives to sharks. Among teleosts, the reason for such an aim is to assess a female's predisposition to mating via olfactory cues (e.g., Miranda et al. 2005; Friberg 2006) which could also be true for sharks (Johnson and Nelson 1978). Since the wounds around the pelvic fins and cloacal area of the examined sharks actually showed bites, with some being rather severe, the purpose of these bites as detecting olfactory cues does not seem likely; neither do they seem to reflect a tactile signal or stimulation of any kind by the male shark.

Mating hormones as a clue for ready-to-mate females

It is known that juvenile female blue sharks, *Prionace glauca*, can store sperm until adulthood is reached (Stevens 1976) and such juveniles already show some of the scarring mentioned here (Calich and Campana 2015). This raises the question of whether mature males are able to distinguish not only between receptive and non-receptive females but also between virgins and recently mated females, as has been suggested by studies on teleost mating systems (e.g., Liley 1968; Liley and Wishlow 1974; Guevara-Fiore et al. 2009). It is plausible that virgins and mated females could be distinguished by differences in the composition of their pheromone releases (e.g., Guevara-Fiore et al. 2009). With reference to the virgin mating of blue sharks, it could also be possible that juvenile males try to mate prior to reaching adulthood for the purpose of honing the skills needed to successfully mate once adulthood is reached. Targeted females may realize that the pursuing males have not yet reached maturity and will thus try to reject them. This then raises the question of how successful male sharks are when trying to mate during their first year of maturity.

Relative size between the two sexes

It has been shown among some teleosts that smaller males attempt more coercive copulations than larger ones (e.g., Parzefall 1969; Clutton-Brock and Parker 1995; Schlupp et al. 2001). Although individual teeth marks of male sharks were identifiable on females throughout this study, the correlations between interdental distances and body size have not been done for any of the presented shark species. However, Calich and Campana (2015) used lateral jaw gape as a size reference for blue sharks when describing mating or courtship scars. Knowing the sizes of the males and females when mating occurs is crucial information to further delve into the idea of coercive mating (e.g., Skomal and Natanson 2003), especially age-related questions. Being able to determine male size relative to the targeted females potentially could also help determine the ratio between soliciting and potential coercive copulation.

Ryan and Causey (1989) showed that larger teleost males mostly court and chase less, and vice versa. Large(r) male sharks could overpower small(er) females; thus, a bigger size would not only be advantageous for possible courting but also for potential coercive copulation. An estimation of female size would have benefited the project, as already mentioned, and will be included in a continuation of this topic. Likewise, the size of males based on tooth imprints will also be included. Such would then allow to answer additional questions like bite numbers in relation to female size or a size comparison between the two sexes.

Independent of sizes, copulations could also depend on the actual ratio between males and females at a mating site. The more this ratio leans towards the males, the more likely a potential coercive mating attempt could occur. At this point, it remains unknown if male sharks actually compete between each other over the opportunity to mate with a particular female or not.

Premating ritual?

Various shark species are known to have some premating rituals (e.g., Gordon 1993; Domi et al. 1999; Whitney et al. 2004). For example, male zebra sharks, *Stegastoma fasciatum*, have been observed touching the tip of the female's caudal fin and initiating a body rotation along her longitudinal axis (Fig. 5). Such behavior could be seen as a tactile premating ritual, or indeed as actual foreplay. In addition, lemon sharks swim next to each other for an extended period of time in a synchronized manner (personal observation), in what could also be interpreted as some form of premating ritual. Similar observations were made by Clark (1963). Such swim patterns could lead a female to a better sexual performance (e.g., Pfaus et al. 2001). Observations like these suggest that the act of mating may not just be guided by a release of sexual hormones by the female shark but also by visual factors such as the already mentioned partner size, or conspicuous mating displays, and the potential tactile stimuli.

On the importance of potential coercive mating in sharks

The advantages of potential coercive mating include increased genetic variability (e.g., Neff et al. 2008), circumvention of female choice (e.g.. Evans et al. 2003), or access to unreceptive females (Liley 1966) to name a few. Although to date these effects have only been studied among some teleost populations, they may also play a role in sharks. Considering the ancient evolutionary origins of sharks, coupled with their use of internal fertilization, some of the known strategies seen within teleosts are likely to be present at least in some of the more modern shark species. It is also essential to further explore how much effort a male actually invests in a receptive female compared to a non-receptive one (e.g., Guevara-Fiore et al. 2010). Besides such investment of effort, it is also paramount to get a better understanding regarding the courtship tactics of male sharks and potential sexual conflicts, as well as a female's preference and her strategy of choosing appropriate males for mating.

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