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## Sexual conflicts in sand tiger sharks *Carcharias taurus* (Rafinesque, 1810) in an artificial environment

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**Abstract**

Understanding reproductive behaviours and the environmental conditions that facilitate reproduction is important for successful reproduction in managed care. Complex reproductive behaviours have been observed in both aquarium and free-ranging elasmobranchs. Sexual conflicts, including pre-copulatory behaviours in sand tiger sharks *Carcharias taurus* in managed care have been previously documented. This study reports observations that corroborate the previous accounts of reproductive behaviours as well as describing novel consensual conflicts between males and detailing the male dominance hierarchy in six sand tigers at the National Aquarium. The observations suggest that male behaviours are not strictly pre-copulatory, as consensual male conflicts occurred to the exclusion of attempted copulation, and in the absence of females. Physical separation of either the dominant or most subordinate male decreased the occurrence of sexual conflicts, suggesting that these individuals are the key sharks in hierarchical settings and that conflicts among sand tigers are not strictly related to reproduction, but may be driven by social, physiological, olfactory and/or electrosensory cues.

### Introduction

Successful breeding in an artificial environment is enhanced by understanding reproductive behaviours exhibited by animals (Henningsen et al. 2004a; 2017). Because of the scarcity of observations of reproductive behaviours in wild animals, observations of reproductive behaviours in animals in managed care contribute the bulk of knowledge on mating behaviours in elasmobranchs (Pratt and Carrier 2001; Carrier et al. 2004; Henningsen et al. 2004a). To expect successful breeding in artificial environments, effects of the environment must be considered since behaviours may be modified or attenuated because of confinement (Henningsen et al. 2004a; Whitney et al. 2004; Pratt and Carrier 2001; 2005). The sand

tiger shark *Carcharias taurus* (Rafinesque 1810), is among the most popular species displayed in aquaria and is a species for which reproductive behaviours have been described (Gordon 1993; Pratt and Carrier 2001; Henningsen et al. 2004b; 2017; Nicholson 2009; Willson and Smith 2017).

Despite the abundance of mature sand tiger sharks in aquaria globally, successful reproduction resulting in live pups in human care is rare (Henningsen et al. 2004b; 2017; Willson and Smith 2017). Artificial reproductive techniques may be useful to increase reproductive success in sand tiger sharks as well as other species in artificial environments, but knowledge on biological status and reproductive stage is critical for optimising the chances for success (Daly and Jones 2017; Henningsen et al. 2017; Wyffels et al. 2019).

Gordon (1993) first described pre-copulatory and copulatory behaviours of captive sand tigers based on behaviours exhibited by two mature males and one mature female. Reproductive behaviours for sand tigers have also been described by Nicholson (2009), Schneble (2014) and Willson and Smith (2017). The terms 'sexual aggression' as well as 'reproductive behaviours' are often used to refer to aggression or conflicts that are sexually related, but 'sexual conflicts' may be a more appropriate term to describe the range of interactions exhibited by both sexes (Birkhead and Parker 1977; Henningsen et al. 2004b; 2017). This study reports pre-copulatory and copulatory behaviours (sexual conflicts) among sand tigers at the National Aquarium (NA), including the male dominance hierarchy. It also documents relationships quantitatively between sexual conflicts and swimming speed and food intake in this group of sand tigers.

## Materials and methods

### Study animals

Adult sand tiger sharks of both sexes were maintained in a recirculating 8.52×105 l racetrack-shaped aquarium system at NA (Sabalones 1995). Photoperiod varied seasonally from 13 hr light:11 hr dark to 11 hr light:13 hr dark for summer and winter, respectively. A 90-min dimming period, from the onset of the cycle, occurred in the morning and at night. Water temperature varied seasonally from January 1998 to September 1999, from 22.8 to 24.4°C. Beginning in September 1999 through 2003, the setpoint was constant at 24.4°C, but ranged from 22.4–26.5°C, with a mean of 24.4±0.02°C SE.

Sharks were fed fresh whole fish twice per week, at a rate of 2.0 to 2.5% body weight per week, depending upon the individual. Food intake was recorded for each shark to the nearest gram. In the investigation, in 1998 the study group consisted of three adult males, Male 1, Male 2 and Male 3 (235, 252 and 236 cm TL, respectively), and two adult females, Female 1 and Female 2 (231 and 266 cm TL, respectively). The death of one male (Male 2) and one female (Female 2) in October and December 1999, respectively, resulted in a population of two males (Male 1 and Male 3) and one female (Female 1) from December 1999 to January 2001. An additional male, Male 4 (228 cm TL), was introduced in January 2001, resulting in a population of three adult males and

one adult female from January 2001 to January 2003 (Table 1). Female 1 was moved to a different aquarium system in January 2003, resulting in an exhibit population of the three adult males from January 2003 to May 2003. Table 1 provides each shark's estimated years of age, years in captivity, and acquired origins.

### Observation of sexual conflicts

Detailed observations of sexual conflicts were made from 1998 to 2003. Observations were conducted by staff monitoring in front of the viewing windows and above the exhibit along a catwalk. Pre-copulatory behaviours were recorded as described in Gordon (1993), Nicholson (2009) and Willson and Smith (2017). An observed behaviour was considered new if it was not previously described, could be clearly defined, and was displayed repeatedly. Initiation of sexual conflict was determined from the date that the sharks displayed the behaviours, and the cessation of these behaviours indicated the end date. Additional sexual conflicts were documented according to similar protocol. Preliminary diurnal and nocturnal observations to determine peaks in sexual conflicts and behaviours allowed establishment of set observation times used in the study. Observations were made during set time periods: before the lights came on via headlamp or handheld torch (07.30–09.00) after the lights came on (09.00–10.30), the middle of the day (12.00–13.30), and in the afternoon (14.30–16.00). Random observations were also conducted between 16.00 and 07.30. Depending upon the severity of sexual conflicts, longer and more frequent observation periods were conducted, including 24-hr monitoring.

Dominance hierarchy in males was determined from observed behaviours, based primarily upon the descriptions given in Gordon (1993) and Pratt and Carrier (2001), but also from observations specific to these sharks, as individuals. Hierarchical status in the three males, dominant to subordinate was represented by  $\alpha$ ,  $\beta$  and  $\gamma$ , respectively.

Because increased swimming speed was reported for males exhibiting pre-copulatory behaviour (Gordon 1993), relative swimming speeds were estimated for all NA sharks throughout the year. Relative swimming speeds were measured as the speed at which the sharks traveled from the edge of one acrylic window panel (n=28 panels) of the exhibit to the other edge, inside (1.59±0.14 m SE) of the columns. Relative speed was calculated

**Table 1.** Sand tiger sharks maintained at the National Aquarium, Baltimore, during the years 1998 to 2003 by identification number, sex, total length (cm), estimated age and duration in the collection. Estimated ages according to length are as of 1998 or upon introduction based on Goldman (2002) by sex and (sexes combined in parentheses). \*Female 1 was 100 cm TL upon acquisition in 1982 and aged at age 0.

Shark identification	Total length (cm)	Estimated age (years)	Origin	Time in captivity at the National Aquarium (total years)
Male 1	235.4	15 (11)	Wild caught (Delaware)	1990–2003 (13)
Male 2	251.7	(15)	Wild caught (Delaware)	1990–1999 (19)
Male 3	235.9	15 (11)	Wild caught (Delaware)	1994–2003 (9)
Male 4	228.3	12 (10)	Wild caught (Maryland)	2001–2003 (2)
Female 1	227	9 (10) *16	Wild caught (New York)	1982–2003 (21)
Female 2	265.5	17 (20)	Wild caught (Delaware)	1990–1999 (9)

for each shark based upon the time required to traverse the 1.59 m distance along the panel. Relative speeds were measured three times a day during the observation periods. Relative swim speed and variation were expressed on a weekly basis throughout the study period for each shark and averaged for monthly values. Since sand tiger sharks adjust their buoyancy through swallowing and expelling air into and out of the stomach (Bass and Bullard 1972; Hussain 1989; Compagno 2001), their speeds ranged from almost motionless (hovering or stalling) to actively swimming. Observations of hovering were excluded. In addition to behavioural monitoring, gross morphological observations were also recorded. These subjective observations included changes in coloration as reported by Gordon (1993) and gross assessment of the claspers and the associated cloacal region in males or the cloacal region and general robustness of the body in females.

### Separation of sharks

Due to animal health concerns from bite wounds inflicted during sexual conflicts, a male was removed from the exhibit in 1998 (Male 1) from 23 April to 15 June 1999 (Male 1) from 6 April to 19 May, and 2002 at the height of sexual conflicts. In 2002, two males were relocated, but not concurrently: Male 4 from 27 February to 1 April and Male 1 from 5 April to 21 May. In 2003, Female 1 was relocated to another aquarium system prior to the onset of sexual conflicts, from 14 January to 14 May.

### Statistical analysis

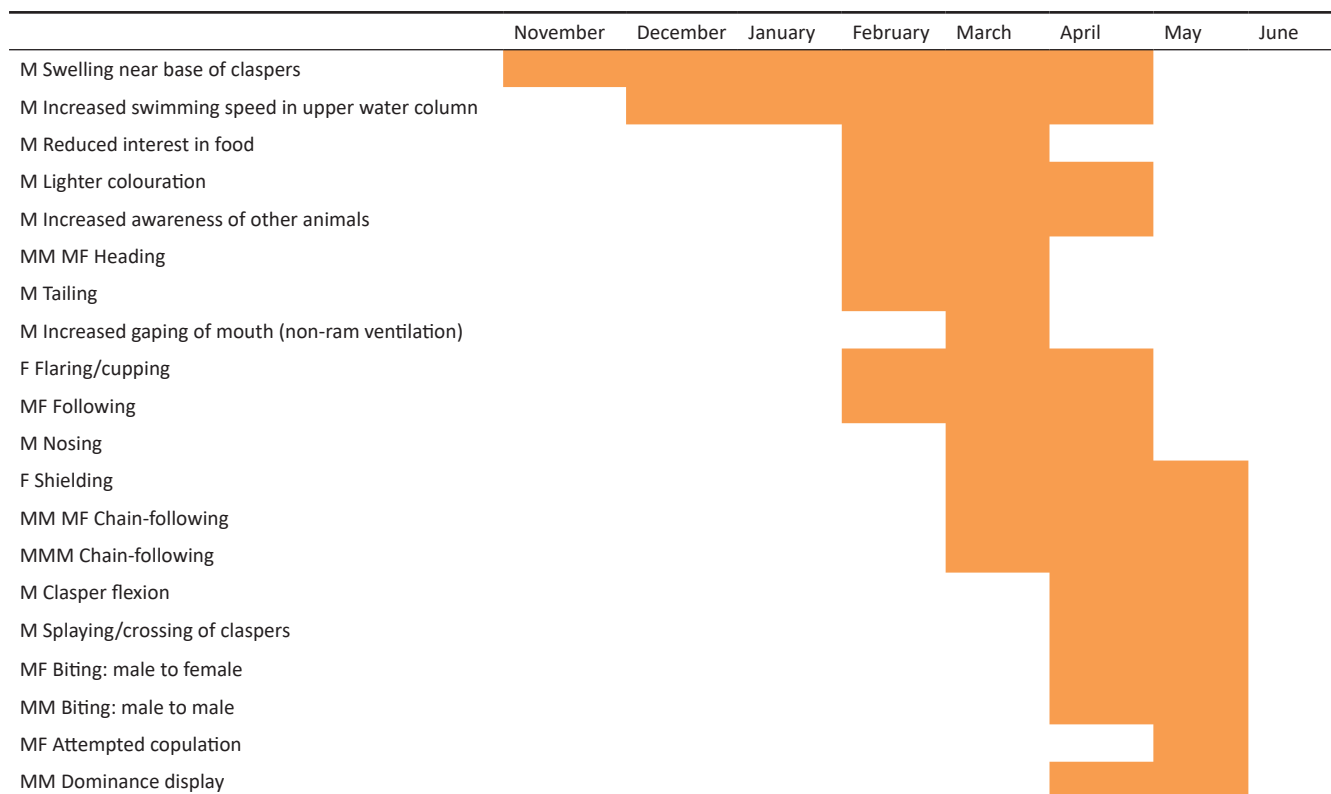
Data on relative swimming speeds were analysed monthly for annual variation in individual sharks, differences between males,

and differences between all sharks. Food intake data were analysed statistically to examine the difference between males based upon hierarchical status and between males and females, particularly for dominant males (Gordon 1993) in comparison to those not involved in sexual conflicts, and females. Data were assessed via single factor ANOVA; all statistical tests were evaluated at the level of significance  $P < 0.05$  and conducted using SigmaStat 3.1 (Systat Software, Inc. Point Richmond, CA. USA). Data that were not normally distributed or of unequal variances were analysed via non-parametric methods. Non-parametric methods included the Wilcoxon signed-rank, the Kruskal-Wallis one way analysis of variance, and the Tukey-Duckworth test. The appropriate post-hoc multiple comparison test based upon conditions of the test by SigmaStat was used to assess differences between sharks and between months.

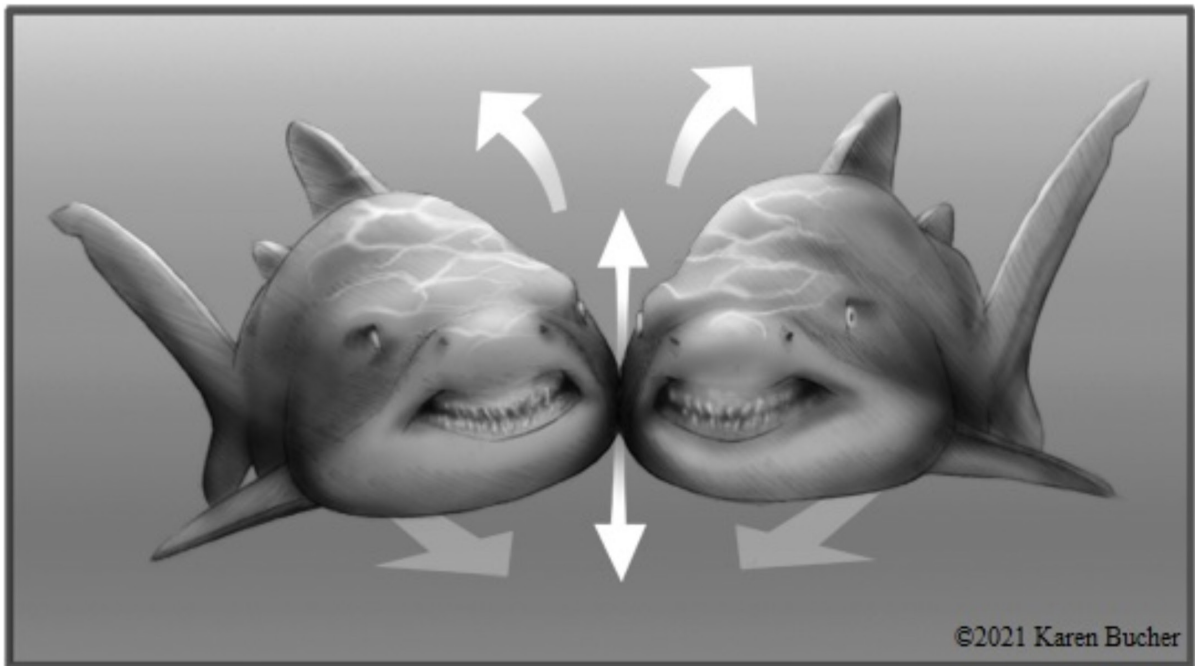
## Results

### Sexual conflicts and male dominance hierarchy

Sexual conflicts were observed every year during the study period, except for 2000, when only increased rates of swimming were observed. Although annual variation existed, the results are summarised here as a generalisation of the observations. Many of the observations corroborate the previous descriptions; however, there were instances of the lack of previously documented behaviours from rapid swimming in males to attempted copulation as well as the occurrence of new behaviours or sexual conflicts (Figure 1). Snapping at or interspecific biting of other inhabitants of the exhibit, as previously described by Gordon (1993), was



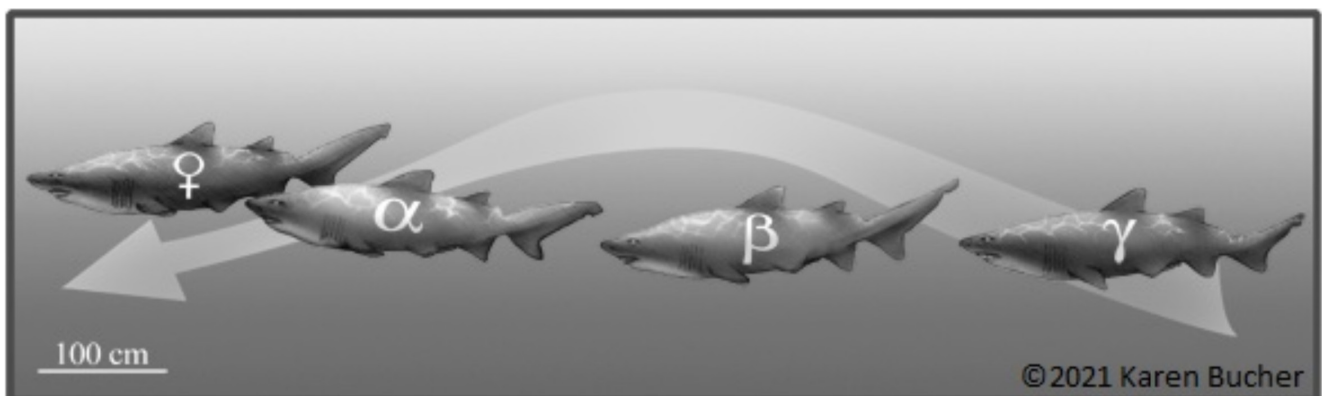
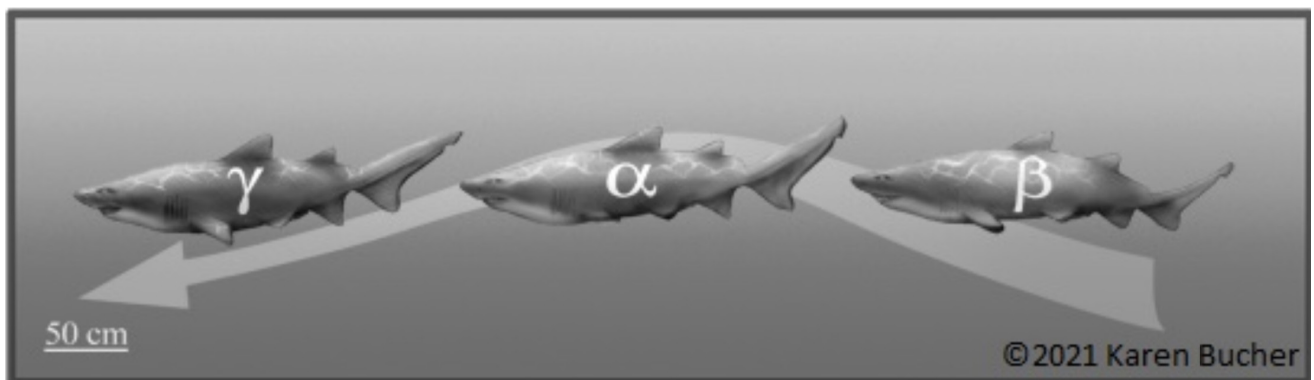
**Figure 1.** Generalised sequence of events of sexual conflicts in captive sand tigers at the National Aquarium, 1998 to 2003. F indicates females and M indicates males. Orange boxes indicates when the behaviour was observed.



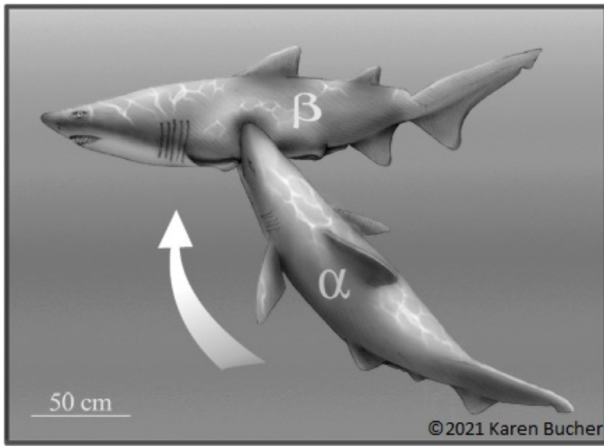
**Figure 2.** Heading behaviour observed in sand tiger sharks at National Aquarium. It was observed between males as well as between a male and a female. Illustrated by Karen Bucher, Department of Art as Applied to Medicine, Johns Hopkins University.

observed in one instance. An increased awareness of other animals was observed in the dominant males that is analogous to the patrolling reported in the earlier study by Gordon (1993),

as the males approached the others to a close proximity (~1 m), but no snapping or biting occurred. In addition, the duration of the sexual conflicts was quite variable and persisted longer than



**Figure 3.** (a) Chain-following behaviour observed in male sharks at the National Aquarium. (b) Chain-following with nosing in male sharks following a nosing male in sand tiger sharks at the National Aquarium. Illustrated by Karen Bucher, Department of Art as Applied to Medicine, Johns Hopkins University.



**Figure 4.** Male-dominance biting observed between a dominant male and a subordinate male sand tiger shark at the National Aquarium. Illustrated by Karen Bucher, Department of Art as Applied to Medicine, Johns Hopkins University.

in the previous reports (Gordon 1993; Nicholson 2009; Willson and Smith 2017). Female behaviours conformed to the previous descriptions of shielding and cupping and flaring. Cupping always preceded flaring. Submissive behaviour was not observed in the females, but retaliatory biting was observed following attempted copulation. Attempted copulation was observed in March 1998 and March 2001. The remnants of infertile egg capsules from a female were discarded and found on exhibit. This event was noted in February, March and October 1998, and again in July 2001.

Novel or previously undescribed behaviours were observed between sexes as well as within sex. Heading, a behaviour in which the sharks swim parallel and slowly and touch regions of the head in the area just posterior to the eye (Figure 2), was observed between males and between a male and a female. Chain-following (Figure 3a) and chain-following with nosing (Figure 3b) was observed between males and between males and a female,

respectively. In these behaviours, the sharks changed direction of movement if necessary, and formed a line directly behind the subordinate male in chain-following and behind the female in chain-following with nosing. The most dramatic behaviour observed within a sex was termed male dominance biting (Figure 4). The dominant male quickly approached the subordinate male from a ventral position and took a directed bite on the ventral surface of the subordinate male between the pectoral fins and pelvic fins remaining locked together for up to a few minutes. The subordinate male occasionally bit back, like retaliatory biting by a female during attempted copulation. The dominance hierarchy in males changed during the study, but the changes occurred at the subordinate position. Tailing, a previously documented behaviour by a dominant male (Gordon 1993) was observed both in Male 1 and Male 3 but more frequently by Male 1. Male 1 was the only male to tail either Male 2 or Male 4. Although male dominance biting was first observed in Male 3 directed at Male 1, all subsequent instances were initiated by Male 1 directed at Male 3 and Male 4. Male 2, although tailed, was not the subject of male dominance biting. The only male that was observed to attempt copulation was Male 1. In all instances, the female bit back in a retaliatory manner and escaped. The dominance hierarchy for the study period then, consisted of Male 1, Male 3 and Male 2 as the  $\alpha$ ,  $\beta$  and  $\gamma$  males, respectively for 1998 and 1999; Male 1 and Male 3 as the  $\alpha$  and  $\beta$  males for 2000 and 2001; and Male 1, Male 3 and Male 4 as the  $\alpha$ ,  $\beta$  and  $\gamma$  males from 2001 to 2003.

In addition to these observations, several other conflicts were inferred based upon bite marks and current sexual conflicts but are not given here as they were not directly observed. These included instances of male dominance biting and attempted copulation. Of note, however, an interesting behavioural sequence ensued following the introduction of Male 4 in January of 2001. Immediately following the introduction into the exhibit, Male 1 swam rapidly and closely behind and snapped at Male 4 but did not bite. The close following continued for five minutes and then Male 3 followed but not as close for an additional 25 minutes. In addition to the interaction between Male 4 and Male 3, Female 1 began shielding immediately after Male 4 was introduced and this persisted for two hours.

The dominant and the most subordinate males are the key sharks in the hierarchy, since removal or physical separation of either resulted in the termination of sexual conflicts. Retaliatory biting and avoidance by the female and occasional cupping and flaring preceded continuous cupping and flaring and submission by the female in previous descriptions (Gordon 1993; Willson and

**Table 2.** Analysis of annual food intake by month (mean $\pm$ SE) for each shark in the study, from 1998 to 2003, exclusive of 2000, analysed by single factor ANOVA. Non-normally distributed data or in which the variance was not equal were analysed using appropriate non-parametric methods. K-W=Kruskal-Wallis, OR=on ranks. Statistical significance at  $P < 0.05$ .

Shark	Test	d.f.	F or H value	P	Significant
Male 1	K-W ANOVA OR Tukey	11	H=25.301	0.008	Yes
Male 2	K-W ANOVA OR	11	H=4.589	0.949	No
Male 3	ANOVA	11	F=0.915	0.534	No
Male 4	ANOVA	11	F=0.838	0.606	No
Female 1	ANOVA	11	F=0.782	0.656	No
Female 2	K-W ANOVA OR	11	H=8.740	0.646	No

Smith 2017), but here only attempted copulation and retaliatory biting were observed following increased cupping and flaring. The relocation of the female in 2003 precluded attempted copulation that year. Sexual conflicts were documented in the males in 2003 despite the female being relocated to another aquarium system. Based upon the sequence of sexual conflicts and timing of the release of infertile ova, it appears that the cycle of the males and the female were not synchronised.

**Food intake**

Interest in food and rate of food intake of the dominant male, Male 1, and Male 3 varied seasonally, declining in January, and returning to previous levels in May. Interest in food and rate of food intake in the other males, Male 2 and Male 4 (Figure 5a), as well as in the females (Figure 5b) did not vary during the study. Monthly food intake values for Male 2, Female 2, Male 4 and Female 1 did not differ (Table 2), while that for Male 3 differed, albeit not significantly. Values for Male 1, however, differed significantly among months (single factor Kruskal-Wallis ANOVA on ranks  $H=25.301$ ,  $d.f.=11$ ,  $P=0.008$ , Table 2), with significantly lower rates between February and April (Tukey’s multiple comparison test). For females, monthly food intake was consistent for Female 1 and Female 2 (single factor ANOVA,  $d.f.=11$ ,  $F=0.864$ ,  $P=0.592$ , Table 2). On an annual basis rate of food intake differed among months for only the dominant male (Male 1) and a subordinate (Male 3) for the year 2000 compared to other years (Kruskal-Wallis single factor ANOVA on ranks  $H=26.076$  for Male 1 and  $H=25.820$  for Male 3) (Figure 5c).

**Swimming speeds**

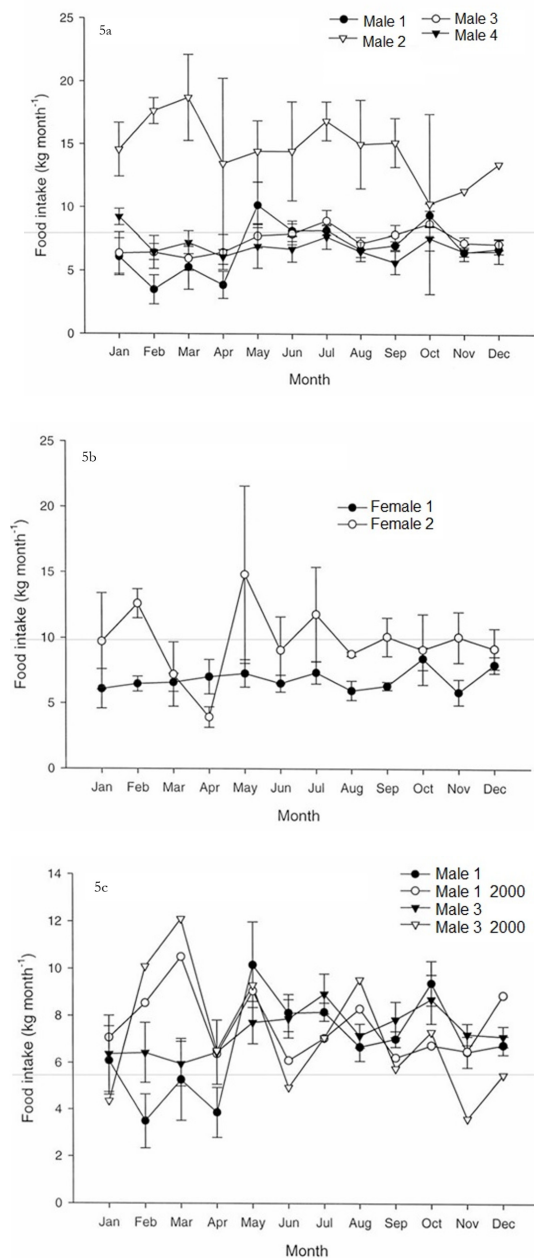
Dominant males at NA were indeed documented to have an increased swimming speed during mating season, compared to subordinate males. Based upon behavioural observations, the relative swimming speed of the males Male 1 and Male 3 increased in January. On a quantitative basis, however, the mean relative swimming speed began to increase for Male 3 and Male 2 in September and October, respectively, while it remained relatively constant for the males, Male 4 and Male 2 (Figure 6a) as well as for the females (Figure 6b). Male 2 (single factor ANOVA  $F=2.265$ ,  $d.f.=11$ ,  $P=0.012$ ) and Male 3 (single factor ANOVA  $F=2.060$ ,  $d.f.=11$ ,  $P=0.0240$ ) had significantly elevated speeds in March all years except 2000 (Figure 6a). For 2000, a significant difference occurred only in April for Male 3 (single factor ANOVA  $F=4.746$ ,  $d.f.=11$ ,  $P<0.001$ ) (Figure 6c). Post-hoc multiple comparisons also confirmed that Male 1 and Male 3 were significantly different (Dunn’s) ( $P<0.05$ ).

Although not included in the initial investigation, qualitative observations were again conducted from 2007–2014. One female (Female 3) and two males (Male 5 and Male 6) were added to the collection in 2007 and 2011, respectively. In 2014, the male hierarchy consisted of Male 3 as the  $\alpha$  male, Male 5 and/or Male 6 as the  $\beta$  male and Male 4 as the  $\gamma$  male (Schneble 2014).

**Discussion**

The sexual conflicts presented here confirm those described previously (Gordon 1993; Pratt and Carrier 2005; Willson and Smith 2017) while also describing new sexual conflicts in captive sand tiger sharks. The sexual conflicts presented here did not result in successful copulation and this may be due to several factors. Since the female was moved prior to the initiation of the behaviours, it is possible that physiological cues, unknown underlying genetic differences, visual cues and electrosensory cues were involved in initiating the conflicts. The continuation of the conflicts in the female’s absence suggests that visual or olfactory cues from the female were not required to maintain the sexual conflicts in the

males. The cessation of the conflicts following the removal of the dominant or subordinate male indicates that they are the key animals in the hierarchy. The cessation of the conflicts following the separation of these two individuals and the re-initiation of the conflicts two to three days after the reintroduction further supports this conclusion regarding this group of male sand tiger sharks. It is also possible that the behaviours are correlated to hormone levels, which has been documented in other vertebrate taxa (Moore 1987; Holst and Eichman 1998). Indeed, reproductive



**Figure 5.** (a) Food intake per month (mean±SE) for male sand tiger sharks, Male 1, Male 3, Male 2 and Male 4, at the National Aquarium for the years 1998 to 2003, excluding 2000; asterisk indicates significance at  $P<0.05$  for 5b. (b) Food intake per month (mean±SE) for female sand tiger sharks, Female 1 and Female 2, at the National Aquarium for the years 1998 to 2003, excluding 2000. (c) Food intake per month for Male 1 and Male 3 for 1998 to 2003 (mean±SE, exclusive of 2000) and for 2000.

hormone levels were related to behavioural status in this group of sharks (Henningsson et al. 2008; 2015).

Contributed information from several colleagues as well as previously summarised information on mating and sexual conflicts in sand tigers in aquaria (Gordon 1993; Henningsson et al. 2004) indicate that these behaviours corroborate Gordon's (1993) descriptions. Successful reproduction through parturition has occurred at only four institutions, in Australia, South Africa and the Middle East (Henningsson et al. 2004; 2017), while mating

and sexual conflicts have been observed in Europe as well as the US. Sea Life Sunshine Coast (Mooloolaba, Queensland, Australia) has recorded eight parturition events since 1992 (Willson and Smith 2017). The novel behaviours of heading, chain-following, and chain-following with nosing described here have not been reported for other captive sand tiger sharks. Interactions between males beyond tailing were not observed by Gordon (1993) and only at two institutions: the NA, as described here, and Jenkinson's Aquarium in New Jersey, US (Smith, Jenkinson's Aquarium, personal communication, April 2003). Additionally, although not observed, bites on the ventral surface of subordinate males appear to be in the same position as those inflicted during male dominance biting (Kinnunen, personal communication, Manly Sea Life Sanctuary, formerly known as Oceanworld Manly).

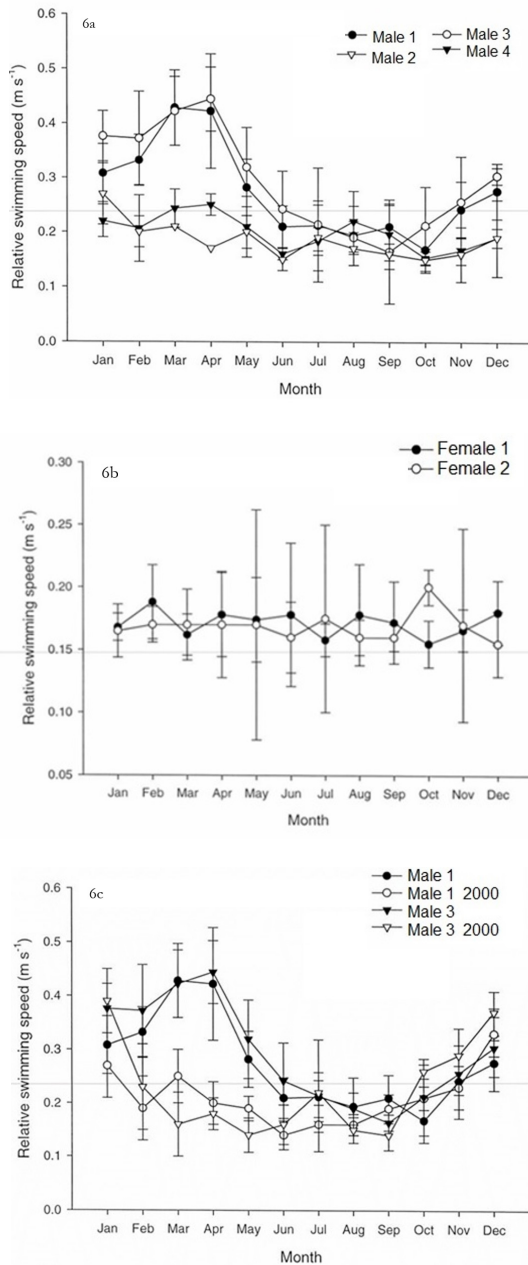
Information from other institutions allowed comparisons not only to the sexual conflicts themselves, but also to the duration of the conflicts. In Gordon's (1993) initial description, behaviours were noted to be 13–14 months apart and to last from 3–4 weeks in duration. In three years of observed sexual conflicts in six male and four adult female captive sand tigers at Ripley's Aquarium of the Smokies, Tennessee, US, from 2002 to 2004, the duration of these conflicts ranged from 23–40 days. In these observations, increased activity was first noted in males, as following, and nosing the females occurred. The smallest male seemed to be the most active. Copulation was observed in all three years and different females were apparently pursued each year by the males (Hodge, Choromanski and Bulman, personal communication).

The following and chain-following behaviours described here are unique with respect to the strictly male composition but have been described previously in elasmobranchs. Although following was described in a group of bonnethead sharks *Sphyrna tiburo*, after the introductions of a new shark, in each case the new shark was a female (Myrberg and Gruber 1974). Pratt and Carrier (2001) noted that sharks of the same sex will closely follow each other during the mating season. Previous observations in this and other species of elasmobranchs strongly indicated the presence of olfactory cues such as pheromones and suggested their importance in mating systems (Johnson and Nelson 1978; Klimley 1980; Gordon 1993; Carrier et al. 1994; Hueter et al. 2004).

The more subjective observations made in the present study may add to the existing knowledge in both captive and wild conspecifics. Lucifora et al. (2002) reported lighter coloured males in wild sand tigers during the mating period in the southwest Atlantic, corroborating the observations by Gordon (1993) as well as in the present study. At NA, Male 1, the  $\alpha$  male, appeared to lighten the most, perhaps indicative of a physiological basis for the hierarchical status.

The difference in feeding interest and intake in males, and relation to male hierarchy presented here quantitatively was described by Gordon (1993), is also consistent with the relationship to reproductive cycle as suggested by Townsend and Gilchrist (2017). The dominant and subordinate males play a key role within the hierarchy; removal of either resulted in a cessation of conflict amongst them within 72 hr (Henningsson et al. 2008). Swimming speed and food intake are two main indicators of determining a shark's position within the hierarchy, not just the size and total length of an animal (Gordon 1993; Henningsson et al. 2004b; 2017).

The importance of documenting sexual conflicts as well as promoting successful reproduction in human care in this species is highlighted by the status of sand tiger sharks in the wild, ranging from vulnerable to critically endangered (Cavanagh et al. 2003; Otway et al. 2004). Information from the present study, as well as that from others, provides evidence that the male dominance hierarchy in this species exists and is not based upon size and varies in intensity. Sexual conflicts occur annually,



**Figure 6.** (a) Relative swimming speed (mean $\pm$ SE) of male sand tiger sharks at the National Aquarium for the years 1998 to 2003, excluding 2000. (b) Relative swimming speed (mean $\pm$ SE) of female sand tiger sharks at the National Aquarium for the years 1998 to 2003, excluding 2000. (c) Relative swimming speed (mean $\pm$ SE) of  $\alpha$  (Male 1) and  $\beta$  (Male 3) male sand tiger sharks for years 1998 to 2003, exclusive of 2000 in comparison to relative speed (mean $\pm$ SE) for 2000.



with males interested in different females and this is consistent with a biennial reproductive cycle in females (Branstetter and Musick 1994; Goldman 2002; Henningsen et al. 2004a), rather than annual (Gilmore et al. 1983; Gilmore 1993). It is necessary to consider how the confinement of the artificial environment impacts behaviour as it may be modified or attenuated as a result of captivity (Henningsen et al. 2004; Whitney et al. 2004). In addition, the occurrence of putatively successful copulations, but the scarcity of successful parturition (Henningsen et al. 2017), indicates the need to investigate physiological factors during reproduction in this species; something which may also be impacted by captivity. Though this investigation sheds new light on the depth of sexual conflicts in sand tiger sharks, its applications and the comparisons to other groups of captive sand tiger sharks are important considerations for this threatened species.

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