

Male mate choice in the spot-tail shark *Carcharhinus sorrah*: are males choosy or opportunistic?

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Male mate choice has been documented in different taxa including insects, lizards, fish, birds and mammals. However, in sharks, male mate choice is not clearly reported but field observations suggest that it is probable. In this study, I tested for evidence of male mating preference of the spot-tail shark *Carcharhinus sorrah* towards three female traits that are typically associated with female fecundity, these are: (1) body size, (2) parasite burden, and (3) mean heterozygosity. I collected data on heterozygosity, age, length and parasite burden of 73 litters of *C. sorrah* females. I found no association between male mating preference and any of the selected female traits. A possible interpretation is that, given the polygamous mating system of sharks and consequent likelihood of sperm competition, *C. sorrah* males focus primarily on obtaining fertilization, rather than adjusting their behavior according to potential fitness differences between females. Future research is needed to gain better understanding on the reproductive behavior and social dynamics of *C. sorrah* to benefit conservation efforts that are needed to effectively manage *C. sorrah*.

Introduction

Mate choice occurs whenever the effect of a trait expressed in one sex leads to non-random allocation of reproductive investment by the opposite sex (Edward 2014, Rosenthal 2017). Mate choice is mostly defined by competitive males and choosy females (Edward & Chapman 2011, Aubier *et al.* 2018, Morina *et al.* 2018). However, increasing evidence show that males can be choosy, even in unexpected situations such as species without male parental care (Sæther *et al.* 2001, Assis *et al.* 2017, Auld *et al.* 2017, Waner *et al.* 2018). For example, if males are involved in a polygamous mating system, sperm competition might be an issue, therefore to increase the chances of fertilization success, males might

need to be strategic about the allocation of their sperm resources to certain females (Parker 1998, Pratt & Carrier 2001, Preston & Stockley 2006, Parker & Pizzari 2010).

Male preference has been documented in a variety of species including insects (Bondurian-sky 2001, Assis *et al.* 2017), lizards (Weiss 2006, Belliure *et al.* 2018), fish (Tudor & Morris 2009, Justus & Mendelson 2018), birds (Amundsen 2000, Sæther *et al.* 2001, Kraaijeveld *et al.* 2004, Rymešová *et al.* 2017) and mammals (Preston *et al.* 2005, Muller *et al.* 2006). Female traits that males showed preference towards include: (1) older females with more experience such as the case in feral pigeons *Columba livia* (Burley & Moran 1979) and the chimpanzee *Pan troglodytes* (Muller *et al.* 2006), (2) younger virgin females

in the bowl and doily spider *Frontinella pyramitela* (Suter 1990) and terrestrial isopod *Armadillidium vulgare* (Fortin *et al.* 2018), (3) larger and more fecund females in the Mormon cricket *Anabrus simplex* (Gwynne 1981), red-spotted newt *Notophthalmus viridescens* (Verrell 1985), plethodontid salamander *Desmognathus ochrophaeus* (Verrell, 1989, 1995), pipefish *Nerophis ophidion* (Berglund & Rosenqvist 1993), the swordtail *Xiphophorus malinche* (Tudor & Morris 2009) and red-legged salamander *Plethodon shermani* (Eddy *et al.* 2016), (4) females showing better parental care as in prairie voles *Microtus ochrogaster* (Verrell 1990, Solomon 1993), (5) more dominant females as in spotted hyenas *Crocuta crocuta* (Szykman *et al.* 2001) and pipefish *Syngnathus typhle* (Berglund & Rosenqvist 2001), (6) less parasitised females as in pipefish *Syngnathus typhle* (Rosenqvist & Johansson 1995), and (7) genetically compatible females as in red junglefowl *Gallus gallus* (Gillingham *et al.* 2009, Hibbit 2015) or genetically dissimilar females as in mangrove rivulus *Kryptolebias marmoratus* (Ellison *et al.* 2013). This indicates that mate choice can evolve under a wider range of circumstances than predicted by parental investment alone (Verrell 1990, Andersson 1994, Rosenqvist & Johansson 1995, Assis *et al.* 2017).

In sharks, most studies focus on reproductive biology (Gilmore *et al.* 1993, Castro 1993, Pratt 1993, White *et al.* 2002, Galvan-Tirado *et al.* 2015, Sulikowski *et al.* 2016, Fujinami *et al.* 2017, Pirog *et al.* 2019), and less on reproductive behavior (reviewed by Pratt & Carrier 2001, Whitney *et al.* 2007, Whitney *et al.* 2010, Chapman *et al.* 2013). Based on field observations it is likely that male mate choice occur in sharks (Springer 1967, Myrberg & Gruber 1974, Johnson & Nelson 1978, Klimley 1980, Carrier *et al.* 1994). The high cost of reproduction for male sharks (limited production of sperm limiting the capacity to mate), combined with the number of available females to mate with that they encounter simultaneously (mate availability) is suggested to promote male mate choice (Edward & Chapman 2011). In this case, male choice is not only based on whether to mate, but also the decision on how many resources to allocate to each female. The high cost of reproduction for male sharks is suggested based on observa-

tions of mature males that were found to have thin livers with low oil content in comparison to females and immature males from the same site during the reproductive season (Springer 1967). This could be due to prolonged fasting or high activity of males during the mating season (e.g. increasing their swimming speed, prolonged chase for a mate; male chase for a female may take five to six hours [Gordon 1993]). Another support to the possibility of male mate choice occurring in sharks is the high likelihood of sperm competition (Bernal *et al.* 2015, Orr & Brennan 2015). Sperm competition is likely to occur in sharks for two reasons, these are: (1) the mating system in sharks is polygamous (Owens & Thompson 1994, reviewed by Edward & Chapman 2011), and (2) female sharks store sperm in the upper oviduct for up to 45 months (Pratt 1993, Bernal *et al.* 2015), which might create an environment for sperm competition. According to Dewsbury (1982), in mating systems with high sperm competition, the best male strategy may not be to inseminate as many available females as possible. A better strategy might rather be to bias mating effort towards particular females to increase a male's fertilization success (Ramm & Stockley 2014). However, male mate choice is not clearly documented, or studied in sharks. Based on my knowledge, this is the first study to investigate male mate choice in sharks.

The spot-tail shark *Carcharhinus sorrah* is a viviparous species with a yolk sac placenta and a gestation period of ten months (Compagno 1984). It gives birth once a year, producing between one to eight pups per litter, with an average of four pups (Compagno 1984). Females mature around two years old and their longevity is around seven years. Male and female *C. sorrah* use different depths of habitat and thus show sexual segregation (Knip *et al.* 2012). Stevens *et al.* (2000) found that although the species is capable of moving long distances (up to 1116 km), almost 50% of their studied specimens were recaptured within 50 km of their tagging site. This suggests that although *C. sorrah* is capable of moving long distances, movement of most individuals is limited, probably resulting in little mixing between sites. The species is currently listed as near threatened on the IUCN red list (Vié *et al.* 2009).

Understanding the reproductive behavior of sharks has become increasingly necessary because of their value in commercial fishery and the need to design proper management plans for their successful conservation (Pratt & Carrier 2001). Knowledge of the male mating preferences is important because it has significant potential to alter population fitness by influencing the contribution made to future generations by non-preferred females (Hibbit 2015), and because assortative mating can have profound influences on the genetics and demographics of populations (Hargeby & Erlandsson 2006).

A polygamous mating system is where an individual, whether a male or a female, mate with multiple individuals during the same reproductive cycle (Zeitzen 2018). In a polygamous system, males and females encounter each other simultaneously. But since their mating ability is constrained, due to their limited sperm reserves and the possibility of high cost of sperm production in sharks, strategic allocation of their sperm resources to certain females is needed to increase their chances of fertilization success (Parker 1998, Pratt & Carrier 2001, Preston & Stockley 2006, Parker & Pizzari 2010). The high cost of sperm production in sharks is suggested based on a tagging study of the Nurse shark *Ginglymostoma cirratum*, which showed that male sharks mate once, leave mating grounds and come back the next day to mate again (Pratt & Carrier 2001). This suggests that sperm or ejaculate protein production is a costly task that might require a day to replenish.

Investigating male mate choice in any new system is a challenge, since multiple factors are predicted to drive male mate choice. In this study, I focused on examining male mating preference towards three female traits that are associated with female fecundity in other taxa. The selected female traits are: (1) body size; studies showed that males commonly prefer larger females when choosing a mate and that female total body length is positively correlated with fecundity, as larger females might provide the capacity physically required to hold a greater number of pups (Côte & Hunte 1989, Honěk 1993, Merrett 1994, Kiørboe & Sabatini 1995, Clobert *et al.* 1998, Kraak & Bakker 1998,

Garcia-Barros 2000, Eddy *et al.* 2016, Barneche *et al.* 2018); (2) mean heterozygosity (Keller & Waller 2002, Durand *et al.* 2015); empirical studies showed that in some taxa, fecundity increases with greater genetic diversity (Keller & Waller 2002, Gijbels *et al.* 2015); (3) parasite burden (Wittman & Fedorka 2015); in stickleback fish, studies indicated that parasite infection can alter mate choice and the likelihood of being selected as a mate (Milinski & Bakker, 1990, Barber *et al.* 2000). The aim of this study was to test for a correlation between any of the three female traits (body size, mean heterozygosity, and parasite burden), with evidence of male preference (number of sires per litter) in the spot-tail shark *Carcharhinus sorrah*.

Methods

Ethical statement

All tissues or specimens were collected from dead animals, and therefore did not require ethical or institutional approval. However, permission to sample at the fish market in Dubai, United Arab Emirates, was authorized under collaboration with the Central Veterinary Research Laboratory.

Sample collection

Fieldwork was conducted from mid-April until the end of May 2013. Samples of pregnant *C. sorrah* were collected from Diera fish market in Dubai (25°16'30.5''N 55°17'55.7''E), the United Arab Emirates (Fig. 1). All *C. sorrah* included in this study were dissected in this study. Before dissecting the pregnant *C. sorrah*, the following data and samples were collected: (1) gill slit clips ($n = 73$), and (2) total body length (TL). After dissection, the following samples were collected: (1) a piece of the vertebrae for age analysis, (2) the gut for parasite burden analysis, (3) litter size (number of pups - in total, 320 pups were sampled), and (4) genetic sample (fin-clip) from each pup to be used in paternity analysis (inferring number of sires per litter).

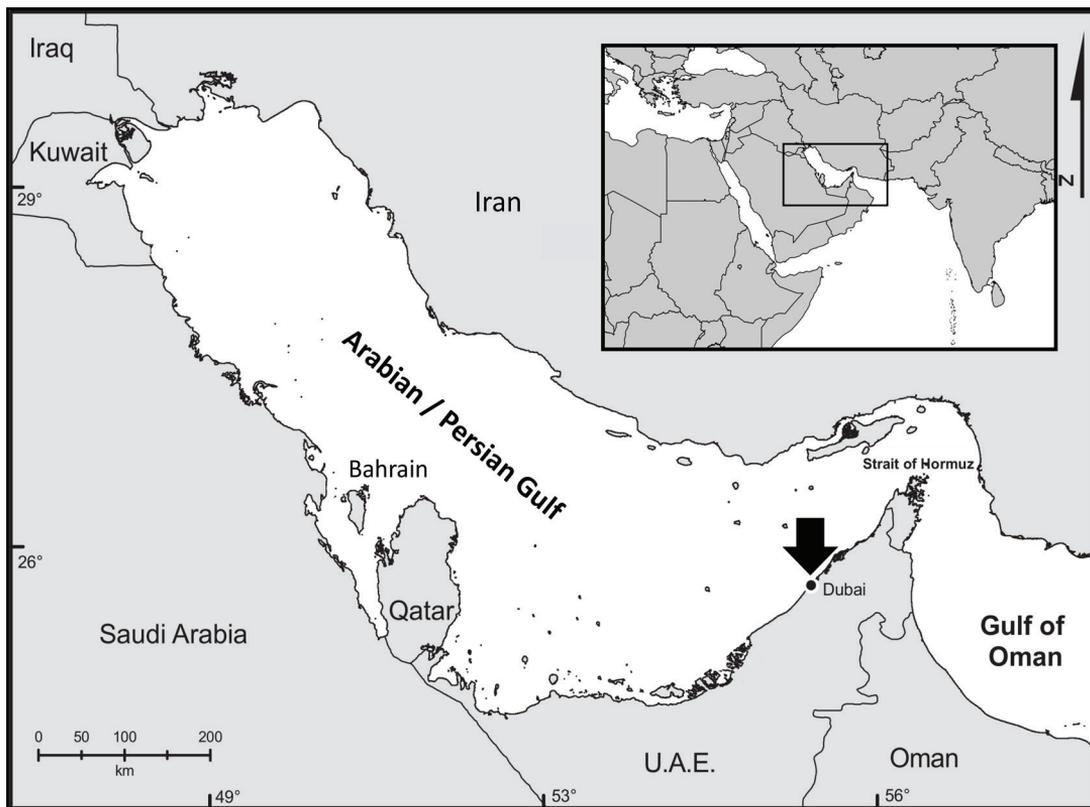


Fig. 1. The study site. The arrow marks the landing site at Diera fish market in Dubai, United Arab Emirates (UAE).

Laboratory work

Genetic work

Fifteen microsatellite loci were used for *C. sorrah* (Almojil *et al.* 2016), following the same protocols and procedures for DNA extraction, PCR amplification, genotyping, allele scoring and quantification of genotyping error as in Almojil *et al.* (2018). The resulting genetic data were used to calculate the homozygosity by loci index (HL). This index is shown to correlate with genome-wide homozygosity (Aparicio *et al.* 2006). The HL index was calculated using the R package *Rhh* (Alho *et al.* 2010), and used to represent mean heterozygosity of all tested females.

The genetic data were also used to calculate the number of sires per litter using the program COLONY 2.0 (Jones & Wang 2010). The full-likelihood analysis method was used with a

medium run length. The generated genotypes were used in the input file for parentage analysis as known mothers. The relation was defined under the maternal sibship/maternity option in the program COLONY to facilitate the assignment of half-sib pups into full-sib pups and thus estimate the number of sires per litter.

Vertebra preparation, sectioning and age determination

Each vertebra was cleaned and aged following the ageing protocol described in Harry *et al.* (2013). Vertebra section was read twice to evaluate the precision between and within reads. The percent agreement and Chang (1982) method of the coefficient of variation (CV) was used as the evaluation measure. The within-reader bias was statistically evaluated using Bowker's test of symmetry (Evans & Hoening 1998). Moreover,

the precision and bias statistics were calculated using the *agecomp* function of the Fisheries Stock Assessment package (FSA) (version 0.4.1) (Ogle 2009, Daniela *et al.* 2015) in R (R version 3.0.2 Development Core Team 2013).

Metazoan parasite burden: isolation and quantification

The collected stomach and intestine of each of the sampled pregnant females were processed at the Central Veterinary Research Laboratory in Dubai, United Arab Emirates. Metazoan parasites were isolated following the precipitation method of Pritchard (1982). The parasite burden was measured as the total parasite burden (count of individual parasites at all families pooled together).

Data analysis

Relationship between explanatory variables

Dependencies between the explanatory variables were tested by generating paired plots (Crawley 2012). Based on the paired plot results, the explanatory variable “Age” was dropped as it showed collinearity with “Total length, TL”. The effect of dropping the explanatory variable “Age” was measured by testing the goodness of fit of the new model (Paul *et al.* 2006).

Hypothesis testing for male mate choice in *C. sorrah*

Given the scarcity of behavioural data and setting aside the possible influence of cryptic female choice, the number of sires per litter in each of the examined females’ *C. sorrah* was used as a representative of a female’s attractiveness to males (i.e. male mate preference) and was treated as a continuous variable. A zero-truncated Poisson model was applied using the *vglm* function in the *VGAM* package (Yee 2015) in R 2.15.1 (R Project Core Development Team 2013). An additive model was used to test for the effect of three possible explanatory

variables, namely: (1) female total body length (continuous), (2) female mean heterozygosity (continuous), and (3) female gut parasite burden (continuous) simultaneously. The distribution was specified under the positive Poisson family, given that our data are without zeros, thus the values are strictly positive Poisson. Therefore, the positive Poisson family was specified via the *pospoisson* function within the *vglm* function of the *VGAM* package (Yee 2015).

Results

Test for male mate choice in *C. sorrah* showed that the number of sires per litter did not significantly correlate with any of the tested explanatory variables: (1) female total body length (Fig. 2), (2) female mean heterozygosity (Fig. 3), or (3) female gut parasite burden (Fig. 4 and Table 1). The average number of sires per litter as shown from the study data was five.

Discussion

This study provided no clear evidence in support of the hypothesis that male *C. sorrah* preferred to mate with females showing any of the selected three potential cues of higher fecundity in females, namely: (1) larger body size, (2) higher mean heterozygosity, or (3) lower levels of parasitism. Such a null result is difficult to interpret since it could also arise from a lack of statistical power. However, our study was based on a substantial sample size ($n = 73$). Therefore, it could be that in this species, males are not adjusting their behavior according to potential differences in fitness between females, but rather capitalizing on any reproductive opportunity that might result in fertilization, especially that sperm competition is highly likely.

In polygamous systems, reduced sperm competition might be a priority in male mate choice (Pardo *et al.* 2016). In theory, sperm competition would be expected to be higher in females that display cues of higher fecundity. Evidence from different taxa showed that some males can adaptively reduce their mating preferences for more fecund females and redirect their mating effort

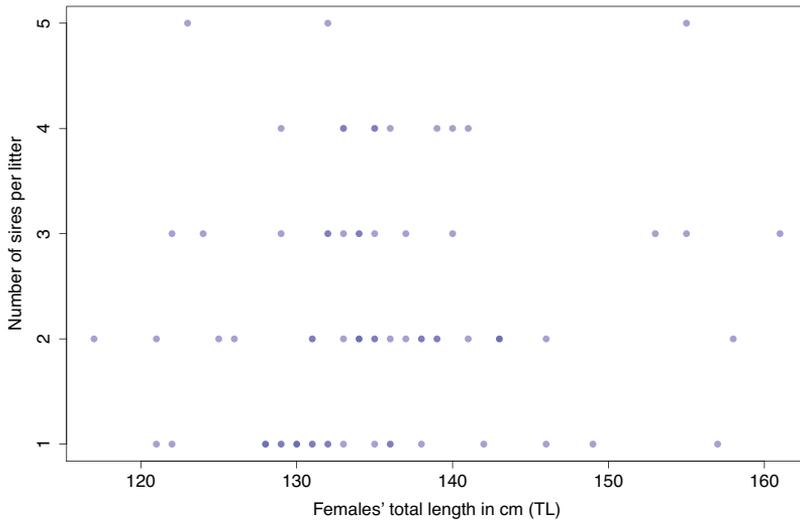


Fig. 2. Relationship between the number of sires in a female's litter, and her total body length ($p = 0.34$ in a zero-truncated Poisson GLM; see text for details). Purple points illustrate the raw data points.

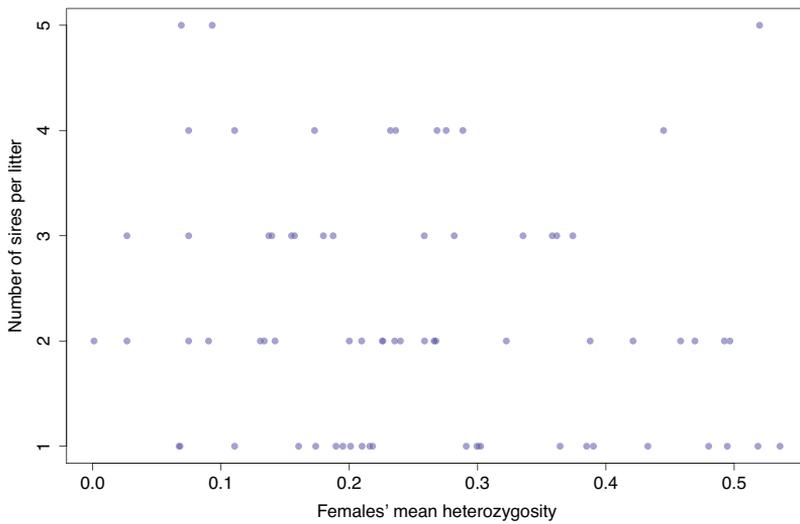


Fig. 3. Relationship between the number of sires in a female's litter, and her heterozygosity ($p = 0.19$ in a zero-truncated Poisson GLM; see text for details). Purple points illustrate the raw data points.

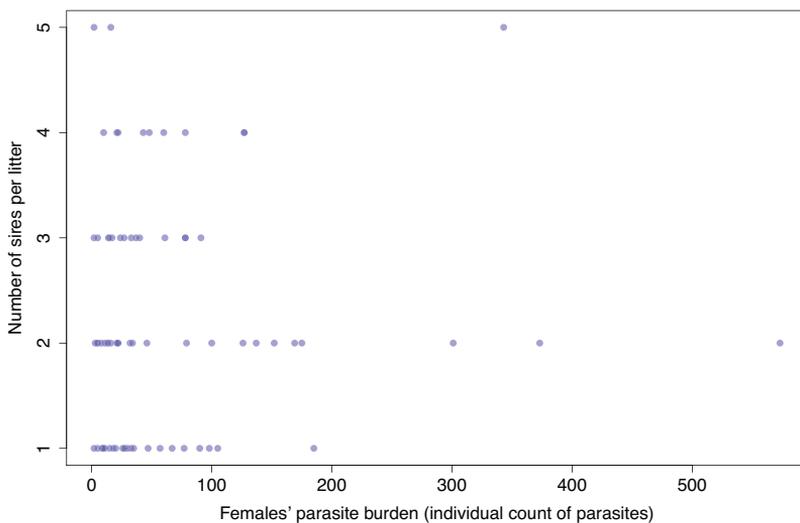


Fig. 4. Relationship between the number of sires in a female's litter, and her gut parasite burden ($p = 0.46$ in a zero-truncated Poisson GLM; see text for details). Purple points illustrate the raw data points.

toward less fecund females, in response to a perceived increase in the risk of sperm competition associated with more fecund females (Dosen & Montgomerie 2004, Jeswiet *et al.* 2012). This can potentially contribute to the maintenance of variation in male mating preferences in the population (Wedell *et al.* 2002, Jeswiet *et al.* 2012). Previous work on male guppies *Poecilia reticulata* showed that male mating preference was only expressed when males were able to assess the mating status of encountered females (Herdman *et al.* 2004). In some spiders, such as the wolf spider *Schizocosa malitiosa* (Baruffaldi & Costa 2014), males showed higher interest in virgin females (e.g. Suter 1990, Simmons 2001, Herberstein *et al.* 2002, Fortin *et al.* 2018). This could be to reduce the risk of female rejection and sperm competition, and thus increase fertilization success and paternity (Suter 1990, Wedell *et al.* 2002). Overall, this suggests that costs of sperm competition can select for accurate male assessment of female mating status in a polygamous mating systems, influencing male mate choice if mating is costly (Edward & Chapman 2011, Rosenthal 2017).

The mechanism of male assessment of females' mating status might depend on chemical signals (Johansson & Jones 2007, Thomas 2011, Coombes *et al.* 2018). Increasing evidence supports that in some species, females stop producing or change the chemical composition of their sex pheromones after mating (reviewed in Johansson & Jones 2007). In sharks, field observations suggest a role of chemical signals in directing mating behavior (Johnson & Nelson 1978). For example, Gordon (1993) noted that males of the sand-tiger shark, *Carcharias taurus*, lost interest in females after copulation. He thus hypothesized that a chemical stimulant, possibly

pheromones, are responsible for males' loss of interest in mated females. This is further supported by the work of Demski (1990a, 1990b), who found that the brain control of testicular and ovarian development in sharks is mediated by gonadotropin-releasing hormones. He then hypothesized that the "follow" behaviour and mate chase observed in sharks (Myrberg & Gruber 1974, Johnson & Nelson 1978, Klimley 1980) is possibly triggered by female pheromones, which trigger sexual behavior in males.

Evidence that sexual behavior in males is triggered by female pheromones is also supported by field observation of the pre-copulatory behavior in both the black-tip reef shark *C. melanopterus*, and the white-tip reef shark *Tri-aenodon obesus* (Johnson & Nelson 1978). In both species a male closely follows a female and orients its snout to her vent, suggestive of male assessment of females' reproductive or mating status. Moreover, males intercept females even when visual and sound cues were absent, and in some cases performed a sudden turn to follow another path that was initially out of sight, which is suggestive of the hypothesized olfaction-mediated recognition (Johnson & Nelson 1978). This behavior is termed as 'close follow' and is suggested to be similar to 'parallel swimming' by Klimley (1980) and 'following' by Carrier *et al.* (1994). Therefore, the pre-copulatory sensory cues are probably mainly olfactory (i.e. pheromones) that might indicate a female's reproductive state. However, further studies are required to ascertain conclusively the role of pheromones in male assessment of female mating status in sharks.

To improve our understanding of male choice in sharks, future research need to incorporate and plan to collect long-term data from tag-

Table 1. Output of the best fit of the zero-truncated Poisson model using the three explanatory variables: (1) female total body length (continuous), (2) female mean heterozygosity (continuous), and (3) female gut parasite burden (continuous) simultaneously; degrees of freedom = 69.

	Estimate	Standard error	z	p
Intercept	-0.55	1.49	-0.37	0.71
Female total body length	0.01	0.01	0.95	0.34
Female mean heterozygosity	-0.97	0.74	-1.31	0.19
Female gut parasite burden	0.0007	0.0009	0.73	0.46

ging studies with direct field observations on reproductive behavior (which male courted with which female), and the use of molecular tools (a database of genotypes of all tagged individuals). Future conservation studies will benefit greatly from incorporating knowledge on shark's reproductive behavior, habitat requirements for mating and pupping grounds as well as focusing on social dynamics and mating behavior to effectively manage shark stocks.

DATA ACCESSIBILITY: The entire data set used in this study is deposited in the Dryad Repository at <https://doi.org/10.5061/dryad.w3r2280mn>.

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