Breaking the patrisharky: Scientists reexamine gender biases in shark, ray mating research

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Sand tiger sharks mating at Georgia Aquarium. Credit: Georgia Aquarium

Shark scientists at Georgia Aquarium, Scripps Institution of Oceanography at UC San Diego, and Dalhousie University are challenging the status quo in shark and ray mating research in a new

study that looks at biological drivers of multiple paternity in these animals. The results were published March 4 in the journal *Molecular Ecology*.

Many species of sharks and rays exhibit multiple paternity, where females give birth to a litter of pups that have different fathers. While widely documented in scientific literature, the drivers of this phenomenon are not well understood. However, previous research has cited male aggression as the reason, claiming that the females are unable to avoid or submit to their advances during mating. This has led to the "convenience polyandry" theory, the assumption that there is a greater cost for females when refusing male mating attempts, as being the most widely credited explanation.

"If convenience polyandry is the only reason we talk about, it takes the agency away from females," said Kady Lyons, research scientist at Georgia Aquarium and lead author of the study. "If she's investing all this energy into making big babies, why doesn't she get a say in who will be the sire of her offspring?"

While multiple paternity has been documented in many elasmobranchs (sharks and rays), this is the first study to evaluate it starting from the female point-of-view. The researchers note that most studies on shark and ray reproduction were conducted by male scientists, and their biases could manifest in their research.

"No matter how objective we try to be as scientists, we're still human and our experiences are brought to the table," said Dovi Kacev, assistant teaching professor at Scripps Oceanography and a co-author of the study.

The researchers developed models based on shark and ray biology and physiology to test whether multiple paternity could be in the best interest

of females or males, or a combination of both. They looked for patterns that they would expect to see if this phenomenon was pushed or pulled by one sex or the other, such as sperm competition or female selection for sperm genetic diversity, and compared it to data from past studies and their own research on these animals. By asking, "Would this benefit a male or a female?" they found no conclusive evidence that multiple paternity is primarily a male-driven advantage. In most instances, the benefits for females and males were the same, challenging previous ideas that male behavior and biology drives multiple paternity.

"Male or female drivers may sometimes produce the same multiple-paternity end result, but more often than not it is the male factors that get the lion's share of the credit," Lyons said. "This seemed odd to me considering how complex and energetically taxing female reproduction is."

The researchers stress that uncovering which sex (or both) may be responsible for the observed patterns is difficult as elasmobranchs have been evolving over many millions of years, and observing shark and ray mating is a rare occurrence. The scientists, however, found clues in what science does know about elasmobranch mating and reproduction.

Elasmobranch mating can be quite violent. In many cases, males bite the females to secure a hold, inflicting injury and leaving scars. This can even be seen in some of the more docile species like manta rays. Females have, however, developed advantages such as thicker skin in bite-prone areas in order to better recover from the mating injuries. In many species, the females are also often much larger than males.

While it does take energy for females to recover from wounds or avoid frisky males by swimming away, this only represents the beginning of their energetic investment into reproduction. The researchers point out that female elasmobranchs devote a lot of resources to the production of

developed young, such as through ovulation of fat-rich eggs and providing nutrition to embryos in species that have internal gestation, which is the norm for most sharks and rays.

"One thing that is underappreciated, even by experts, is how diverse sharks and rays are," said Christopher Mull, postdoctoral fellow at Dalhousie University and a co-author of the study. "When it comes to reproduction, sharks and rays use every mode that has been described in vertebrates, from laying eggs to giving live birth with a placenta, similar to humans."

This diversity of sharks and rays makes them an interesting animal group to study multiple paternity, and for examining sex roles in the animal kingdom, said the researchers. The typical number of offspring can vary widely between species, from a single pup up to several hundred. The smallest of sharks can fit in the palm of a human hand, while the largest can grow to the size of a school bus. Despite these differences in biology and physiology, the phenomenon of multiple paternity appears to be a common trait across sharks and rays.

This evolutionary advantage, and the idea that it could be driven by the biology of the females, has been of keen interest to Lyons throughout her research. In a previous study, she found that round stingrays, native to the California coast, can exhibit different patterns of paternity. These rays have two uteri, and Lyons showed that in some females, one uterus held offspring with the same father while the other held offspring of a different father. In other individuals, offspring paternity was mixed between the two uteri. This was hypothesized as females ovulating in different patterns, which may give them some control over which males were able to fertilize their eggs.

Female elasmobranchs have other physiological abilities that suggest they might be behind multiple paternity. Some species have serial

ovulation, in which one egg at a time is produced and fertilized. It has been shown that some can store sperm, thereby preventing the sperm from one male from fertilizing an egg, or using this ability to save sperm from another male that could be used in the future. Essentially, females have the anatomical tools that may allow them to control which sperm fertilize their eggs.

From past data, the researchers found many examples of pregnant female sharks with "failed ova" (those that were in the process of being resorbed) alongside normally developing embryos. If reproduction was driven by males, the scientists asked, why would the female miss the opportunity to pass on her genes as well? These examples bolster their idea that the reasons for multiple paternity cannot be attributed to only one sex.

"Female elasmobranchs have these incredible physiology mechanisms that give them a reproductive advantage, but these are largely ignored in the literature," Lyons said.

"I think a key takeaway from our work is challenging the dog(fish)ma that female sharks and rays are passive players in the mating process," said Mull. "But demonstrating these mechanisms at work can be really challenging, so we focused on developing a series of testable hypotheses that other researchers can apply to their own work."

The researchers note that while this study is on sharks and rays, it has implications for the larger animal kingdom, and for diversity in science.

"Diversifying perspectives at the table will enrich scientific studies," said Kacev. "We're not saying the male perspective is wrong, or that male sharks aren't at all responsible for multiple paternity, but it takes two to tango."

"Perspective is completely shaped by background," said Lyons. "If you don't have a diverse background, your perspective will be limited."

More information: Kady Lyons et al, An inconvenient tooth: Evaluating female choice in multiple paternity using an evolutionarily and ecologically important vertebrate clade, *Molecular Ecology* (2021). DOI: 10.1111/mec.15844