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Digest: Female squid influence insemination success after mating to show a preference for smaller males*

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In systems where females mate with multiple males, females can influence insemination success to favor the males they find most attractive. When a female influences insemination success, it is known as cryptic female choice (CFC) because her influence often occurs after mating (post copulation) inside the reproductive tract and out of sight. For example, female fowl show CFC by ejecting sperm from subdominant males after forced mating (Pizzari and Birkhead 2000), while female yellow dung flies can alter the paternity outcomes of their multiple partners (Ward 2000). Historically, it has been difficult to disentangle both the mechanisms and outcomes of CFC from those of male–male competition, such as sperm competition, as both influence sperm storage and paternity (Birkhead and Pizzari 2002). Furthermore, CFC is hard to observe, so studies of CFC have had to rely on indirect measures such as second male paternity, where CFC is inferred if offspring paternity does not reflect a male's mating success (Ward 2000).

In the Japanese pygmy squid, females are polyandrous and mate with multiple males. Male squid grasp females and ejaculate branching tubes (spermatangia) from spermatophores by a modified arm (hectocotylus). They then place several spermatangia on the female's body where they release many spermatozoa that then migrate to her seminal receptacle within 24 h of copulation (Sato et al. 2014a). A female can remove the spermatangia from her body before spermatozoa transfer by blowing water on them with her siphon, or by removing and eating them. This behavior makes the pygmy squid an excellent system for directly observing CFC and its outcomes.

Sato et al. (2016) combined direct observation of CFC with second male paternity measures to see which male traits females found most attractive and how female choice influenced the insemination success of attractive and unattractive males. The team measured CFC by counting the number of spermatangia placed, removed, and remaining on the female's body after each copulation act. They also examined each male to determine traits such as body size and duration of copulation. Finally, second male paternity was used to measure the insemination success of each male. Second male paternity was an important inclusion as it allowed Sato et al. to compare observed CFC with offspring paternity and to rule out potential bias toward the sperm of the last male to mate.

The team found that female squid preferentially removed the spermatangia of larger males who copulated quickly—a surprising result after a previous study found that females preferentially removed spermatangia from larger males who copulated for a long time (Sato et al. 2014b). Sato et al. (2016) suggest that female preference for small male body size and long ejaculation duration demonstrate CFC and not sperm competition because they are female-driven choices. However, Sato et al. (2016) found that CFC did not strongly influence final male paternity, suggesting that while females may bias the spermatangia of some males, male-driven sperm competition may still play a role in this system.

Sato et al. conclude that female preference for small males may have arisen in the Japanese pygmy squid to counter the large volume of spermatozoa produced by large males. However, it is unclear whether CFC has any strong consequences for the evolution of this species, since CFC did not alter the share of paternity

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achieved by preferred males. Future studies may investigate the consequences of CFC in these squid and compare the predictive power of second male paternity for mating systems where CFC is inferred and not observed.

LITERATURE CITED

Birkhead, T. R., and T. Pizzari. 2002. Postcopulatory sexual selection. Nat. Rev. Genet. 3:262–273.

Pizzari, T., and T. R. Birkhead. 2000. Female feral fowl eject sperm of subdominant males. Nature 405:787–789.

Sato, N., T. Kasugai, and H. Munehara. 2014a. Spermatangium formation and sperm discharge in the Japanese pygmy squid *Idiosepius paradoxus*. Zoology 117:192–199.

———. 2014b. Female pygmy squid cryptically favour small males and fast copulations as observed by removal of spermatangia. Evol. Biol. 41:221–228.

Sato, N., M. Yoshida, and T. Kasugai. 2016. Impact of cryptic female choice on insemination success: larger sized and longer copulating male squid ejaculate more, but females influence insemination success by removing spermatangia. Evolution. doi:10.1111/evo.13108.

Ward, P. I. 2000. Cryptic female choice in the yellow dung fly *Scathophaga stercoraria* (L). Evolution 54:1680–1686.

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