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Function of an extraordinary display in Sarcastic Fringeheads (*Neoclinus blanchardi*) with comments on its evolution

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Sexual selection is well-known for leading to elaborate traits and behaviors in animals (Andersson, 1994), but the context in which these unusual features evolved and function is often unclear. Understanding the mechanism behind such extraordinary features allows us to better understand the evolution of the organism. Here, we highlight an exaggerated trait in a tube blenny (Teleostei: Blenniiformes, Chaenopsidae) known as the Sarcastic Fringehead (*Neoclinus blanchardi,* Figure 1A; Video S1). Sarcastic Fringeheads, much like their relatives, reside within vacant invertebrate tests (e.g., gastropod shells) or rock crevices in the temperate eastern Pacific (Love, 2011; Hongjamrassilp et al., 2020). The name Sarcastic Fringehead is derived from its charismatic gaping display when encountering another individual (Figure1 B, C). The display starts with an individual opening its mouth, bending its head backward, and flaring its large upper jaw laterally exposing its colorful buccopalatal membranes to another individual. Despite the reputation of the display in popular culture, which can be seen in social media, the behavior was only recently briefly described in the scientific literature (Hongjamrassilp, 2016; Hongjamrassilp et al., 2018).

Sarcastic Fringeheads are set apart from their congeners through several anatomical features. In particular, this species has elongated maxillary bones with an unossified portion, extending well past the head in adult males. This trait, in combination with modified lacrimal bones that permit the upper jaw to be rotated laterally, enables the Sarcastic Fringehead to have a considerably wider gape than other related fishes that also perform a gaping display (Hongjamrassilp et al., 2018). In addition, the margin of the maxilla is yellow, and the buccopalatal membrane reflects UV light and is fluorescent. These features are hypothesized to further enhance the display. Even though Hongjamrassilp et al. (2018) described the special features related to the gaping display in Sarcastic Fringeheads and hypothesized possible

function of this display as a part of the agonistic behavior, the real functions of this extraordinary gaping display have never been accurately quantified.

While both males and females Sarcastic Fringeheads perform the gaping display, males have a bigger mouth, larger overall body size, and a more vivid buccopalatal membrane than females. Two main questions have arisen from this unique behavior and corresponding dimorphism. Do Sarcastic Fringeheads perform this behavior for territorial defense, courtship purposes, or both? Gaping displays that function in territory defense are known in other species of *Neoclinus* (Murase and Sunobe, 2011), in other chaenopsids (e.g., Robins et al., 1959; Hastings pers. observ.), and in other blenniiforms (e.g., Sauzima et al., 2002). The uniquely exaggerated display in the Sarcastic Fringehead also serves this defense function (Hongjamrassilp et al., 2018), but epigamic selection (or intersexual selection) may have also played a role in elaborating this display, especially given the flexible, unossified posterior extension of the maxilla that at first glance does not appear to enhance an individual's fighting ability. This leads to a second question: What are the selective pressures leading to the evolution of this unique display? In this study, we document the function of the extraordinary gaping display in Sarcastic Fringeheads and explore the possible sexual selection mechanism behind it.

During 2016 – 2019, we observed Sarcastic Fringeheads at field sites at Redondo Beach in Los Angeles and La Jolla Canyon in San Diego (California, USA) through SCUBA dives. Sarcastic Fringeheads favored rock crevices or vacant wavy turban snail shells (*Megastraea undosa*) as shelters. Most of the time, adult Sarcastic Fringeheads concealed themselves within a shelter with only their head protruding (Figure 1A). They were observed preying on small invertebrates such as skeleton amphipods (Family Caprellidae) and tuna crabs (*Pleuroncodes planipes*), with the size of its prey ranging from 0.2 cm to 7.5cm. When heterospecific non-prey

intruders such as humans, octopuses, and other fishes came within the shelter's proximity, rather than perform the gaping display, the Sarcastic Fringeheads instead chased the intruder via burst swimming and in some instances by biting the intruder. In contrast, if the intruder was a conspecific, the resident would signal to the intruder by gaping their mouth (Figure 1B).

We also collected live specimens of male Sarcastic Fringeheads (N=15 individuals) at around 20–30 meters depth near La Jolla Canyon using several vacant wavy turban shells as traps. Sarcastic Fringeheads were kept in captivity in flow-through seawater and fed pieces of squid every 2–3 days until satiation. To observe the gaping display in staged interactions, two males were introduced to a 10-gallon tank with a single turban snail shell placed in the center of the tank. After one individual took over the shell, subsequent interactions were recorded with a digital video camera. Based on 25 interaction observations (19 from staged tank observations and 6 from *in situ* observations), we generated an ethogram (Appendix S1: Table S1) and a kinematic diagram of the gaping display (Figure 2). In staged interactions, male Sarcastic Fringeheads performed a full gaping display in 68.42% of the encounters when a conspecific approached their shelter. In response, intruders would either retreat or return a gaping display. The gaping display was always performed before physical contact (i.e., fighting, including biting). In the case of physical contact, both fish swam at each other while holding a continuous gape and proceeded to collide with each other—mouth to mouth. The two fish—mouths still agape—then pushed each other, mouth to mouth, until one of the individuals terminated the attack by biting the other's head (or other parts of the body). Sarcastic Fringeheads that have larger body size (and thus longer jaws) were more victorious during these bouts (N = 40 interactions, $\chi^2 = 29.66$, $p < 0.001$) (Figure 1C).

Non-agonistic interactions were also observed between Sarcastic Fringeheads. Males, both *in situ* and in laboratory settings, were observed courting females by protruding their heads out of their shelter and rapidly shaking their heads side to side with their mouths closed or only slightly open (Video S2). This headshaking behavior is also observed in male Moss Fringeheads (*N. bryope*) (Murase and Sunobe, 2011) and *N. nudus* (Hongjamrassilp pers. observ.). In one *in situ* instance, the Sarcastic Fringehead's courtship display lasted around 10 minutes before the female stuck her head into the male's shelter, presumably to inspect the suitability of the refuge. This was followed by the female inserting the posterior part of her body into the male's shelter. As seen in Video S2, receptive females returned the lateral shake prior to entering the shelter. While the female was inside the shelter, the male continued to shake his head and patrol around the shelter. After the female deposited her eggs, she left the shelter, and the male entered it apparently to fertilize the eggs. The male then remained in the shelter, guarding, and fanning the eggs using pectoral and dorsal fin movements indicating paternal care in this species (Video S3). Eggs hatched about two weeks post-fertilization. It is important to note that the male never performed the gaping display to the female as part of the reproductive repertoire. Therefore, we suggest that the gaping display in Sarcastic Fringeheads functions specifically as an agonistic display for intraspecific communication. This may differ from their relative's western Pacific species such as *N. bryope*, which perform a gaping display to both conspecific and heterospecific intruders alike (Murase and Sunobe, 2011).

Combined with the combative interactions we observed between males, we believe that this exaggerated gaping display is primarily driven by male-male competition. Mate choice criteria in female Sarcastic Fringeheads is unknown. Females of other chaenopsids prefer to mate with large males (Hastings and Petersen, 2010), but it does not appear that male Sarcastic

Fringeheads use their elongate jaws for advertising their body size to females during courtship, at least not using the gaping display.

Alternatively, the large jaws in this species may have evolved to permit feeding on large prey. Most fishes are gape limited in the size of prey they can ingest (Hambright, 1991) and because of its large jaws the Sarcastic Fringehead is able to consume relatively large prey (Video S4). However, a study of its kinematics of feeding (Baettig et al., 2013) revealed it combines ram and suction feeding but does not utilize its maximum gape during prey capture. Instead, it typically uses less than half of its maximum gape and does not flare the maxillae laterally or tilt the head backwards. This suggests that these fish are capable of modulating their gape size differently when feeding versus displaying to conspecifics.

From a developmental perspective, the elongate jaws of the Sarcastic Fringeheads evolved via two forms of peramorphosis (Hongjamrassilp et al., 2018): acceleration in which the growth of jaws of males is positively allometric compared to those of females (and males of other species of *Neoclinus*), and hypermorphosis in which the jaws grow relatively longer in this, the largest species in the genus. The underlying selection for large body size in this species is unknown. Still, the availability of relatively large shelter and spawning sites, such as wavy turban shells, may have removed a constraint on maximum body size (see Hastings, 1988 for a discussion of shelter size constraints). However, these shells may be relatively rare, enhancing male-male competition for this limited resource. While we have not conducted experiments to test shelter limitation in this species, it has been shown for other shelter-dwelling chaenopsids (Hastings and Galland, 2010), and via anecdotal evidence in Sarcastic Fringeheads. This includes their well-known use of artificial shelters such as discarded cans (Love, 2011) and our ability to use vacant shells to attract and capture individuals. Thus, the large body size of Sarcastic

Fringeheads may have led to increased competition for shelters sites, resulting in selection for increased jaw size and exaggeration of the gaping display.

While extraordinary traits and behaviors in animals are well-known to result from sexual selection, the mechanism(s) behind elaboration and diversification of sexually selected traits remain poorly understood (McCullough et al., 2016). Many tube blennies exhibit sexual dimorphism and have diverse morphological characters and behavior (Hastings, 2019), but only a few studies have been conducted to investigate the evolutionary mechanism behind their unusual traits. Based on our behavioral study of Sarcastic Fringeheads, we postulate that the elaborate display and exaggerated morphological characters of this fish result from male-male competition for shelters in a highly competitive habitat. Moreover, the colorful mouth membrane of Sarcastic Fringeheads may play a role in signaling to inform an intruder regarding resource holding potential. Having a colorful mouth membrane for signaling in this fish supports "conspicuous signaling theory" which predicts that while a weapon is useful for fighting, the conspicuousness of the evolved weapon depends on the surrounding environment (McCullough et al., 2016). In this case, the coloration and fluorescence of Sarcastic Fringeheads mouth membrane may help the fish to communicate more effectively in the relatively deep ocean environment (20–30 or more meters) where light is reduced (Michiels et al., 2008; Britten et al., 2017). Nevertheless, whether females play a role in selecting males with larger jaws as mates needs to be addressed. In the realm of interesting traits, Sarcastic Fringeheads are a unique study organism and may offer new insights into sexual selection.

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Literature cited

Andersson, M. B. 1994. *Sexual selection*. Princeton, N.J.: Princeton University Press.

Baettig, C. G., L. B. Miller, P. A. Hastings, and R. S. Mehta. 2013. "Kinematics of Feeding in Sarcastic Fringeheads, *Neoclinus blanchardi* (Teleostei: Blenniiformes)." In *Integrative and Comparative Biology*, Vol. 53, E241–E241. Cary, N.C.: Oxford University Press.

Bitton, P. P., U. K. Harant, R. Fritsch, C. M. Champ, S. E. Temple, and N. K. Michiels. 2017. "Red fluorescence of the triplefin *Tripterygion delaisi* is increasingly visible against background light with increasing depth." *Royal Society Open Science*. 4:161009. doi: 10.1098/rsos.161009

Hambright, K. D. 1991. "Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth". *Transactions of the American Fisheries Society* 120: 500–508.

Hastings, P. A. 1988. "Female choice and male reproductive success in the angel blenny, *Coralliozetus angelica* (Chaenopsidae)". *Animal Behaviour* 36: 115–124.

Hastings, P. A. 2019. "Evolution of sexual dimorphism in tube blennies (Teleostei: Chaenopsidae)." *Integrative Organismal Biology* 1(1): 1–22.

Hastings, P. A., and G. R Galland. 2010. “Ontogeny of microhabitat use and two-step recruitment in a specialist reef fish, the Browncheek Blenny (Chaenopsidae).” *Coral Reefs* 29(1): 155 –164.

Hastings, P. A. and C. W. Petersen. 2010. “Parental care, oviposition sites and mating systems of blennioid fishes.” pp. 91–116, *In*: Cole, K. S. (ed), *Reproduction in marine fishes: Evolutionary patterns and innovations.* Berkeley, C.A.: University of California Press.

Hongjamrassilp, W. 2016. “Heterochrony and the evolution of an aggressive display of the Sarcastic Fringehead (Blenniiformes: *Neoclinus blanchardi*)” (Unpublished Master's thesis, UC San Diego).

Hongjamrassilp, W., A. P. Summers, and P. A. Hastings. 2018. “Heterochrony in fringeheads (*Neoclinus*) and amplification of an extraordinary aggressive display in the Sarcastic Fringehead (Teleostei: Blenniiformes)”. *Journal of Morphology* 279(5): 626–635.

Hongjamrassilp, W., A. Murase, R. Miki, and P. A. Hastings. 2020. “Journey to the west: trans-Pacific historical biogeography of fringehead blennies in the genus *Neoclinus* (Teleostei: Blenniiformes).” *Zoological Studies* 59: 1–12.

Love, M. S. 2011. *Certainly more than you want to know about the fishes of the Pacific Coast: a postmodern experience*. Santa Barbara, C.A.: Really Big Press.

McCullough, E. L., C. W. Miller, and D. J. Emlen. 2016. “Why sexually selected weapons are not ornaments.” *Trends in Ecology & Evolution* 31(10): 742 –751.

Michiels, N. K., N. Anthes, N. S. Hart, J. H. Alfred , J. Meixner, F. Schleifenbaum, G. Schulte, U. E. Siebeck, D. Sprenger, and M. F. Wucherer. 2008. "Red fluorescence in reef fish: a novel signalling mechanism?." *BMC Ecology* 8(1): 1–14.

Murase, A., and T. Sunobe. 2011. “Interspecific territoriality in males of the tube blenny *Neoclinus bryope* (Actinopterygii: Chaenopsidae).” *Journal of Ethology* 29(3): 467 –472.

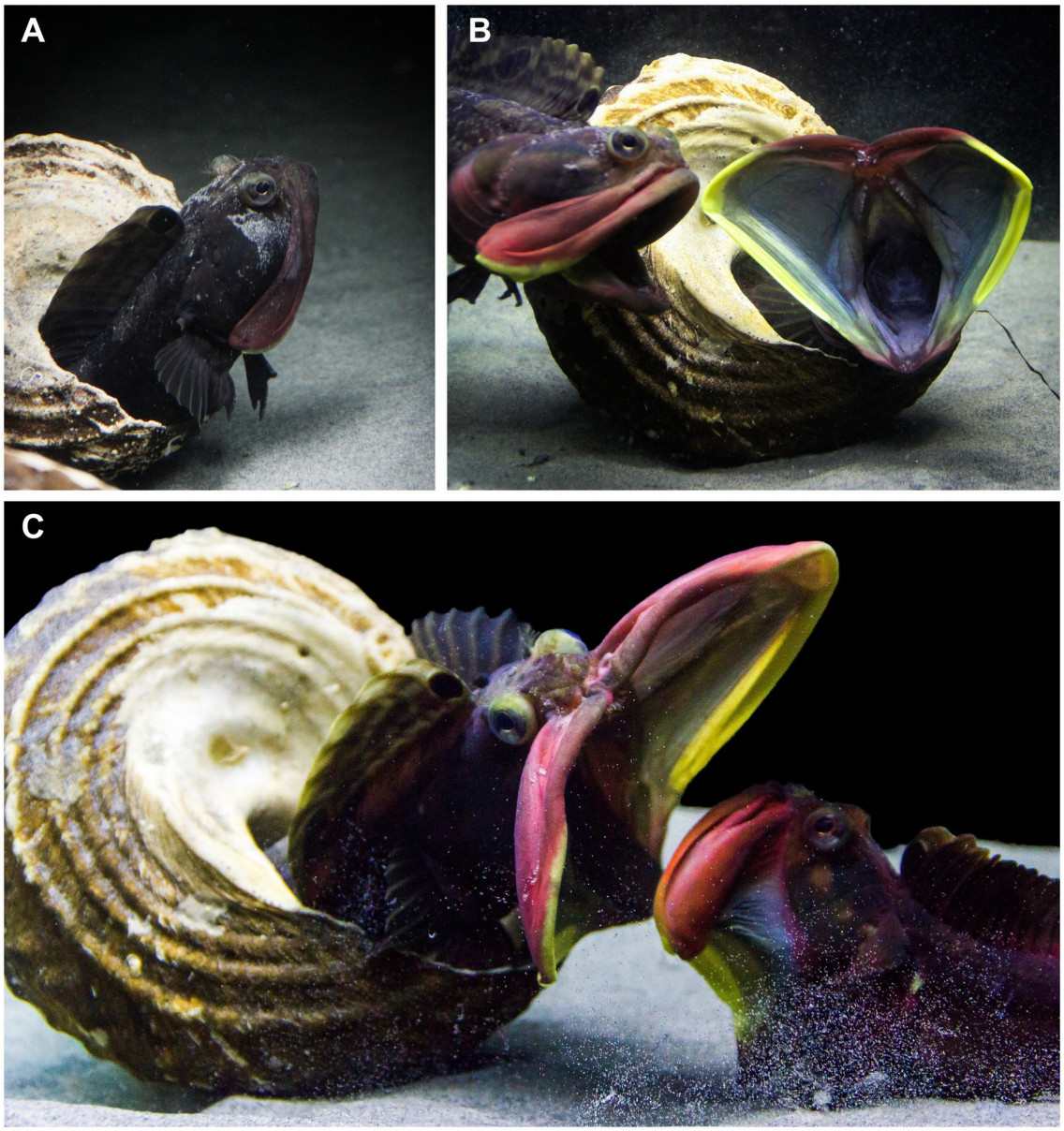
Robins, C. R., C. Phillips, and F. Phillips. 1959. “Some aspects of the behavior of the blennioid fish *Chaenopsis ocellata* Poey.” *Zoologica* 44(2): 77–84.

Sazima, I., J.L. Gasparini, and R Leão de Moura. 2002. “*Labrisomus cricota,* a new scaled blenny from the coast of Brazil (Perciformes: Labrisomidae).” *Aqua* 5: 127–132.

Figure legend

Figure 1 (A) A Sarcastic Fringehead (*N. blanchardi*) guards its shelter, a wavy turban snail shell, which is important for its survival and reproduction. **(B)** A Sarcastic Fringehead signals to the conspecific intruder by gaping its mouth displaying a colorful membrane and teeth to the intruder. **(C)** A Sarcastic Fringehead with a bigger mouth tends to win the fight and is ultimately able to occupy the shelter.

Figure 2 Kinematic diagram of transitions of behaviors of Sarcastic Fringeheads. This kinematic diagram was made from observations of 25 interactions. Please refer to Appendix S1 for the description of each behavior.



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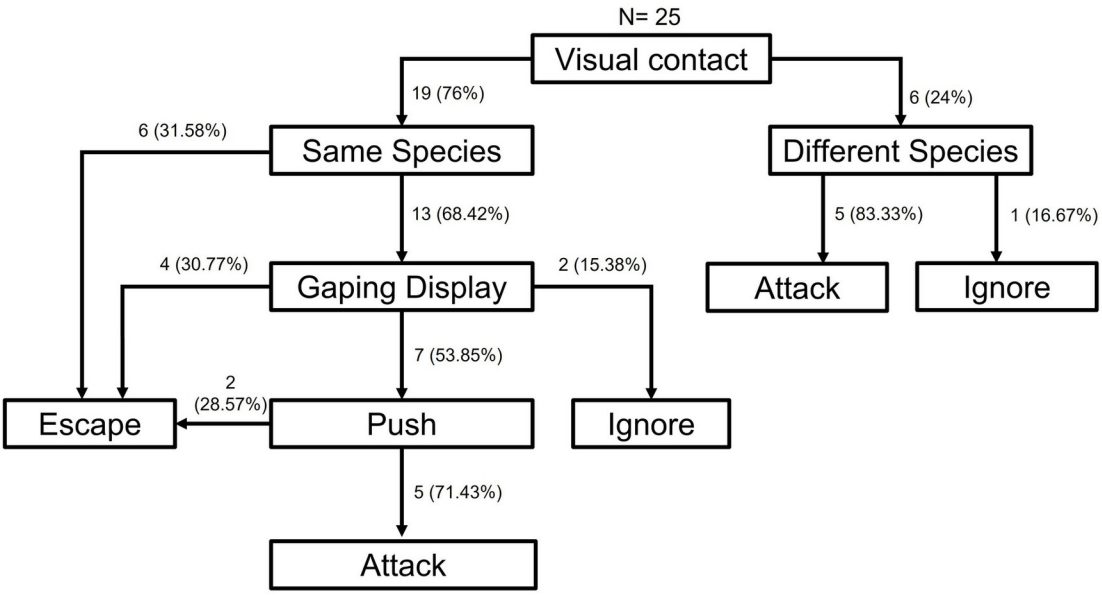

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