Diel activity patterns and habitat preferences of stonefish (*Synanceia* spp.) in captivity

Danica LENNOX-BULOW

Australian Institute of Tropical Health and Medicine, James Cook University, Cairns, Queensland.
danica.lennoxbulow@my.jcu.edu.au

Robert COURTNEY

Australian Institute of Tropical Health and Medicine, James Cook University, Cairns, Queensland.

Brendan C. EBNER

Australian Centre for Tropical Freshwater Research, James Cook University, Townsville, Queensland.
Department of Primary Industries NSW, Grafton Fisheries Centre, Grafton, NSW 2460, New South Wales.

Jamie SEYMOUR

Australian Institute of Tropical Health and Medicine, James Cook University, Cairns, Queensland.

https://doi.org/10.17082/j.2204-1478.65.2024.2023-04

Citation: Lennox-Bulow, D., Courtney, R., Ebner, B.C. & Seymour, J. (2023). Diel activity patterns and habitat preferences of stonefish (*Synanceia* spp.) in captivity. *Memoirs of the Queensland Museum* **|** *Nature 65*: 1–7. Brisbane ISSN 2204-1478 (Online), ISSN 0079-8835 (Print). Accepted: 7 November 2023. Published online: 9 January 2024.

Keywords:
Habitat use | diel activity | stonefish | *Synanceia* | crypsis | ambush predator.

Danica LENNOX-BULOW, Robert COURTNEY, Brendan C. EBNER, Jamie SEYMOUR

ABSTRACT

Synanceia verrucosa (reef stonefish) and *Synanceia horrida* (estuarine stonefish) are known as the world's most venomous fishes. However, little is known about their habitat preference and activity patterns. This study aimed to determine the habitat preferences and diel activity patterns of stonefish. The movements of four adults of each species that were offered complex and simple habitats in captivity were recorded by filming during day and night periods. Generally, both species exhibited similar behaviour, though *S. verrucosa* travelled further per movement than *S. horrida*. Collectively, stonefish spent 94% of their time associated with complex habitat and moved significantly less frequently on complex (1.6 movements per hour) relative to simple habitat (17.3 movements per hour). Stonefish were least active around sunset in the late afternoon and evening, which may relate to an active feeding period during the morning or paradoxically to a higher probability of ambush feeding success near sunset. These findings have enhanced our current understanding of the ecology of these species.

Figure 1. Side view of two stonefish species found in Queensland (North-Eastern Australia) waters, *Synanceia horrida* (estuarine stonefish, left) and *Synanceia verrucosa* (reef stonefish, right).

The reef stonefish (*Synanceia verrucosa*) and the estuarine stonefish (*Synanceia horrida*) are members of the Synanceiidae family (Fig. 1) and are known as the world's most venomous fishes (Isbister 2001; Meyers 1999). Stonefish are widely distributed in both the tropical and sub-tropical coastal marine waters of the Indian and Pacific oceans, including around northern Australia (Saggiomo et al. 2021). *S. verrucosa* is found on reef flats, shallow lagoons and in small intertidal pools, while *S. horrida* inhabits estuaries and near shore areas (Williamson et al. 1996; Grobecker 1981; Endean 1961). Stonefish are cryptic ambush predators that remain motionless for extended periods of time (Williamson et al. 1996; Grobecker 1981; Endean 1961), but will engulf nearby prey with explosive speed (Ferry-Graham and Lauder 2001; Grobecker 1981; Endean 1961).

Research conducted on stonefish has primarily focused on their venom and venom delivery system (Isbister 2001; Williamson et al. 1996; Kizer et al. 1985; Endean 1961), particularly their associated medical significance (Ngo et al. 2009; Brenneke and Hatz 2006). In contrast, apart from Grobecker's paper (1981), scant attention has been directed toward the ecology of these species, particularly their feeding behaviours, habitat preferences and activity patterns. Unlike fast-swimming pursuit predators that rely on speed and agility to capture prey (Juanes et al. 2002), stonefish are slow-swimming ambush predators that mimic benthic microhabitat (Grobecker 1981; Endean, 1961). Stonefish are highly cryptic, a common morphological adaptation to avoid detection by prey and predators that are visually oriented (Hairston et al. 1982; Endler 1981). Furthermore, stonefish can change colour to better match their environment (Loannou and Krause 2009; Grobecker 1981; Endean 1961). Background matching is less effective when animals are in motion; therefore, many cryptic animals tend to stay still (Loannou and Krause 2009; Zhang and Richardson 2007). Evidence also suggests that crypsis and lack of motion form a synergistic relationship, reducing the probability of detection (Loannou and Krause 2009). Additionally, stonefish encourage algal growth on their body surfaces, which enhances their ability to blend into their surrounding environment (Ballantine et al. 2001; Williamson et al. 1996) and may also attract herbivorous fish and invertebrates into the animal's strike range (Grobecker 1981).

Habitat type has proven to be an important factor that contributes not only to background matching, but also to the efficiency of foraging success for many ambush predators (Horinouchi et al. 2009; Schultz et al. 2009; Laurel and Brown 2006; Savino and Stein 1989). Structurally complex environments have been shown to reduce the efficiency of pursuit predators through reduced mobility and decreased vision (Laurel and Brown 2006; Abrahams 2005). However, the foraging efficiency of ambush predators in structurally complex environments is helped by their mode of predation, where these predators capitalize on their ability to ambush prey (Schultz et al. 2009; Stephens and Krebs 1986). Stonefish are commonly associated with complex environments, though they can also be found buried in the sand of simple environments (Williamson et al. 1996; Grobecker 1981; Endean 1961). It is unknown which habitat type is preferred by stonefish during the day or night. Subsequently, the aims of this study were to determine the habitat preferences and diel activity patterns of *S. verrucosa* and *S. horrida* in captivity to better understand the ecology of these medically important species.

MATERIALS AND METHODS

A total of four *S. verrucosa* and four *S. horrida* were used in the study. Two of each species (330–410 mm LT) were housed in each of two aquaria (dimensions L x W x D: 2.3 x 1.2 x 0.6 m) with substrate comprised of sand (0.1 m deep) in one half (termed simple habitat) and rock and large coral rubble in the other half (termed complex habitat) (Fig. 2). A ten-day acclimation period was provided before filming commenced. The aquariums were exposed to natural light and shielded from direct sunlight. Filming of the aquariums took place over a total of 72 hours, which was divided into two 9-hour day sessions from 08:00 to 16:50, and two 9-hour night sessions from 20:00 to 04:59. Both aquariums were filmed simultaneously during these four sessions. These time frames were chosen to compare behaviour patterns between light and dark conditions.

Figure 2. View from above of one of the experimental aquariums used in the study. Two substrate types were used; simple (left) comprised of sand-only and complex (right) containing a mixture of sand, rock, and large coral rubble. Arrows indicate the location of stonefish on complex habitat.

We quantified the time that each individual spent occupying each habitat type from film footage. The position of individuals resting on the boundary between two habitat types was classified according to the habitat containing the majority of the fish's body. A three-way analysis of variances (ANOVA) was conducted using the statistical package SPSS v. 17 to determine the effect of habitat type (complex, simple), condition (light, dark) and species (*S. verrucosa* and *S. horrida*) on the total amount of time spent in each environment. A further three-way ANOVA was conducted to explore the frequency of movements by each species per hour in relation to habitat type and period in the diel cycle (day, night).

Distance was calculated from film footage by marking the initial position of each stonefish, tracking their movement on a display monitor and measuring the on-screen distance travelled. This measure was then converted to the true scale movement distance ± 0.05 m and movements under 0.1 m were excluded. The time each movement occurred was recorded and rounded to the nearest minute. The movement times were then divided into hourly intervals. Using the statistical package R, a two-way repeated measures ANOVA and post-hoc least significant difference (LSD) was conducted to explore if the average distance travelled per movement differed between species and if the frequency of movement differed according to the time of day or night (among hourly intervals).

RESULTS

Stonefish habitat preference

There was no significant interaction between habitat, species, and/or period in the diel cycle in relation to total amount of time spent in each habitat (species × habitat × diel cycle) [$F_{1, 24} = 0.72$, $p = 0.40$]. There was also no significant interaction of the mean time spent in each habitat between the species (species × habitat) [$F_{1, 24} = 1.79$, $p = 0.19$]; or significant interaction between substrate type and period in the diel cycle (habitat × diel cycle) [$F_{1, 24} = 0.43$, $p = 0.52$]. However, stonefish spent significantly longer in the complex habitat (94%, $M = 1016$ min) than in the simple habitat (6%, $M = 73$ min) [$F_{1, 24} = 566$, $p < 0.001$] (Fig. 3).

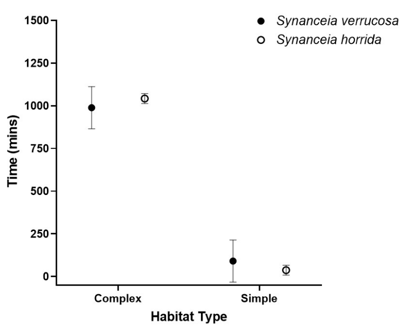

Figure 3. Stonefish (*Synanceia* spp.) habitat preferences. The mean amount of time (minutes) that reef (*S. verrucosa*, •), and estuarine (*S. horrida*, ∘) stonefish spent amongst simple (i.e., sand-only) and complex (i.e., a mixture of sand, coral rubble and rocks) habitats measured over 18 cumulative hours of day and night (i.e., between 08:00 ~ 16:59 hours and 20:00 ~ 04:59 hours). Error bars represent 95% CI.

Stonefish movement frequency and distance

There was no significant interaction between the mean frequency of movement per hour and species, habitat, or period in the diel cycle (species × habitat × diel cycle) [$F_{1, 22} = 0.13$, $p = 0.72$]. However, stonefish occupying the complex habitat moved significantly less frequently on average (1.6 movements per hour) than in the simple habitat (17.3 movements per hour) [$F_{1, 22} = 45.90$, $p < 0.001$] (Fig. 4A). There was no significant interaction between the mean number of movements in each habitat type per hour and species (species × habitat) [$F_{1, 22} = 0.64$, $p = 0.43$]; habitat and diel cycle (habitat × diel cycle) [$F_{1, 22} = 0.65$, $p = 0.43$]; or species and diel cycle (species × diel cycle) [$F_{1, 22} = 0.06$, $p = 0.81$].

There was no significant interaction in the average distance travelled per movement between the two species and the time each movement occurred (species × time) [$F_{13, 712} = 0.91$, $p = 0.54$]. However, *S. verrucosa* travelled further per movement ($M = 0.94$ m; $SD = 0.68$ m) than *S. horrida* ($M = 0.67$ m; $SD = 0.37$ m), [$F_{1, 712} = 53.20$, $p < 0.001$] (Fig. 4B).

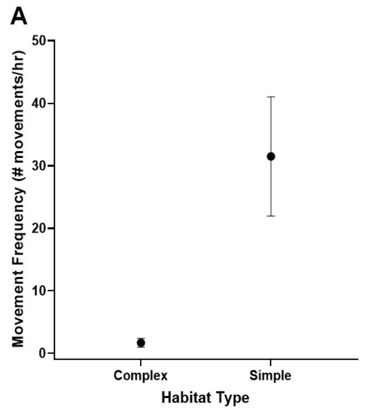

Figure 4. Movement patterns of stonefish. **A** Mean movement frequency (number of movements per hour) of stonefish (both *S. verrucosa* and *S. horrida*) over 18 hours (08:00 ~ 16:59 hours and 20:00 ~ 04:59 hours) in complex (sand, rock, and large coral rubble mixture) and simple (sand-only) habitat types. Error bars represent 95% CI.

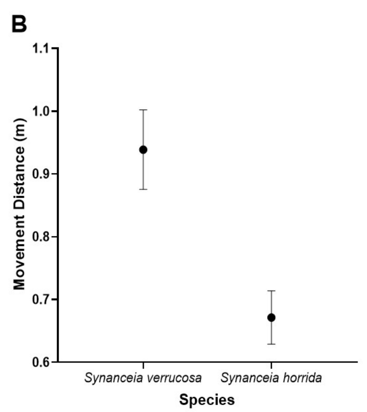

Figure 4. Movement patterns of stonefish. **B** Mean movement distance (metres) of *S. verrucosa* and *S. horrida* over 18 cumulative hours (08:00 ~ 17:00 hours and 20:00 ~ 05:00 hours) in both complex and simple habitat types. Error bars represent 95% CI.

Stonefish diel movement trends

There was a statistically significant effect for the time each movement occurred, and a post-hoc LSD analysis revealed stonefish travel further per movement during 10:00–10:59 hours (*M* = 1.26 m; *SD* = 0.92 m) and 09:00–09:59 hours (*M* = 1.14 m; *SD* = 0.84 m).

The shortest average distance per movement occurred during 16:00–16:59 hours (*M* = 0.63 m; *SD* = 0.44 m) and 20:00–20:59 hours (*M* = 0.65 m; *SD* = 0.43 m), [$F_{17, 712} = 2.76$, $p < 0.001$] (Fig. 5). There was a bimodal distribution corresponding to a decrease in the distance travelled per movement that related to reduced movement during transitional periods between light and dark.

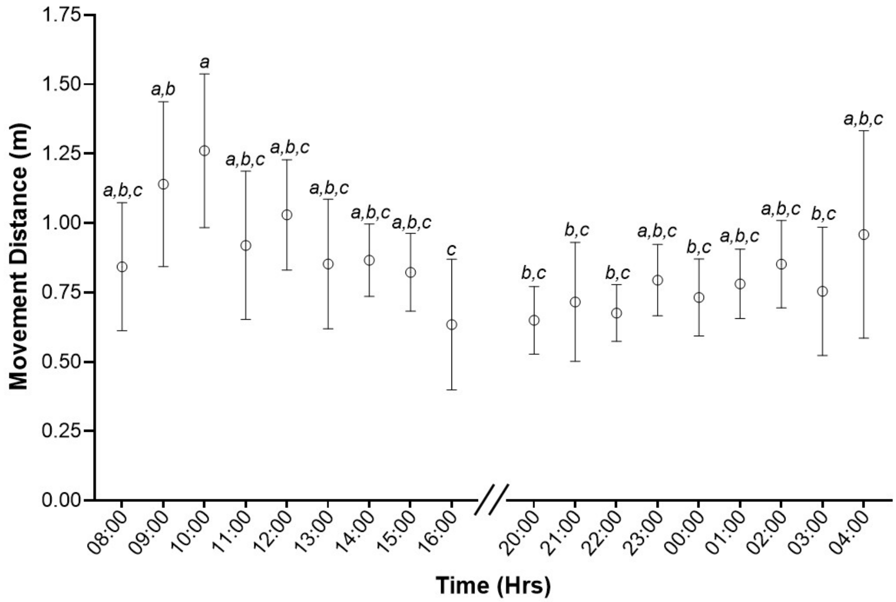

Figure 5. Stonefish diurnal movement distance. The mean distance (metres) that stonefish (both *S. verrucosa* and *S. horrida*) travelled within hourly intervals (i.e., 8:00 = 8:00 ~ 8:59 hours) over day (08:00 ~ 16:59 hours) and night (20:00 ~ 04:59 hours) periods. Error bars represent 95% CI. Means sharing the same letter grouping are not significantly different according to Fishers LSD (α = 0.05).

DISCUSSION

A key finding from the study was that both *S. verrucosa* and *S. horrida* exhibited a strong preference for spending time in complex benthic habitats (94%) over simple habitats (6%). This trend was not significantly different between the two species or the time of day. As with other ambush predators, stonefish presumably benefit from increased feeding efficiency and concealment from visual predators in complex habitats (Horinouchi et al. 2009; Schultz et al. 2009; Laurel and Brown 2006).

The difference in average distance travelled per movement between species in the study may indicate a real ecological and/or evolutionary difference in behaviour of these species in the field. For instance, *S. horrida* may rely on mobility of prey fishes in tidal estuaries where high turbidity prevails, whereas *S. verrucosa* may need to relocate ambush position in relation to site-attached and highly visual reef fishes that become aware of a predator's position. The differences in movement may also be an artefact of holding these species in close confines in captivity, although this is unlikely since antagonist interactions were not observed.

Alternatively, the small differences in average distance moved by two stonefish in the study may be statistically significant but have no functional basis (Underwood 1990).

Conversely, activity levels were substantially different between habitat types, with stonefish moving less in complex (1.6 movements per hour) than in simple habitats (17.3 movements per hour). This is consistent with other cryptic animals, which tend to stay still to avoid detection (Loannou and Krause 2009; Zhang and Richardson 2007). Specifically, the increased probability of predators or prey detecting the presence of stonefish in simple habitats may explain the increased frequency of movement on sand by stonefish in the current study. While this study investigated the effect of substrate complexity and time of day on habitat preference and activity patterns in reef and estuarine stonefish species, it is important to consider that various additional factors, such as turbidity, as well as physical substrate attributes like colour, brightness, and texture may also influence these behaviours *in situ*.

The diel activity patterns observed of stonefish in the current study may have a functional and possibly an evolutionary basis. Morris and Whitfield (2009) found that the scorpaenid, *Pterois volitans*, fed mostly in the early morning between 08:00–11:00 hours. Similarly, in this study, stonefish were most active at that time, and were least active during the late afternoon (between 16:00 and 16:59) and night (20:00 to 03:00). Reduced activity of stonefish around sunset may be an adaptation to ambush feeding during the transition from light to dark conditions. Paradoxically, whereas many predatory coral reef fishes become more active in association with crepuscular feeding (Helfman 1986), ambush predators such as stonefish may actually move less at that time, enhancing the advantage of crypsis and heightening the element of surprise for capturing mobile prey. Numerous studies have focused on the ecological advantages of crypsis in the context of predator-prey interactions (Théry and Casas 2002; Grobecker 1981) and recently the synergy between prey crypsis and reduced movement has been shown to confer additional protection to prey than can otherwise be explained by the additive effects of crypsis and movement (Loannou and Krause 2009). Whether such synergistic benefits are afforded to other cryptic ambush predators remains to be tested. In conclusion, this study suggests that there is an intrinsic link between stonefish movement patterns, time of day, and substrate complexity allowing for a better understanding of the ecology of these species.

ACKNOWLEDGEMENTS

This study was conducted under James Cook University Animal Ethics Committee Reference A1570. Brendan Ebner photographed the stonefish in Fig 1. The authors would also like to acknowledge the contributions of Megan Harris whose feedback greatly improved a late draft of this manuscript.

LITERATURE CITED

Abrahams, M. (2005). The physiology of antipredator behaviour: What you do with what you've got. *Fish Physiology*. **24**, 79–108. https://doi.org/10.1016/S1546-5098(05)24003-7.

Ballantine, D.L., Navarro, J.N., & Hensley, D.A. (2001). Algal colonization of Caribbean scorpionfishes. *Bulletin of Marine Science*. **69**(3), 1089–1094.

Brenneke, F., & Hatz, C. (2006). Stonefish envenomation — A lucky outcome. *Travel Medicine and Infectious Disease*. **4**(5), 281–285. https://doi.org/10.1016/j.tmaid.2005.09.001.

Endean, R. (1961). A study of distribution, habitat, behaviour, venom apparatus, and venom of the stone-fish. *Australian Journal of Marine and Freshwater Research*. **12**(2), 177–190, https://doi.org/10.1071/MF9610177.

Endler, J.A. (1981). An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society*. **16**(1), 25–31. https://doi.org/10.1111/j.1095-8312.1981.tb01840.x.

Ferry-Graham, L.A., & Lauder, G.V. (2001). Aquatic prey capture in ray-finned fishes: A century of progress and new directions. *Journal of Morphology*. **248**(2), 99–119. https://doi.org/10.1002/jmor.1023.

Grobecker, D.B. (1981). *The 'lie-in-wait' feeding mode of a cryptic teleost, Synanceia verrucosa*. Paper presented at the 3rd biennial conference on the Ethology and Behavioral Ecology of Fishes, held at Normal, Illinois, USA, May 19–22.

Hairston Jr, N.G., Li, K.T., & Easter Jr, S.S., (1982). Fish vision and the detection of planktonic prey. *Science*. **218**(4578), 1240–1242. https://doi.org/10.1126/science.7146908.

Helfman, G.S. (1986). Fish behaviour by day, night and twilight. In T.J. Pitcher (Ed.), *The behaviour of teleost fishes* (pp. 366–387). Springer. https://doi.org/10.1007/978-1-4684-8261-4_14.

Horinouchi, M., Mizuno, N., Jo, Y., Fujita, M., Sano, M., & Suzuki, Y. (2009). Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. *Marine Ecology Progress Series*. **377**, 43–49. https://doi.org/10.3354/meps07869.

Isbister, G.K. (2001). Venomous fish stings in tropical northern Australia. *The American Journal of Emergency Medicine*. **19**(7), 561–5. https://doi.org/10.1053/ajem.2001.28325.

Juanes, F., Buckel, J.A., & Scharf, F.S. (2002). Feeding ecology of piscivorous fishes. In P.J.B. Hart & J.D. Reynolds (Eds.), *Handbook of fish biology and fisheries: Fish biology*. **1**, (pp. 267–283). Blackwell Publishing. https://doi.org/10.1002/9780470693803.ch12.

Kizer, K.W., McKinney, H.E., & Auerbach, P.S. (1985). Scorpaenidae envenomation. A five-year poison center experience. *JAMA*. **253**(6), 807–810. https://doi.org/10.1001/jama.253.6.807.

Laurel, B.J., & Brown, J.A. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. *Journal of Experimental Marine Biology and Ecology*. **329**(1), 34–46. https://doi.org/10.1016/j.jembe.2005.08.003.

Loannou, C.C., & Krause, J. (2009). Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. *Biology Letters*. **5**(2), 191–193. https://doi.org/10.1098/rsbl.2008.0758.

Meyers, R.F. (1999). *Micronesian reef fishes: A comprehensive guide to the coral reef fishes of Micronesia* (3rd ed.). Coral Graphics.

Morris Jr, J.A., & Whitfield, P.E. (2009). Biology, ecology, control and management of the invasive Indo-Pacific lionfish: An updated integrated assessment. **99**, (pp. 57): National Oceanic and Atmospheric Administration Technical Memorandum.

Ngo, S.Y., Ong, S.H., & Ponampalam, R. (2009). Stonefish envenomation presenting to a Singapore hospital. *Singapore Medical Journal*. **50**(5), 506–509. https://www.ncbi.nlm.nih.gov/pubmed/19495521.

Saggiomo, S.L., Firth, C., Wilson, D.T., Seymour, J., Miles, J.J., & Wong, Y. (2021). The geographic distribution, venom components, pathology and treatments of stonefish (*Synanceia* spp.) venom. *Marine Drugs*. **19**(6), 302. https://doi.org/10.3390/md19060302.

Savino, J.F., & Stein, R.A. (1989). Behavior of fish predators and their prey: Habitat choice between open water and dense vegetation. *Environmental Biology of Fishes*. **24**, 287–293. https://doi.org/10.1007/BF00001402.

Schultz, S.T., Kruschel, C., & Bakran-Petricioli, T. (2009). Influence of seagrass meadows on predator–prey habitat segregation in an Adriatic lagoon. *Marine Ecology Progress Series*. **374**, 85–99. https://doi.org/10.3354/meps07779.

Stephens, D.W., & Krebs, J.R. (1986). *Foraging theory* (**Vol. 6**). Princeton University Press.

Théry, M., & Casas, J. (2002). Predator and prey views of spider camouflage. *Nature*. **415**, 133–134. https://doi.org/10.1038/415133a.

Underwood, A.J. (1990). Experiments in ecology and management: Their logics, functions and interpretations. *Australian Journal of Ecology*. **15**(4), 365–389. https://doi.org/10.1111/j.1442-9993.1990.tb01464.x.

Williamson, J.A., Fenner, P.J., Burnett, J.W., & Rifkin, J.F. (1996). *Venomous and poisonous marine animals: A medical and biological handbook*. UNSW Press.

Zhang, Y., & Richardson, J.S. (2007). Unidirectional prey–predator facilitation: Apparent prey enhance predators' foraging success on cryptic prey. *Biology Letters*. **3**(3), 348–351. https://doi.org/10.1098/rsbl.2007.0087.