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Individuality matters for substrate-size preference in the Nile tilapia juveniles

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ABSTRACT

Preference tests have usually been used to identify nonhuman animal preferences for welfare purposes (environmental enrichment), but they are mostly at the group level—that is, group preferences for resources or environmental conditions. However, a more robust method was developed to analyze animal preference, and this method detected clear individual variation in preferences of Nile tilapia fish (*Oreochromis niloticus*) selecting different background colors. Here, a clear individual variability of preference was found for another type of enrichment—the sizes of substrate. Despite this variability, a consistent response was detected at the group level: Small gravel was less frequently preferred than avoided, and the more decided fish (those who preferred only one substrate size) never preferred gravel over sand-size substrate. That is, Nile tilapia avoided gravel and preferred smaller substrate, and this finding was possibly associated with their mouth gap. Considering that small gravel is a substrate often used for fish rearing, these findings highlight fish keepers' incorrect perception of fish needs, based mostly on arbitrary criteria instead of actual fish preferences and without considering individual needs.

KEYWORDS

Preferred options; individual variability; gravel; sand

Detecting preference responses of nonhuman animals is an approach widely used to determine animal preferences to improve their welfare conditions. In this line, many studies involving preference tests have been applied for animals selecting different kinds of resources to detect animals' preferred options (e.g., Bartoshuk, Harned, & Parks, 1971; Basolo, 1990; Braithwaite & Barber, 2000; Girguis & Lee, 2006; Levy, Lerner, & Shashar, 2014). Preference responses have usually been inferred from momentary choices determined in trials conducted over a maximum of a few days, based on the assumption that a momentary choice should represent a preference (e.g., Gonçalves & Oliveira, 2003; Levy et al., 2014; Liao & Lu, 2009; Schlupp, Waschulewski, & Ryan, 1999; Webster & Hart, 2004). Moreover, in such tests, the individual variation of choice response was usually ignored, even when considering that significant individuality concerning preferred options of the animals was already demonstrated in tests conducted for a few days or trials (Browne, Caplen, Edgar, Wilson, & Nicol, 2010; Godin & Dugatkin, 1995; Johnsson, Carlsson, & Sundström, 2000; Wolfgang & Birkhead, 2004).

Recently, we demonstrated a method that identified two patterns of response from a set of choice tests: preferences and nonpreferences (Maia & Volpato, 2016). Accordingly, a preference response is a choice consistent over time, while a nonpreference response (hereinafter dispreference, based on Larrinaga, 2011) is a not consistent momentary choice, thus indicating that a choice response does not necessarily represent a preference of the animal. In this same study, we also found significant individual variability in preference responses for the Nile tilapia when choosing different background colors during several test days. This finding indicated that individuality of preferences can be

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maintained over time and therefore reinforced individual preferences in a group of fish. Once animal preference is investigated to support environmental enrichment, more attention and deeper investigation for other environmental resources considering individual responses are needed.

Substrate traits have been shown to improve growth, production, and even survival in the cichlid Nile tilapia (Uddin et al., 2007), indicating that substrate should be an important resource for environmental enrichment to improve the welfare conditions of this species. Furthermore, the type of available substrate affects the digging behavior of Nile tilapia (Mendonça & Gonçalves-de-Freitas, 2008). In fact, a previous study showed that the Nile tilapia preferred a particular size of substrate (Freitas & Volpato, 2013). However, these authors tested the Nile tilapia choices in only 4 daily consecutive tests, which was recently demonstrated to be insufficient to determine consistent preferences (Maia & Volpato, 2016). Considering the short-term nature of preference tests and the possibility of individual variability in such tests, we evaluated preference responses of Nile tilapia for different sizes of substrate in a set of 10 consecutive daily choice tests, while trying to identify the role of individual variability in such responses.

Materials and methods

Nonhuman animals and holding conditions

We tested juvenile Nile tilapias (*Oreochromis niloticus*; $M \pm SD$ = 6.93 ± 0.36 cm total length and 5.45 ± 0.90 g total weight), who came from commercial hatcheries and were kept in indoor tanks (1000 L–1700 L) for at least 30 days prior to the experiment. Fish were maintained at a low density (one fish/5 L) and were fed once a day in excess (5% of biomass/day) with commercial food for tropical fish (36% crude protein). Water was changed fortnightly, which maintained the water quality with pH ≅ 6.8, ammonium < 0.3 ppm, and nitrite < 0.05 ppm. Aeration was constant, and water temperature was maintained by heaters at 25°C to 27°C. The photoperiod was maintained from 6 am to 6 pm with white light (~ 300 lx).

Experimental strategy

To determine the preference responses of individual fish (n = 23), we tested 24-hour isolated fish for choices of four sizes of substrate in 10 consecutive daily tests. During each test day, fish were individually placed in the test apparatus (details in Figure 1) inside a transparent cylinder. After 5 minutes, fish were released to freely swim among the four compartments, and their positions were registered every 30 seconds for 1 hour, totaling 120 registers/test. Fish were then returned to their individual isolation aquaria, where they were fed, until the next daily test. These registers were used to determine the preference index (PI) and preference rate (PR), as described in Maia and Volpato (2016).

Specific procedures

The test apparatus was circular (⌀ = 40 cm), with size-matched compartments of each substrate size disposed peripherally to a central area (⌀ = 15 cm; Figure 1). The compartments for substrate choice contained the same amounts of substrates and differed only by particle sizes—fine sand (0.12 ± 0.04 cm), thick sand (0.57 ± 0.07 cm), small gravel (1.04 ± 0.16 cm), or large gravel (1.64 ± 0.29 cm)—based on Stoner and Abookire (2002; details in Figure 1). A circular acrylic piece was maintained in the central area of the test apparatus on the bottom (Figure 1), which worked as a platform from which the fish could access the four choice compartments.

Fish were weighted, and total length was measured before isolation for 24 hours. Then, we selected only fish with paler eyes for experimentation, as paler eyes are an indicator of a low level or lack of stress response in Nile tilapia (Freitas, Negrão, Felício, & Volpato, 2014). Water conditions

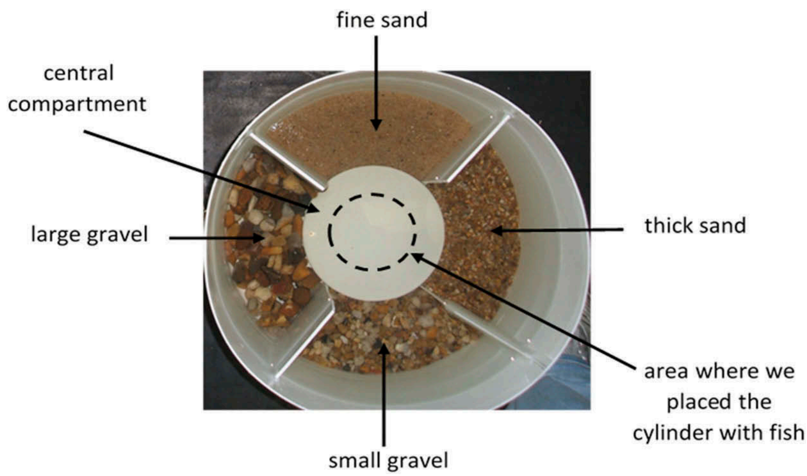

Figure 1. Top view of a test apparatus indicating the four similar choice compartments of the same volume and area. Each compartment was internally covered by a thin layer (~ 2 cm) of a substrate of a different size (fine sand, 0.12 ± 0.04 cm; thick sand, 0.57 ± 0.07 cm; small gravel, 1.04 ± 0.16 cm; or large gravel, 1.64 ± 0.29 cm). The central compartment was made of a white and circular piece of acrylic on a piece of cylindrical PVC (2 cm height). This compartment was used to place individual fish in the test apparatus, inside a transparent plastic cylinder (~ 8 cm in diameter), which was removed after a five-minute acclimation period. Aquarium diameter = 40 cm; water column height = 15 cm.

in isolation aquaria (40 cm × 20 cm × 25 cm) were similar to those in holding tanks. We siphoned water and conducted changes in isolation aquaria one to three times per week, always in the morning, while fish were in the test apparatuses. Individual heaters were used to maintain a stable temperature during all experimental procedures in isolation aquaria and test apparatuses. The light over the test apparatuses was white (~150 lx at the water surface level).

Preference index and preference rate calculations

To determine individual preferences and nonpreferences and the intensity of such responses, we calculated the PI values for each substrate size option for each fish, as described in Maia and Volpato (2016). Basically, for each individual, we summed the position registers over the test days for each substrate size option, resulting in a cumulative frequency for each option. Based on this result, we calculated the areas above the cumulative-frequency line, which were summed and then resulted in cumulative areas. Such calculated areas increase with the value of frequencies obtained in the most recent tests—a step based on the assumption that the more recent the choice is, the higher the impact for the calculations, as the preference responses may vary over time (details in Maia & Volpato, 2016). According to this index, positive PI values represent preference responses and negative values represent nonpreference responses. Moreover, each PI value indicates the intensity of preferred and nonpreferred responses. Thus, the most preferred option is indicated by the highest positive PI value, while the avoided (mostly dispreferred) option corresponds to the highest negative PI value of each fish.

Some fish showed preference for only one substrate size, and thus, they were qualitatively different from those who preferred two or more options (based on Maia & Volpato, 2016). For the other fish who preferred more than one substrate size, we decided among these preferred options by calculating the PR, a PI-derived calculus. PR indicates a response relative to the other preferred items, and thus, it is used to determine how much the fish prefer the most preferred option compared to the other preferences (described in Maia & Volpato, 2016).

Statistical analyses

For comparisons of frequencies of preferences or nonpreferences of different sizes of substrate, we used Goodman's proportion test among multinomials (Goodman, 1964). For comparisons between frequencies of preference and nonpreference for the same size of a substrate, we used Goodman's proportion test within multinomials (Goodman, 1965). For all these comparisons, $\alpha = .05$ was used.

Results

Fish varied their choices for preferred and nonpreferred sizes of substrate, with no clear association between the responses (Table 1). Such variation in responses included individuals with just one ($n = 7$) or two ($n = 15$) preferred items (Figures 2 and 3) and one fish who preferred all but one of the four available options (Fish 23, Figure 3). The intensity of each individual response also varied among fish, as indicated by a PI range from 148.00 to 9085.00 for preferences and from −9.75 to −5134.25 for nonpreferences (Figures 2 and 3). For fish who expressed two or more preferences ($n = 16$), the intensity responses of the first preference compared with the other preferences also varied considerably, as PR ranged from −50.23 to 89.26 (Figures 2 and 3). Moreover, one-preference fish (the most decided fish) never preferred gravel for substrate (Figure 2).

Although individual variation was high, as mentioned earlier, small gravel was more frequently a dispreferred than a preferred option (Figure 4a). Moreover, this size of substrate was more frequently an avoided option (the most dispreferred option) than the most preferred option (Figure 4b).

Discussion

Here we found that preferences of Nile tilapia for different particle sizes of substrate are a matter of individuality. Individual variation depended on preferred options, number of preferences, and intensity of response for substrate sizes. Despite these responses, a pattern was detected: Fish avoided small gravel substrate and the most decided fish (one-preference fish) always preferred sand sizes, not gravels. As small gravel is a common substrate size used in ornamental fishkeeping, to improve fish welfare conditions based on what is considered a good option, we highlight that our options for preferred items should consider the fish's own preferences. Thus, when it is possible, several substrate sizes should be made available for fish, and when it is not possible, at least small gravel should be avoided. Moreover, these fish options indicate that the ability of fish to remove substrate particles with the mouth is an important element of substrate preference.

Individual variability was expressed by fish in terms of different substrate sizes preferred by each fish and the different intensities of preferences/dispreferences (PI and PR values, Figures 2 and 3). This response ranged from a clear preference for one substrate size to a preference for three out of four choice options; the latter case indicates a rejection response for one item. Such variability in preference/dispreference does not seem to be related to the resource type, because it has also been reported for background colors in this same species (Maia & Volpato, 2016). Thus, the factors

Table 1. Lack of association between individual choices for the most preferred and the most nonpreferred options of substrate size.

Most nonpreferred option (columns) / Most nonpreferred option (rows)		Sand		Gravel		
		Fine	*Thick*	*Small*	*Large*	TOTAL
Sand	*Fine*	—	2	5	3	10
	Thick	4	—	1	0	5
Gravel	*Small*	2	0	—	0	2
	Large	2	1	3	—	6
TOTAL		8	3	9	3	23

Note. Data are from 23 fish. Each fish was added based on the association of his/her most preferred and most nonpreferred options.

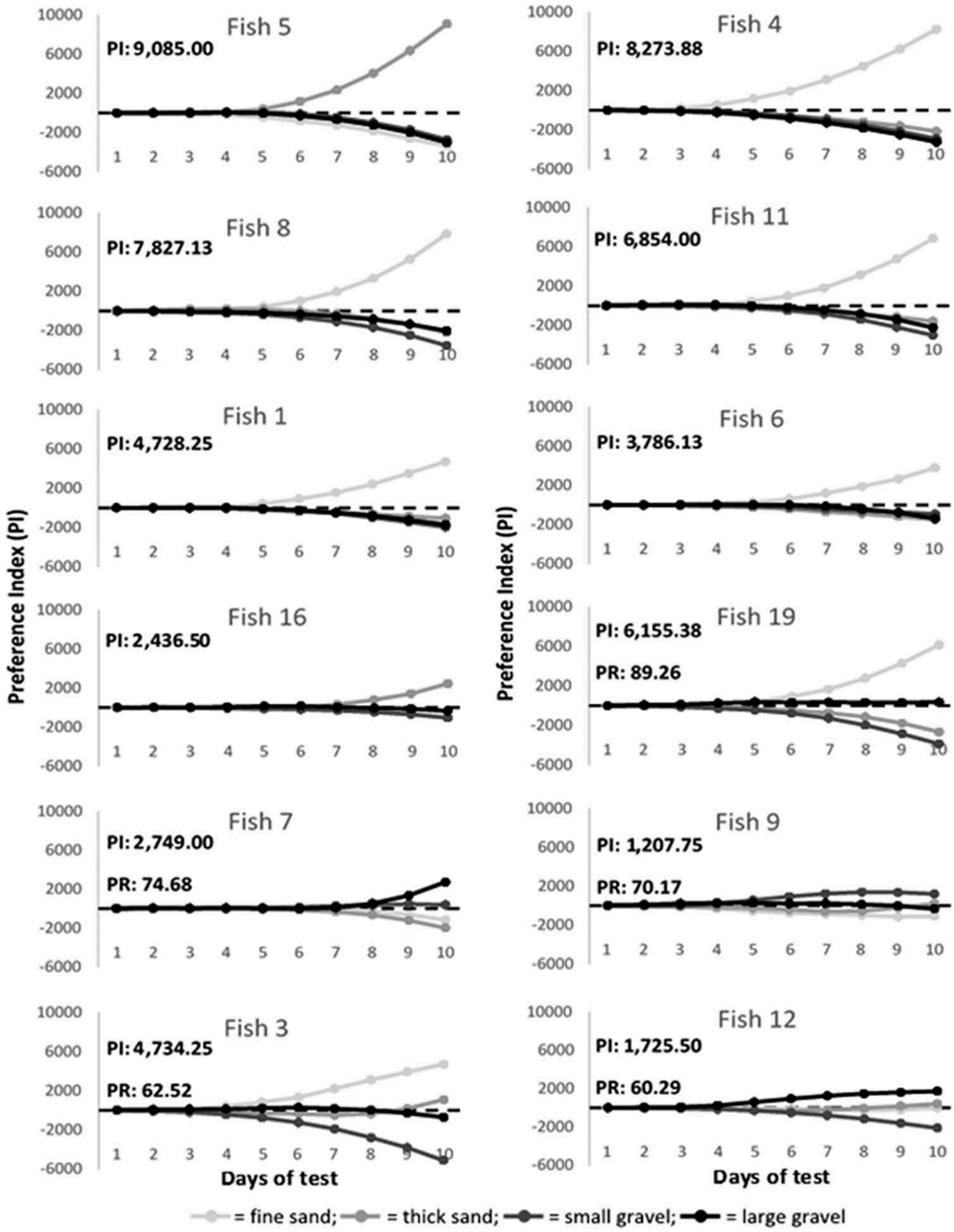

Figure 2. Individual profiles of preference (positive preference indices [PIs]) and dispreference (negative PIs) responses for different sizes of substrate, including one-preference fish. Fish 1, 4, 5, 6, 8, 11, and 16 expressed just one preference response. Thus, only PI values are indicated above lines for these fish. For other fish, PI values for the most preferred option and PR values are indicated above lines.

involved in such individual variability for substrate size seem to be more complex. Variability of preference for substrate size could not be explained in terms of the individual dispreference (Table 1). On the other hand, choice for specific substrate granulometry has been associated with mouth-gap size (Freitas & Volpato, 2013). Although this finding could explain most of the choices for sand instead of gravel, the very narrow range of fish size in our sample (coefficient of variation of 5.2% and 16.5% for total length and body mass, respectively) suggests that the association might be

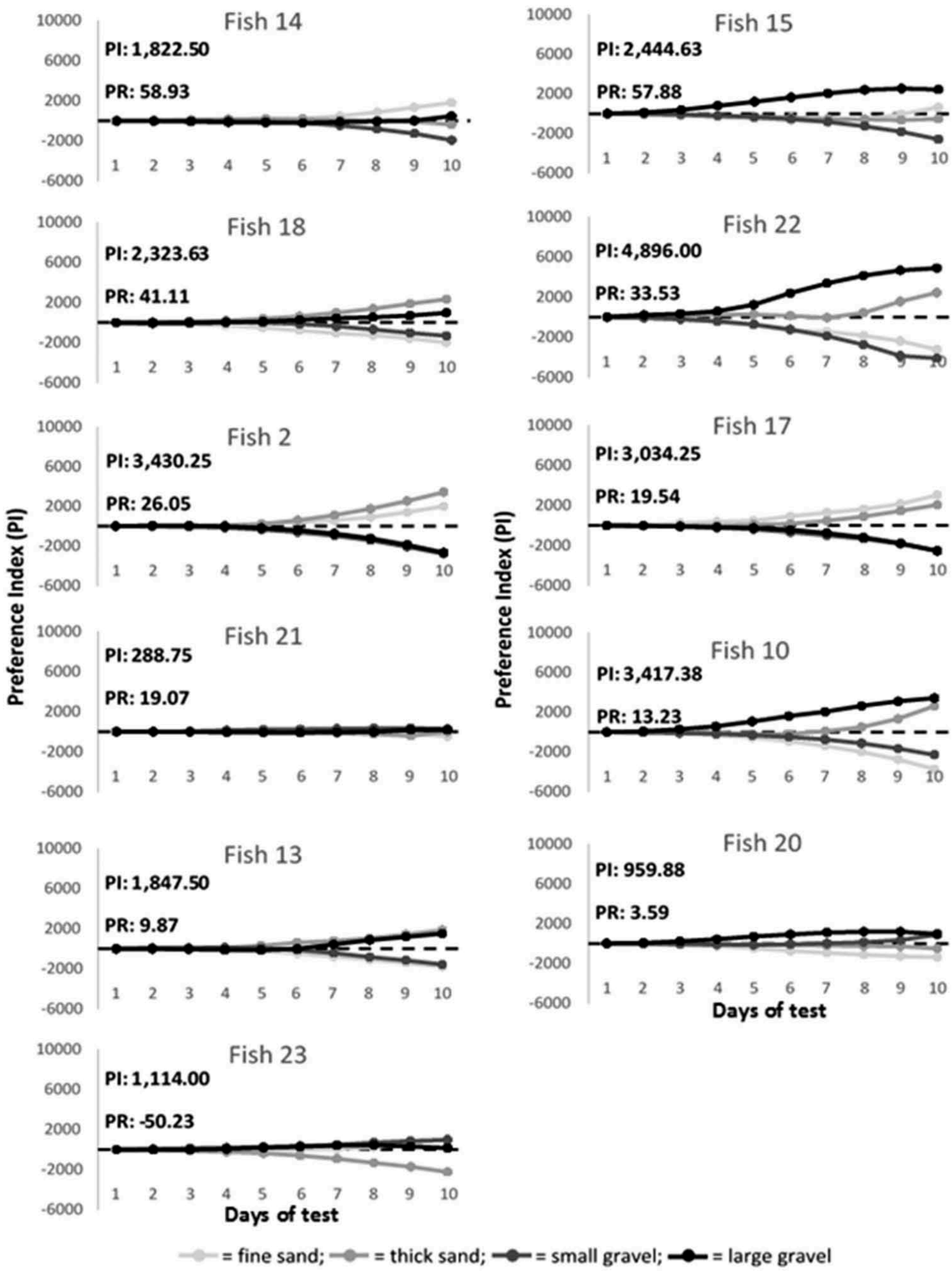

Figure 3. Individual profiles of preference (positive preference indices [PIs]) and dispreference (negative PIs) responses for different sizes of substrate. All fish here expressed more than one preference response, and thus, PI values for the most preferred option and preference response values are indicated above lines in all cases.

more complex (e.g., it includes the desire to move the substrate and not only the ability to do so). However, as we did not measure specifically the mouth gap of fish tested here, we suggest that future studies better investigate the relationship between the mouth-gap size of each fish and the individual variability of response for different sizes of substrate.

The Nile tilapia is a species that builds nests on the bottom by removing substrate particles with the mouth to make a depression in the substrate where eggs are laid. In this context, substrate

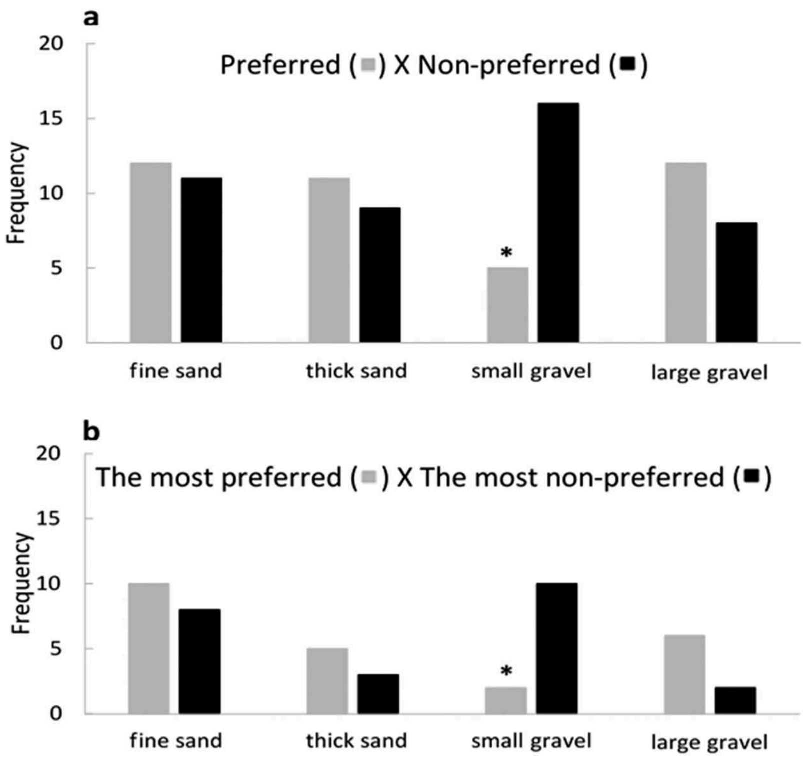

Figure 4. Frequencies of preference and dispreference responses for each substrate size. In (a), all responses were considered, while in (b), only the most preferred and the avoided options of each fish were considered. *Significant differences for the same size of substrate (Goodman's [1965] proportion test, $p < .05$). There was no difference of frequency among different sizes of substrate (Goodman's [1964] proportion test; $p > .05$).

particle size should be relevant for this species. However, we studied sexually immature juvenile Nile tilapia, suggesting that substrate particle size should not be so relevant at this developmental stage. This fact could better explain the high variability for the preferences detected here. In fact, Nile tilapia clearly preferred fine sand (~ 0.12 cm in diameter) compared with thick sand or gravel sizes of substrate when building nests (Freitas & Volpato, 2013). Moreover, Nile tilapia males preferred pure sand or a mixture of sand and shell substrates to build nests when females were present (Mendonça, Volpato, Costa-Ferreira, & Gonçalves-de-Freitas, 2010). However, Nile tilapia also moved substrate particles when feeding on the bottom, suggesting that the particle size should be an important factor for foraging, independently of mating purposes. Thus, as preference responses for substrate were inferred based on a few days of tests (up to five days) in Freitas and Volpato (2013) and Mendonça et al. (2010), further investigation is needed to elucidate if older and mature Nile tilapia would usually select a specific size of substrate consistently over time. Moreover, future studies should better clarify whether there is a difference between males and females, even when considering individual conditions of reproductive phases of preferences for substrate sizes.

Considering that fish with just one preference response always preferred sand sizes, thus avoiding gravels (small or large; Figure 2), we suggest that gravel should not be used as an environmental enrichment for the Nile tilapia. In fact, in preference tests with substrate particles sized similarly to the particles we used here, Nile tilapia preferred substrate sized similarly to our thick sand (~ 0.57 cm) but not gravels (Freitas & Volpato, 2013). According to Phelan, Manderson, Stoner, and Bejda (2001) and Stoner and Abookire (2002), the choice response for particle size of substrate depends on fish size. Based on Freitas and Volpato (2013), fish with ~ 7.1 cm of standard body length have a mouth gap of ~ 0.95 cm. In our tests here, fish were smaller than that (~ 6.9 cm of total body length).

It is possible that the most decided Nile tilapia (one-preference fish) avoided gravels because these substrates were larger (~ 1.04 cm and ~ 1.64 cm) than their largest mouth gap, but as earlier, we did not measure the individual mouth gap of fish, and thus, this finding needs further investigation. Despite this finding, an intriguing fact reported here is that fish, irrespective of number of preferences, avoided only small-sized gravel but not large-sized gravel (Figure 4). A putative explanation is that larger gravels can be more easily foraged without removal of the gravel.

Moreover, we should also consider that the colors and shapes of different sizes of substrate, which varied from a more homogeneous to a more heterogeneous substrate (Figure 1), may have influenced the individual fish preferences, especially considering that Maia and Volpato (2016) have demonstrated great individual variability of preferences for background colors in the same fish species tested here. Thus, the specific relation among colors, shapes, and substrate sizes influencing each individual preference response of fish is an issue for future studies. However, it does not invalidate the main pattern of Nile tilapia usually avoiding gravel, at least the smaller one, as this response was independent of individual variation of preferences/dispreferences for the substrate sizes tested here.

This study also raises an important issue for fish welfare. Ornamental fish keepers have usually used gravels as substrate for several species. This practice contradicts our findings reported here for species for whom substrates are biologically important. On one hand, individual variability suggests that fish should be more individually treated whenever possible. Thus, in cases where fish are more individualized and maintained at a low density of individuals, such as in ornamental aquaria, it is possible to offer more than one and even several sizes of substrate. On the other hand, the most avoided substrate size (small gravel) is the most used in ornamental fish-holding conditions, which reinforces Dawkins' (2006) warning that we should take into account animal preferences.

Conclusion

Here we found that what we think is a good option for environmental enrichment for animals does not necessarily represent their preferred option. As we considered gravel according to the fish's ability to move substrate particles, our study adds to this issue the importance of fish being able to physically interact with enrichment items. Moreover, our findings also highlight the need, wherever possible, to offer several substrate sizes for fish, and in situations in which it is impossible, at least small gravel should be avoided.

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References

Bartoshuk, L. M., Harned, M. A., & Parks, L. H. (1971). Taste of water in the cat: Effects on sucrose preference. *Science*, *171*, 699–701. doi:10.1126/science.171.3972.699

Basolo, A. L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science*, *250*, 808–810. doi:10.1126/science.250.4982.808

Braithwaite, V. A., & Barber, I. (2000). Limitations to colour-based sexual preferences in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, *47*, 413–416. doi:10.1007/s002650050684

Browne, W. J., Caplen, G., Edgar, J., Wilson, L. R., & Nicol, C. J. (2010). Consistency, transitivity and inter-relationships between measures of choice in environmental preference tests with chickens. *Behavioural Processes*, *83*, 72–78. doi:10.1016/j.beproc.2009.10.004

Dawkins, M. S. (2006). Through animal eyes: What behaviour tells us. *Applied Animal Behaviour Science*, *100*, 4–10. doi:10.1016/j.applanim.2006.04.010

Freitas, R. H. A., Negrão, C. A., Felício, A. K. C., & Volpato, G. L. (2014). Eye darkening as a reliable, easy and inexpensive indicator of stress in fish. *Zoology*, *117*, 179–184. doi:10.1016/j.zool.2013.09.005

Freitas, R. H. A., & Volpato, G. L. (2013). Motivation and time of day affect decision-making for substratum granulometry in the Nile tilapia *Oreochromis niloticus*. *Journal of Applied Ichthyology*, *29*, 239–241. doi:10.1111/jai.2012.29.issue-1

Girguis, P. R., & Lee, R. W. (2006). Thermal preference and tolerance of alvinellids. *Science*, *312*, 231. doi:10.1126/science.1125286

Godin, J. J., & Dugatkin, L. A. (1995). Variability and repeatability of female mating preference in the guppy. *Animal Behaviour*, *49*, 1427–1433. doi:10.1016/0003-3472(95)90063-2

Gonçalves, D. M., & Oliveira, R. F. (2003). Time spent close to a sexual partner as a measure of female mate preference in a sex-role-reversed population of the blenny *Salaria pavo* (Risso) (Pisces: Blenniidae). *Acta Ethologica*, *6*, 1–5. doi:10.1007/s10211-003-0083-8

Goodman, L. A. (1964). Simultaneous confidence intervals for contrasts among multinomial populations. *The Annals of Mathematical Statistic*s, *35*, 716–725. doi:10.1214/aoms/1177703569

Goodman, L. A. (1965). On simultaneous confidence intervals for multinomial proportions. *Technometrics*, *7*, 247–254. doi:10.1080/00401706.1965.10490252

Johnsson, J. I., Carlsson, M., & Sundström, L. F. (2000). Habitat preference increases territorial defence in brown trout (*Salmo trutta*). *Behavioral Ecology and Sociobiology*, *48*, 373–377. doi:10.1007/s002650000244

Larrinaga, A. R. (2011). Inter-specific and intra-specific variability in fruit color preference in two species of Turdus. *Integrative Zoology*, *6*, 244–258. doi:10.1111/j.1749-4877.2011.00249.x

Levy, K., Lerner, A., & Shashar, N. (2014). Mate choice and body pattern variations in the Crown Butterfly fish *Chaetodon paucifasciatus* (Chaetodontidae). *Biology Open*, *3*, 1245–1251. doi:10.1242/bio.20149175

Liao, W. B., & Lu, X. (2009). Male mate choice in the Andrew's toad *Bufo andrewsi*: A preference for larger females. *Journal of Ethology*, *27*, 413–417. doi:10.1007/s10164-008-0135-7

Maia, C. M., & Volpato, G. L. (2016). A history-based method to estimate animal preference. *Scientific Reports*, *6*, 28328. doi:10.1038/srep28328

Mendonça, F. Z., & Gonçalves-de-Freitas, E. (2008). Nest deprivation and mating success in Nile tilapia (Teleostei: Cichlidae). *Revista Brasileira De Zoologia*, *25*, 413–418. doi:10.1590/S0101-81752008000300005

Mendonça, F. Z., Volpato, G. L., Costa-Ferreira, R. S., & Gonçalves-de-Freitas, E. (2010). Substratum choice for nesting in male Nile tilapia *Oreochromis niloticus*. *Journal of Fish Biology*, *77*, 1439–1445. doi:10.1111/jfb.2010.77.issue-6

Phelan, B. A., Manderson, J. P., Stoner, A. W., & Bejda, A. J. (2001). Size-related shifts in the habitat associations of young-of-the-year winter flounder (*Pseudopleuronectes americanus*): Field observations and laboratory experiments with sediments and prey. *Journal of Experimental Marine Biology and Ecology*, *257*, 297–315. doi:10.1016/S0022-0981(00)00340-3

Schlupp, I., Waschulewski, M., & Ryan, M. J. (1999). Female preferences for naturally occurring novel male traits. *Behaviour*, *136*, 519–527. doi:10.1163/156853999501450

Stoner, A. W., & Abookire, A. A. (2002). Sediment preferences and size-specific distribution of young-of-the-year Pacific halibut in an Alaska nursery. *Journal of Fish Biology*, *61*, 540–559. doi:10.1111/jfb.2002.61.issue-3

Uddin, M. S., Farzana, A., Fatema, M. K., Azim, M. E., Wahab, M. A., & Verdegem, M. C. J. (2007). Technical evaluation of tilapia (*Oreochromis niloticus*) monoculture and tilapia-prawn (*Macrobrachium rosenbergii*) polyculture in earthen ponds with or without substrates for periphyton development. *Aquaculture*, *269*, 232–240. doi:10.1016/j.aquaculture.2007.05.038

Webster, M. M., & Hart, P. J. B. (2004). Substrate discrimination and preference in foraging fish. *Animal Behaviour*, *68*, 1071–1077. doi:10.1016/j.anbehav.2004.04.003

Wolfgang, F., & Birkhead, T. R. (2004). Repeatability of mate choice in the zebra finch: Consistency within and between females. *Animal Behaviour*, *68*, 1017–1028. doi:10.1016/j.anbehav.2004.02.007