



Three-spined sticklebacks show dimension-specific preferences for shelter

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Shelter is an important resource, serving as protection from rivals, predators and environmental stressors. The physical dimensions of a potential shelter are an important factor that can affect decisions about potential shelter options. Animals must select a shelter that they can fit into and use as a refuge, but beyond that, do they show fine-scale preferences based on shelter dimensions? This question has been actively studied for species whose shelter use is closely connected to their life cycles, such as obligate shell dwellers and nest-inhabiting species. However, preferences and decision making for temporary shelters has received less attention. We tested whether three-spined sticklebacks, *Gasterosteus aculeatus*, a common laboratory model, exhibit preferences in shelter use (actively entering and spending time within a shelter) between shelters with different dimensions. We used PVC tubes of different dimensions as shelters and conducted a simultaneous choice assay where individual fish were presented with each of three tubes available for use as shelter. The fish showed a clear preference, using larger diameter shelters more frequently than either of the other two options. There was no difference in the number of nonsheltering visits fish made or time to enter a shelter across tube sizes, which suggests an active selection by the fish rather than passive bias. There was no difference in duration of time spent within a shelter, suggesting that despite these preferences, actual benefit derived by the fish may be decoupled from the shelter dimensions. Our results offer opportunities for future research that addresses longer term questions in both behavioural ecology and welfare. What drives the preference for larger diameter tubes, and are there long-term benefits to shelter with preferred dimensions? Certainly, our results suggest that housing sticklebacks with larger diameter shelters may be a simple and convenient means to improve welfare.

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Animals must distinguish between similar resources and make choices about which to exploit. This often involves choosing between objects with different physical attributes. Many nest-building species show clear preferences between nests or parts of a nest with different dimensions (Buhot, 1989; Healy et al., 2023; Pärssinen et al., 2019); similarly, hermit crabs show dimension-specific preferences for shells (Conover, 1978). However, animals frequently also need to use structures that afford temporary shelter, and here there has been less research interest into aspects that influence choice, especially in fish. In such situations, such as when under imminent threat of predation, or immediately after escaping an attack, we might expect that any refuge is better than none, but do the dimensions of potential shelter have an influence on choice?

Shelter plays a fundamental role in the survival of animals. It provides refuge from predation and competitors as well as from environmental extremes, and allows recovery from psychological costs of exertion, aggression and stress (Berryman & Hawkins, 2006; Soukup et al., 2022). The availability of shelter can impact behaviour and have ecological consequences in fishes. For example, the availability of shelters affects spatial and foraging behaviour in juvenile Arctic charr, *Salvelinus alpinus* (Benhaïm et al., 2009). It can drive agonistic interactions over shelter as a resource or refuge from aggression, by disrupting visual communication in aggressive encounters (Frommen, 2020). Coral reef fishes show preferences for coral that provides shelter (Kerry & Bellwood, 2012; Ménard et al., 2012), choosing structures that maximize protection from ultraviolet wavelengths (Kerry & Bellwood, 2015). In a laboratory study, stream fish with shelter available had higher growth rates and body condition measures than those with low shelter availability, and for

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some species negative effects attributed to the presence of invasive predators were reduced (Matsuzaki et al., 2012). Similarly, shelter, or lack thereof, can also have important consequences in captive settings within laboratories and aquaculture (Näslund & Johnsson, 2016; Arechavala-Lopez et al., 2022). The mere presence of shelter in aquaria can have physiological benefits, for example captive Atlantic salmon, *Salmo salar*, showed reduced resting metabolism when provided with shelter (Millidine et al., 2006). This may explain the improved growth rates and behavioural performance observed in salmon housed with more shelter (Finstad et al., 2007). Similarly, Näslund et al. (2013) found that presmolt Atlantic salmon reared without environmental enrichment showed higher basal plasma cortisol levels than individuals reared with enrichment, which indicates shelter can reduce other physiological measures, in this case stress. Considering these results, availability of enrichment objects providing shelter can greatly benefit fish welfare by reducing responses to stress.

The beneficial influence of shelter on fish is not, however, consistently found across studies. In some cases, the addition of shelter can result in negative effects on some measurable benefits. Salmon parr raised with different levels of shelter showed no difference in postrelease survival, and even grew more slowly in more enriched rearing environments (Rosengren et al., 2016; Solås et al., 2019). A major factor here is fish density which may override or counteract effects of shelter: smolts held at high densities showed reduced growth, more fin damage and impacted intestinal function (Rosengren et al., 2016). Another reason for mixed results can be, at least partially, linked to species differences. For example, there were no differences in metabolism across conditions with and without shelter detected in the false clownfish, *Amphiprion ocellaris* (Kegler et al., 2013). Similarly, species with high intraspecific aggression may show increased levels of aggression with shelter, especially if they compete over it, for example in African catfish, *Clarias gariepinus* (Boerrigter et al., 2016). Many other factors may underlie the different usage patterns and effects of access to shelter across studies. Time of day can play a role, for example, as shown by a study on Eurasian minnows, *Phoxinus phoxinus*, where the influence of shelter varied between day and night (Chrétien, Boisclair et al., 2021). Social context, such as level of dominance, has also been shown to influence shelter use, in species such as smallmouth bass, *Micropterus dolomieu* (Chrétien, Cooke et al., 2021) and the cichlid *Neolamprologus pulcher* (Reddon et al., 2019). More pertinently, the metabolic effect of shelter may depend on the type of shelter. This aspect is largely overlooked, but whether an object is used as shelter may be driven by its attributes and whether it is perceived as shelter by the animal tested. Indubitably, different species have different shelter requirements, or preferences, and this may drive differences in shelter effects between studies. A recent study highlights this: species richness increased with diversity of type of refuge available in a habitat (Hall & Kingsford, 2021). Yet, the attributes of the objects provided for shelter are frequently not considered: a review of studies of physical enrichment in fishes revealed that the ecological basis for use of specific objects for shelter is infrequently provided in the majority of studies (Jones et al., 2021) and suggested more attention should be focused on the type, amount and dimensions of the shelter provided. For most species of fish, and other animals that use temporary shelters, there are still fundamental questions to address, the first being 'do fine-scale differences in the dimensions of the shelter shape usage and preferences'?

Studies that explore shelter preferences have tended to focus on objects used as long-term shelter; in hermit crabs, studies have shown that attributes of shells strongly influence shelter preferences (Bertness, 1981; Conover, 1978; Reese, 1962; Wada et al., 1997). Similarly, shell attributes have been shown to be

important in a recent study of *Neolamprologus multifasciatus*, shell-dwelling cichlids from Lake Tanganyika, which use empty snail shells extensively, as egg deposition and brood care chambers and as shelters to avoid predation (Bose et al., 2020). This study explored the influence of specific attributes and dimensions of shelters on the cichlids' preferences and shelter selection. The fish had significant preferences for shell attributes, including length and aperture width (Bose et al., 2020), suggesting that the small-scale differences in dimensions are worth paying attention to. These and other shell-dwelling cichlids, however, do not move far from their selected shell(s) (Saeki et al., 2022). What about preferences in species that are less closely tied to shelter, and use it more temporarily?

In this study we tested the open-ended hypothesis that the dimensions of objects will influence which objects are used as shelter. We used a common laboratory model species, three-spined sticklebacks, *Gasterosteus aculeatus*. Stickleback shelter use is typically studied in contexts of an antipredator response (Näslund, Bererhi et al., 2015), or in terms of physical enrichment in captivity (Brydges & Braithwaite, 2009). For example, sticklebacks increase shelter use when a predator is present (Ajemian et al., 2015). However, there have been very few empirical tests of their shelter preferences. More importantly, they are highly adaptable to different habitats (Smith et al., 2022; Spence et al., 2013) with no clear association with any specific forms of shelter, making them suitable for investigating shelter preferences in a more general species. We aimed to test whether fish exhibit preferences in shelter use (when the fish fully enters a shelter) for specific dimensions of PVC tube in a free-choice testing arena. We used PVC tubes primarily because they are commonly provided as shelter for captive fish, for many species (Näslund & Johnsson, 2016), including sticklebacks (Ressel et al., 2022; Velema et al., 2012), and because tubes of different dimensions are easy to obtain.

METHODS

Subjects and Husbandry

We collected 45 three-spined sticklebacks from the Kinness Burn, a stream in Scotland, in February 2022 in two batches of sampling due to low catches on the first sampling event. We collected the fish using funnel-traps, keeping the traps in the water for 15 h in an attempt to reduce the inherent sampling bias (Webster & Rutz, 2020) of passive fish traps (Álvarez-Quintero et al., 2021; Kressler et al., 2021). Fish were moved to the laboratory and kept in group tanks for 2 weeks to acclimatize to the laboratory conditions; water was maintained at room level at 10.0 °C, with a 12:12 h photoperiod. Fish were then transferred into individual 45-litre aquaria for 3 weeks before testing began. We used fish of undetermined sex that had body lengths between 4.5 and 5.0 cm and were not showing any breeding coloration. Each housing aquarium was aerated with an air stone and contained the same physical enrichment: gravel (natural mixed colours, grain size 3–5 mm, 0.5 cm depth covering 100% of the bottom of the tank), one artificial plant (8 cm tall, light green leaves, 2 cm maximum leaf breadth), and shaded with black opaque plastic covering circa one-third of the surface area of the tank. Fish were fed daily ad libitum with commercial frozen bloodworms defrosted, at the end of each day, after any trials were completed. After the experiment was complete fish were released back to the point of capture.

Experimental Set-Up

We used a selection of three PVC tubes with different dimensions, but the same colour (grey). Two tubes had equal

diameters (2.2 cm) but one, called the short-narrow tube, was shorter, at 5 cm long (just long enough for most of a 4–5 cm fish to fit in), and the other 10 cm long, the long-narrow tube. The third, long-wide tube, was 10 cm long with a 5 cm diameter. The tubes were based on the use of a small narrow tube as enrichment of sticklebacks in previous studies (Divino & Schultz, 2015; Jones et al., 2023). As there was no previous work on this question, we used simple changes in dimensions, doubling the diameter and the length of previously used tubes. The testing arena was an 80 cm diameter plastic pool with opaque black sides (Fig. 1). The bottom was covered in white sand for easier visual tracking of the fish. Water depth was maintained at 10 cm, from the top of the sand to the surface. In each trial the tubes were arranged such that they were equidistant from the midpoint of the arena with their openings oriented towards the central point, and well within the visual range of sticklebacks held at the midpoint of the arena (Näslund et al., 2017; Sibeaux et al., 2022). A wide-angle video camera (USB 5 megapixel) was mounted directly above the set-up for a top-down view of the arena.

Procedure

Fish took part in one trial per day for up to 4 consecutive days. The first batch of 15 fish were tested in a single trial. We used three arenas to run simultaneous tests. The second batch of 25 fish were tested in four trials each across consecutive days. Trials were conducted in the morning of each day, and the fish were selected pseudorandomly so that they were not tested in the same order every day. At the beginning of each trial the fish was netted from its housing tank and placed into the starting zone within the testing arena. It was held in the starting zone with a circular, transparent, plastic enclosure, 7 cm in diameter, placed in the middle of the arena. The fish was held there for ca. 30 s, so it had the opportunity to view the shelters before the trial began. The starting enclosure was then raised out of the water and the trial began. The fish's behaviour was recorded using a video camera (USB 5 megapixel) for 10 min. It was then caught and returned to its housing tank. The position of the tubes within the arena was changed between trials to control for potential side bias and the water was drained and refilled with new aerated water from a reservoir tank kept in the laboratory at the same temperature (10 °C) to mitigate scent biases affecting consecutively tested fish.

Measurements

Behaviours were scored using the BORIS software (Friard & Gamba, 2016). For each trial we measured (1) shelter use, where

fish fully entered the shelter, (2) the number of visits to each shelter type, where a visit was counted if a fish came within one body length of the shelter, (3) duration, the amount of time (s) spent within a shelter and (4) the latency to enter a shelter. In some instances fish rapidly left the starting zone as the door was opened in a 'flight' response and then maintained a frozen position, a common response to being startled (Kalueff et al., 2013; Näslund, Lindström, et al., 2015). In these instances, if a fish 'froze' within one body length of, but outside, a shelter we scored this as a visit rather than shelter use as they did not actually enter the shelter.

Analysis

All analyses were conducted using the R base package (R Core Team, 2022). The lme4 package (Bates et al., 2015) was used to fit the multilevel generalized linear mixed models (GLMMs) and post hoc Tukey pairwise comparisons (where reported) were performed using the emmeans package (Lenth et al., 2018). Diagnostics, including over- or under-dispersion of non-Gaussian models, were evaluated with the DHARMA package (Hartig, 2022).

We fitted different models to investigate whether the dimensions of a shelter affected preferences. First, to address the primary question and explore differences in shelter use we fitted a generalized linear model (GLM) with the number (count) of shelter use events as the response variable and trial number as a fixed (continuous) factor. We included subject identity as a random factor and used a Poisson family log link function. We chose to use the log link function within GLM rather than log transforming the response data before modelling (which is a common approach). Both approaches are valid, but GLMs with appropriate link functions are more flexible than transformations of the response; this approach allows separate modelling of linearity and variance relationships and typically leads to better fits (Bolker et al., 2009). It also allows the model to return estimates without back-transforming, which is more convenient, and in some cases can avoid errors associated with transformation. We note that we get similar results (and level of significance) with either approach with our data. There was no evidence for dispersion in the fitted model (dispersion = 1.232, $P = 0.16$). We also tested whether there was a difference in amount of time spent in each shelter. Here, we used a GLMM with a Gaussian family log link function duration, with duration of time spent in a shelter fitted against type of shelter and trial with the subject identity term as a random factor. This model was also not over- or under-dispersed (dispersion = 0.994, $P = 0.968$).

Preferences in choices, specifically shelter use in this study, may most parsimoniously be attributed to bias for specific tubes; for

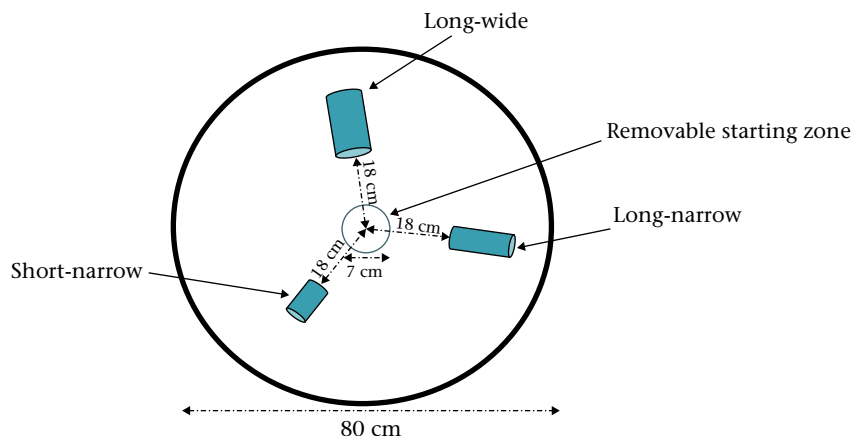


Figure 1. Sketch of the assay set-up showing the starting zone and three shelter choices of different dimensions with tubes drawn to scale.

example, fish may enter a larger tube because they are more likely to encounter it when swimming. As one test for whether bias may account for our results, we compared differences in the number of times a fish visited each tube (nonsheltering visits were counted as occasions when fish came within one body length of a shelter but did not enter). To do this we fitted counts of visits to each shelter in a GLM with subject identity and trial as random factors and used a Poisson family log link function. We also checked to see whether there was any evidence of bias in terms of fish being faster to enter any tubes. Here, we fitted time to enter a shelter (seconds after the starting chamber was removed) in a model with shelter type as the predicted factor in a GLM with a gamma family distribution and ('log') link function to account for distribution inherent to latency data. We included fish identity and trial as random factors.

Our repeated measures approach for one batch of fish afforded us the opportunity to test individual differences, specifically the level of repeatability (Bell et al., 2009), in shelter use. For analysis we used the approach of Biro et al. (2010) and compared the full model we used to quantify the effect of shelter type on shelter duration (as above), where fish identity was specified as a random effect, with a null model, where the individual identity was removed, using a likelihood ratio test (LRT). A significant difference between the two models indicated that there were consistent differences in behaviour at the individual level across the three treatments (LRT: subject: χ^2_{27} , $P < 0.001$). To formally test for repeatability at the level of fish we calculated an estimate of 'R' using the 'rptR' package (Stoffel et al., 2017). This package builds on the functions developed for mixed model analysis with the addition of parametric bootstrapping to provide reliable estimates for 'R' and the uncertainty surrounding those estimates (Stoffel, Nakagawa, & Schielzeth, 2017; Stoffel et al., 2017).

Ethical Note

The experiments adhered to the Guidelines for the treatment of animals in behavioural research and teaching (ASAB Ethical Committee & ABS Animal Care Committee, 2012). The procedures performed were in accordance with the ethical standards and approval of the University of St Andrews Ethics Committee. The principal source of potential stress was in transferring fish between tanks and the testing arena. Only experienced handlers caught the fish, and transfer time was kept to a minimum. Fish were monitored for at least 15 min immediately after any movement between tanks. We checked for changes in colour and behaviour that might indicate fish stress or a lack of wellbeing. Fish only showed minimal signs of stress and in all cases colour changes and sheltering ended within 15 min, and all fish maintained a healthy appetite throughout the study. All individuals were retained in the laboratory for a further 3 weeks, and as none showed visible symptoms of disease they were returned to the point of capture.

RESULTS

Three-spined sticklebacks exhibited shelter use that differed significantly across types of shelter (LRT on 'Shelter type' predictor: $\chi^2_2 = 84.979$, $P < 0.001$; Fig. 2). Post hoc tests revealed that fish sheltered within the long-wide tube significantly more frequently than the other two tube types (versus long-narrow: emmean contrast -2.09 ; z test: $z = 6.892$, $P < 0.001$; versus short-narrow: emmean contrast -2.01 ; z test: $z = 6.868$, $P < 0.001$). There was no indication of an order effect as trial number had no significant influence in the model (LRT on 'Trial' predictor: $\chi^2_1 = 1.189$, $P = 0.276$).

This difference did not appear to be driven by biases outside a shelter use context, as fish did not visit the long-wide shelter more

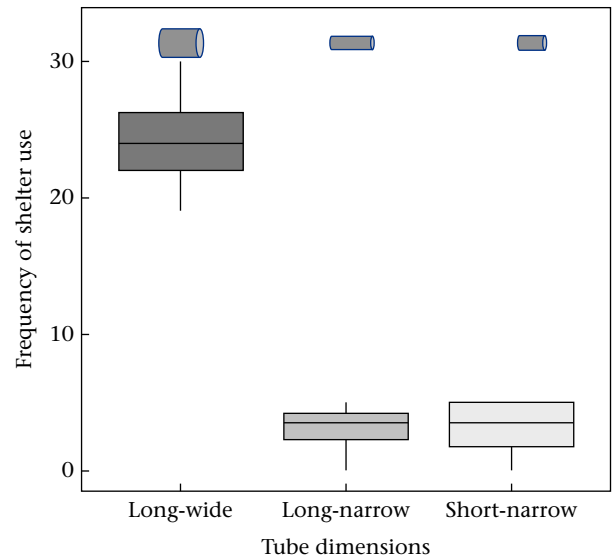


Figure 2. The number of times fish sheltered within each tube type across all trials. Box plots show the median, 25th and 75th percentiles; the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2). $N = 40$ fish tested once and a subset of 25 tested three more times each.

than the other shelters. The number of nonsheltering visits did not differ significantly between the three shelters (LRT: $\chi^2_2 = 4.947$, $P = 0.084$; Fig. 3). Similarly, there was no effect of time to enter a shelter after the start of a trial (LRT: $\chi^2_2 = 0.780$, $P = 0.677$; Fig. 4). On the occasions when fish did use a shelter, there was no significant difference in duration of time spent per shelter type (LRT: $\chi^2_2 = 2.637$, $P = 0.268$; Fig. 5, A1), nor was there an effect of trial (LRT on 'Trial' predictor: $\chi^2_1 = 0.310$, $P = 0.579$).

With repeat testing across 4 days the frequency of sheltering was strongly related to fish identity: specific fish were more likely

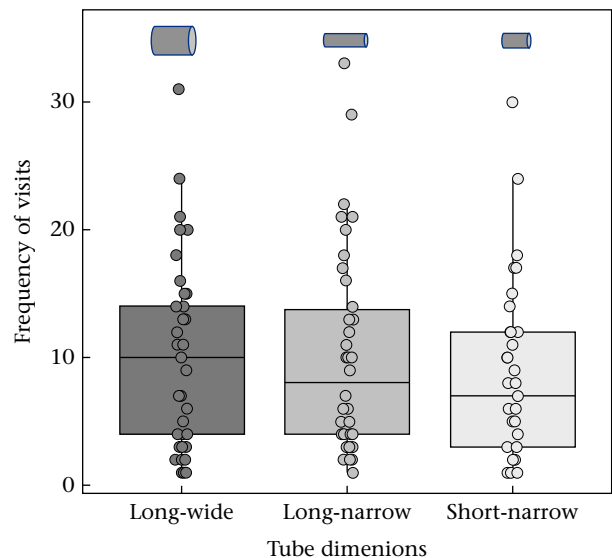


Figure 3. Number of nonsheltering visits (where fish swam within one body length of a PVC tube) made by fish across shelter types. Points show the number of occasions where fish visited a shelter per trial. Box plots show the median, 25th and 75th percentiles; the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2). $N = 40$ fish tested once and a subset of 25 tested three more times each.

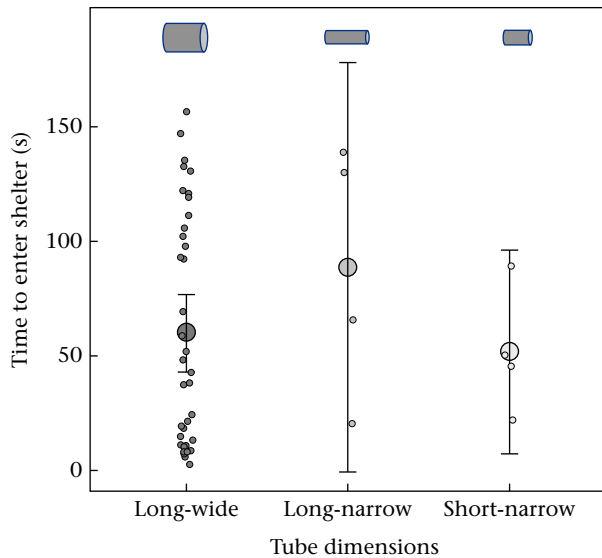


Figure 4. Time to enter a shelter across shelter types. The large points show the mean latency to enter a shelter with 95% confidence intervals for each tube type, the small (jittered) points show the latency for each individual shelter occasion. $N = 40$ fish tested once and a subset of 25 tested three more times each.

to seek shelter than others across trials. Repeatability ‘ R ’ of shelter duration across trials was moderate ($R \pm SE = 0.272 \pm 0.166$, 95% confidence interval = $0-0.624$, $P < 0.029$) and some fish spent little or no time in shelter in any trials (Fig. A2).

DISCUSSION

When sticklebacks in this study used shelters, they used larger diameter PVC tubes far more often than narrower ones. This supports the hypothesis that the dimensions of objects influence animal shelter decisions, in this case for temporary, often time-critical, shelters. These results highlight the importance of taking

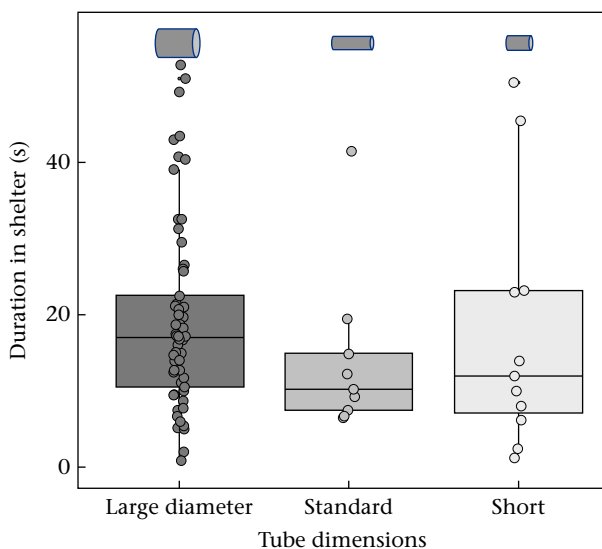


Figure 5. Shelter use and duration of time spent in shelter. Points show instances when fish entered a shelter. Box plots show the median time spent within a shelter, 25th and 75th percentiles; the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2). $N = 40$ fish tested once and a subset of 25 tested three more times each.

dimensions of shelters into account for this species, and probably fish in general. We found no statistically significant difference in duration of time spent in a shelter across shelter types: fish did not spend more time within the larger shelter than in the other two tubes. This suggests that any benefit derived by being inside a shelter, such as recovery from stress, in this situation, may be decoupled from or less influenced by the dimensions of the shelter or by preferences for the structure. However, the sample size for comparing durations across tube dimensions was limited by the number of times fish entered the less preferred shelters; few fish sheltered within the two narrower tubes. Establishing any differential benefits across shelter types will require longer term testing. Small but continual effects of sheltering in preferred shelters over other forms of shelter may only become apparent over longer observation periods. Our results also reinforce the expectation that shelter and enrichment requirements will depend on the individual, as some fish used a shelter over multiple trials and others did not. This is consistent with previous predictions (Huntingford et al., 2006; Maia & Volpato, 2018) that shelter use will vary with behavioural type of the individual (Laskowski et al., 2022) and ability to recover from stress (coping style; Koolhaas et al., 1999). Together our results show that fine-scale preferences for shelter driven by differences in dimensions provide a platform from which further advanced questions can be developed and addressed.

Our results are consistent with the fish making an active choice, that is, having a preference for the larger diameter shelter rather than a bias, as fish did not visit the larger shelter more frequently than the others. Additionally, when fish did use a shelter there were no differences in time taken to enter it as we would expect if there was a bias for the larger diameter tube, due, for example, to the larger tube simply being more obvious. However, the P value for the shelter visits results was marginal (see Fig. 3); hence, a larger sample size may detect such a bias as well as other more subtle ones. Also note that we did not address the functional reason for the preference for using larger tubes as shelter in this study. There are both ecological drivers for this preference, discussed below, and aspects that may influence the design of shelters in further studies. When choosing which shelter to use, the fish may be avoiding the smaller tubes, for example due to reduced visibility within the tube, or reduced ability to manoeuvre within the more confined space relative to the tube with the larger internal volume. The preference for a larger diameter shelter is likely to be some combination of these and other factors and would make interesting follow-up research questions. For instance, it may be worthwhile to compare differences in shelter preferences across species with different modes of swimming such as those that employ labriform and carangiform swimming.

The question of what drives the preference for larger tubes remains to be addressed. In another study, other small, temperate, freshwater species, notably bullheads, also preferred overturned terracotta pots over other shelter options, including plastic plants (Kessel et al., 2011). However, the strong preference for the larger shelters in our study was slightly surprising. Our initial, and naïve, prediction, based on observations of fish using the narrower tube as shelters and our expectation that shelters with narrower openings might provide a more protective refuge from predators, was that fish would prefer the narrower but longer tubes. Croak et al. (2008) found that geckos and snakes preferred narrow crevices that provided a tight fit as shelters and suggested this may reduce the threat from larger predators. Certainly, predation is an important driver of shelter selection. For example, preferences in fishes in general for number, type and size of shelter are influenced by levels of predation threat from other larger piscivorous fish (Freudiger et al., 2021; Groenewoud et al., 2016; Josi et al., 2018). In freshwater streams, such as those from where our study animals came,

predators, including kingfishers and herons, are more likely to attack from above. This may explain the sticklebacks' preference for a refuge with larger overhead cover, which was also found in a previous study where sticklebacks favoured shaded areas over both unshaded areas and areas with plastic plants (Jones et al., 2019). Certainly shaded areas are important for fishes in general (Kerry & Bellwood, 2012; McCartt et al., 1997; Ribeiro et al., 2022). It is possible that the larger tubes were more attractive to sticklebacks in our study, simply because they afforded a larger shaded area. This preference for shaded areas may also be linked to sensitivity to light which can be a stressor in captivity and may even drive shelter-seeking behaviour in both captive fish (Cerri, 1983; Rahman et al., 2020; Schulte, 2014) and wild fish; for example, large reef fishes use shelter as shade and protection from harmful UV-B irradiance (Kerry & Bellwood, 2015). Future work may compare shelter preferences and behaviour at different light levels, and with different colours and shading of the substrate, as sticklebacks also change colour to match their backgrounds to avoid the risk of predation (Tibblin et al., 2020), as do many other fish (Sumner, 1935). This work could also be extended to compare sheltering in contexts with different types of predators, for example populations from areas with predominantly avian predators versus areas with suction-feeding predatory fishes. A final consideration is whether fish will select shelter nonrandomly when there is an immediate threat, and they are not given time to observe their options (as with our study).

Our finding has practical implications, for behavioural and cognitive assays and for husbandry and welfare. Our results suggest that designing assays with sticklebacks should take the dimensions of shelters provided into account. This builds on work showing that the physical design of arenas used for behavioural assays can matter for behavioural expression (Näslund, Lindstrom et al., 2015). It is also important to consider dimensions of objects used as shelter in experimental set-ups where physical enrichment is provided to encourage engagement in tests, for example where presence of plant shelter was provided to manipulate risk in behavioural assays of foraging minnows (Webster & Laland, 2008). With regard to welfare and enrichment, our results provide empirical evidence to suggest that the provision of larger diameter PVC tubes, or alternative shelters such as commonly used clay pots (Frommen & Bakker, 2004), with a greater area of overhead shelter, may afford a simple to implement and low-cost method to improve enrichment. This is a small but potentially valuable contribution to the understanding of enrichment requirements of an important and commonly used model species of fish. Sticklebacks, and fish generally other than zebrafish, *Danio rerio*, and salmonids, have received relatively little empirical research effort on understanding their physical enrichment needs (Näslund & Johnsson, 2016). Few studies have actively explored enrichment for sticklebacks (Brydges & Braithwaite, 2009; Toli et al., 2017), and, given their importance as a model species (Norton & Gutiérrez, 2019), this is an area that must be addressed for better research validity (Browman et al., 2018; Newberry, 1995). The essential points to address are whether access to shelters with preferred dimensions results in more beneficial welfare outcomes, and whether the preferences we observed hold for other populations and ecotypes of sticklebacks which can live in dramatically different habitats (Smith, 2009; Spence et al., 2013). Another area of practical concern to address is whether in-tank shelters such as PVC tubes afford similar or other benefits to even simpler forms of external shelter such as partial tank covers which are increasingly suggested as convenient ways to improve welfare of captive fish (Saraiva et al., 2021; Arechavala-Lopez et al., 2022).

Our results also suggest an opportunity to develop alternative methodologies for studies of cognition and resource selection in this easily studied species. Compared with more traditional food-

rewarded choice tasks in fishes, shelter preferences can be manipulated to explore cost–benefit differences in decision making in tests without food, akin to the work done with colonies of ants where experimenters manipulate cost–benefit trade-offs over shelter and collective decision making (Franks et al., 2003; Sasaki et al., 2015; Stroeymeyt et al., 2011). For example, varying the distance of the shelters from the starting point or extending this study to explore preferences at a more nuanced level, such as having more gradual differences in size between shelters, may help researchers explore visual and search capabilities in sticklebacks.

In conclusion, this study suggests three-spined sticklebacks show short-term preferences for shelters based on their dimensions. This opens avenues for further work on decision making, cognition more generally and welfare of a common model species which researchers can take advantage of to develop further studies.

Author Contributions

N.A.R.J. conceived of the study, received funding, conducted the statistical analyses and drafted the manuscript; N.A.R.J., G.G. and M.M.W. planned the experiment; N.A.R.J. and G.G. cared for the animals, established the set-up, ran the experiment and analysed the videos; N.A.R.J., G.G. and M.M.W. worked on the drafts.

Data Availability

Data are available via an OSF link: https://osf.io/gqke3/?view_only=5b1c739258e641cf9ffee13d930ae2ce.

Declaration of Interest

The authors declare no conflicts of interest.

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Appendix

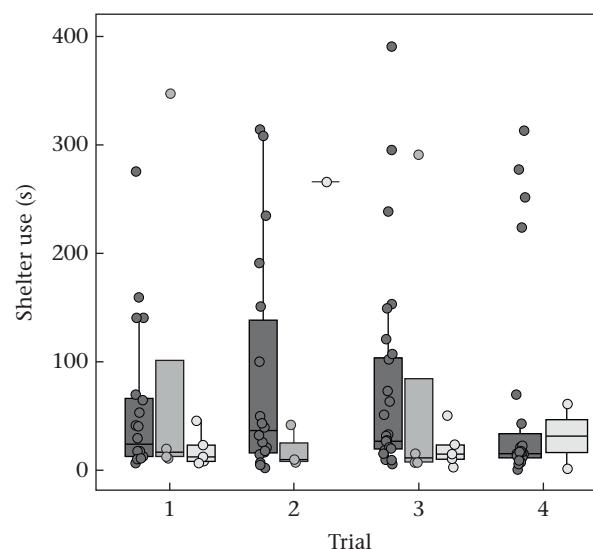


Figure A1. Shelter use and time spent in each shelter across trials. Points show instances when fish entered a shelter, and box plots show duration of time spent within shelter, the median time spent in a shelter, 25th and 75th percentiles; the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2). $N = 25$.

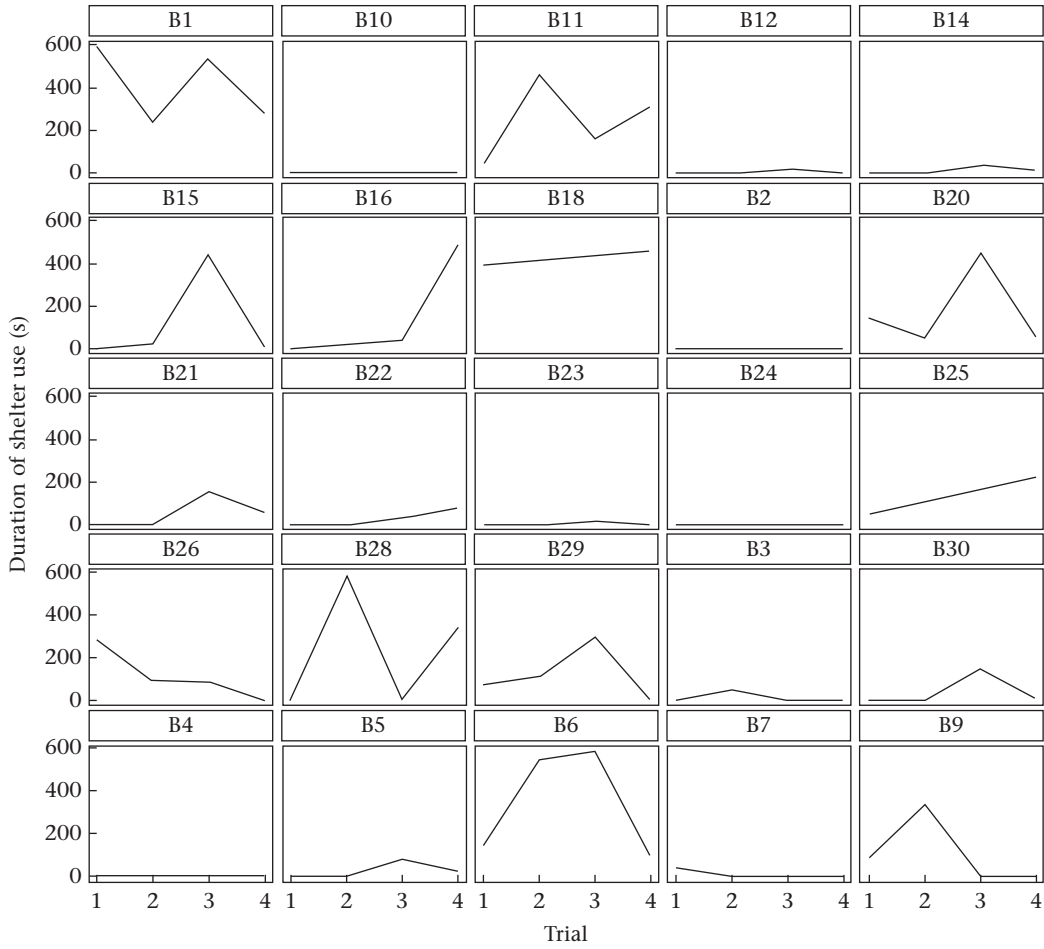


Figure A2. Total time spent in any shelter across all 25 fish tested in all four trials. Lines represent the total shelter use across the four trials.