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Passive traps and sampling bias: Social effects and personality affect trap entry by sticklebacks

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Abstract

Researchers routinely quantify the behaviour of subsets of animals, using their findings to make inferences about wider populations. Broader conclusions, however, may be inaccurate if the subjects that are tested are not representative of these populations. One way that this can arise is through sampling bias, which can occur if the method of collecting the test subjects disproportionately selects those with particular attributes, such that they end up being over- or under represented within the sample. Passive traps are associated with such sampling biases and have been shown to target certain behavioural phenotypes in a range of species. Here we asked whether funnel-type fish traps were more likely to target more active and more social sticklebacks (*Gasterosteus aculeatus*). We found that more subjects entered the traps when they already contained conspecifics and that individual measures of activity predicted trap entry, with more active fish being captured sooner both when the traps already contained conspecifics and when they were empty. Unexpectedly, less-social fish were captured sooner when the traps contained conspecifics. Sampling biases have the potential to skew the data collected by researchers and we therefore highlight the need to acknowledge and discuss potential for sampling biases and any consequences that may arise from this in published work. In the longer term, research that estimates the potential for sampling biases for various collection methods and species would be a valuable resource for helping to devise more representative sampling designs.

KEYWORDS

behavioural syndrome, boldness, methods, personality, reproducibility, STRANGE

1 | INTRODUCTION

Researchers perform experimental investigations into animal behaviour in order to learn about its functions and origins and to draw inferences about its ecological and evolutionary significance. By necessity, only a small subset of animals representing a given population or species can usually be tested, but with rigorous analyses and grounded, realistic extrapolation, findings can be extended to the wider population or even to other species. While this is standard practice, problems may arise if the pool of test subjects are not representative of the population being studied, and if the researchers are unaware of this (Webster & Rutz, 2020).

One way in which this can occur is through sampling biases. Some sampling methods have been shown to be biased towards capturing individuals of a particular size, life stage, sex, body condition or with particular behavioural tendencies (Biro & Dingemanse, 2009). Such effects have been demonstrated in a variety of species. For example, trappability of badgers (*Meles meles*) differs between cubs and adults

and between populations, and also with season and sampling year (Tuyttens et al., 1999). In sea lampreys (*Petromyzon marinus*), sampling bias effects varied with trap type: one type of trap captured more females, smaller males, and females with a lower gonadosomatic index compared to an alternative design. The same trap types were also more likely to recapture individuals that had already been captured once (Reinhardt & Hrodey, 2019).

Personality has been linked to likelihood of capture in a variety of species. Personality refers to the parts of an individual's behaviour that are repeatable (Dingemanse & Wright, 2020). In a classic study, Wilson et al. (1993) showed that pumpkinseed sunfish (*Lepomis gibbosus*) that were captured using funnel-traps behaved differently in the laboratory, being more likely to accept food in feeding trials, compared to those collected using the presumably more indiscriminate methods of seine netting. Among male collared flycatchers (*Ficedula albicollis*) more exploratory individuals, and those with a shorter flight initiation distance measure, were more likely to enter nest box traps than those that were less exploratory and more sensitive to predation threat (Garamszegi et al., 2009). Carter et al. (2012) found that male Namibian rock agamas (*Agama planiceps*) with lower flight initiation distances entered baited traps sooner and were more likely to be successfully captured than those with greater flight initiation distances. In a laboratory study of the freshwater crayfish *Cherax destructor*, bolder individuals that spent more time in open areas away from their burrow were more likely to be captured in a trapping trial than shyer ones that didn't stray far from cover (Biro & Sampson, 2015). It is worth noting that not all studies of trapping methods have found associations with personality biases, however. Michelangeli et al. (2016) found no relationship between any of five behavioural traits and susceptibility to being captured using three trapping methods in delicate skinks (*Lampropholis delicata*). In a rodent, the grassland melomys (*Melomys burtoni*), neither emergence latency nor neophobia measures were related to likelihood of capture in a study using passive rodent traps (Jolly et al., 2019).

All sampling approaches, no matter how carefully designed, are likely to be associated with some degree of bias. A challenge for researchers is to minimise this, through sampling design coupled with knowledge of the target species' behaviour and biology. Research into the susceptibility of different collection methods to these kinds of sampling bias is therefore valuable, both because it has the potential to enable investigators to better interpret the findings of existing work and because, moving forward, it will inform the design of less discriminatory sampling methods. In this study, we investigated whether commonly used (Budria et al., 2015) passive funnel-type minnow trap, widely used by researchers to capture small fishes, were biased towards capturing individuals with particular behavioural characteristics. These traps consist of a wire mesh cylinder with an inwards pointing funnel at either end (Figure S1). Fish swim through the funnel opening and become contained within the trap. Traps do not need to be baited with food for fish to enter, and they may function by exploiting thigomotaxic (wall-following) behaviour by the fish, which leads them towards the trap entrance as they move along the concave outer surface of the trap. They may be susceptible to sampling biases if more active individuals are more likely to encounter them, or less neophobic ones are more likely to approach them (Wilson et al., 1993). Moreover, because they can hold multiple fish, a confined aggregation may act as a social stimulus, drawing in further individuals. Using threespined sticklebacks (*Gasterosteus aculeatus*) a widely employed model organism (Barber & Nettleship, 2010), we tested three predictions. First, we predicted that more active fish would be captured sooner than less active ones; second, that traps already containing fish would capture more subjects, and sooner, than those without; and third, more social subjects would be captured sooner when the traps contained fish.

2 | METHODS

Sticklebacks were collected using dipnets from the Kinnessburn stream in St Andrews, UK in October 2017 and again in October 2019. We collected approximately 30 fish in each year. They were initially housed in groups of 10–15 in 90 L aquaria for one month until testing. From amongst these, we used unsexed adults 35–40 mm long, displaying no signs of reproductive condition. Initially, we tested 16 fish from the 2017 subject pool and 20 from the 2019 subject pool, though some were subsequently excluded, as described below. Aquaria and all of the testing arenas described below were held at 10 ˚C on a 12:12 photoperiod. Each aquarium contained sand and artificial plants and was equipped with an external canister filter. Fish were fed daily with frozen bloodworm unless otherwise stated below. After the study period, they were released at the point of capture. Given the large local population and short (typically < 2 years) lifespan of these fish, we think it very unlikely that individual fish collected in 2017 were resampled in 2019, though this cannot be completely ruled out.

The experiments described in the manuscript were approved by the Animal Welfare and Ethics Committee of the University of St Andrews, and complied with the ARRIVE guidelines for using animals in research (Percie du Sert et al., 2020) and with the laws of the United Kingdom.

Tests took places between November 2017 and January 2018 and November 2019 and January 2020 (hereafter 2018 and 2020 sets). We tested 16 fish in the 2018 set and 20 fish in the 2020 set. Three fish were subsequently excluded (described below) giving a sample size of 33 subjects. Test subjects were divided into groups of four in 90 L aquaria that were separated into four equally sized compartments using perforated, colourless plastic tank dividers (Penn Plax brand), with each fish placed in its own compartment. This allowed us to recognise individual fish without the need for tagging. We provided sand substrate and an artificial plant in each compartment. No external filtration was used on these aquaria, but each compartment was aerated. Each fish was fed 5 bloodworms per day. Test subjects were added to their compartments seven days prior to the beginning of the experiments.

Each subject was tested twice for activity and shoaling behaviour and once in each of two trap tests, within a four-day testing period. Subjects received their first shoaling and activity test on day 1 and their second on day 4 in a randomised order, with the two trap tests occurring on the intervening days, with the order of these also randomised. Fish were fed at 1,700 GMT, after testing on each test day.

Activity assays were performed in an open arena (50 × 50 × 15 cm, 10 cm water depth, Figure S2) with a sand substrate. The testing arena was surrounded by white, opaque plastic screening to prevent the fish from being disturbed by external movement. The subject was introduced into the centre of the arena within a clear, perforated holding unit (10 cm in diameter and was 25 cm tall, Penn Plax brand) and allowed to settle for 15 min. The holding unit was then carefully removed, and the fish released and allowed to move freely for 30 further minutes, during which time it was filmed from above. Every 6 s we recorded whether the fish was stationary or actively swimming, and whether or not it was within 10 cm of the arena wall, producing 360 counts for each measure. These provided two continuous measures of activity, proportion of time spent swimming and proportion of time in the open (>10 cm from the walls).

Shoaling behaviour was measured using a binary choice assay, in which the subject was presented with two enclosures at either end of an aquarium (45 × 30 × 30 cm, 15 cm water depth, Figure S3). Each enclosure measured 10 cm in diameter and was 25 cm tall. They were constructed from perforated, colourless plastic (Penn Plax brand). One contained a group of four conspecifics, while the other was empty, with the shoal designated to an enclosure at random. The whole apparatus was surrounded by white, opaque plastic screening to minimise external disturbance. The subject was introduced to the centre of the tank in a holding unit identical to the enclosures and allowed to settle for 15 min. This was then raised and removed, releasing the subject and allowing it to move freely for 15 further minutes. During this period the apparatus was filmed from above and the amount of time (to the nearest second) that the subject spent within 5 cm of either enclosure was recorded. We used the proportion of time spent within 5 cm of the group of conspecifics as a continuous measure of shoaling for each subject.

Two traps tests were performed, one in which four conspecifics were present inside the trap and one in which the trap was empty. We used a funnel-trap measuring 40 cm long, 22 cm maximum diameter, with 25 mm entrance holes. We modified the trap to prevent the subject from mixing with the four conspecifics in the treatment where they were present. The modifications used in the 2018 and 2020 sets differed (Figure S1). In 2018 we used a cylinder of perforated, colourless plastic to connect the entrance holes of the trap, preventing the subject from entering its interior. In 2020 the conspecifics were housed within a colourless plastic box (15 × 7.5 × 6.5 cm, perforated with 48.8 mm diameter holes) placed within the trap. The cylinder and box were retained for the empty trap treatments too. Year was included as a factor in our analyses, reported below, allowing us to account for any differences between the two approaches (none was detected, see results).

The trap was placed in the centre of a round pool (1.6 m diameter, 30 cm water depth, Figure S4). The pool contained four white 15 cm ceramic tiles raised 4 cm above the floor of the pool were included as refuges. The whole apparatus was placed within a 180 cm cube-shaped white photography tent. A covered opening in one wall allowed us to introduce the test subject. An aperture in the roof allowed us to record the trap within the pool using a Logitech C900 webcam. Two banks of LED strip lights, one on the floor either side of the pool were pointed directly upwards. These were reflected by the photography tent walls back into the pool, creating even lighting within the arena. The test subject was introduced to the pool 10 cm from the edge and directly opposite the centre of the trap, within a 10 cm diameter, 30 cm tall perforated plastic holding unit and was allowed to settle for 30 min. After this period the holding unit was carefully removed and the subject was allowed to swim freely for 120 min. Using a video recording we noted whether, and how long, it took the subject to enter the trap.

2.1 | Statistical analysis

One fish was excluded from the 2018 set because of a corrupted video file for one of the activity measure trials and two were excluded from the 2020 set because they behaved abnormally (they failed to move) in the activity trials, leaving a sample size of 33. We used Pearson's product-moment correlations to gauge the repeatability of the three pairs of activity and shoaling measurements. These were then reduced into two dimensions, Movement (34.5% variance) and Sociability (27.0% variance) using a Principal Components Analysis with varimax rotation. We compared capture rates of the two trap treatments using a Cox regression, including the Movement and Sociability PCs as continuous covariates. Year of testing and trap condition testing order (empty or containing conspecifics) were included as fixed factors. Censoring was used to identify whether a fish did or did not enter the trap for each trial.

2.2 | STRANGE declaration

We do not anticipate that our sample is biased or limited with respect to social background, trappability and self-selection, rearing history, natural changes in responsiveness or experience (Rutz & Webster, 2021; Webster & Rutz, 2020). Test subjects were collected from the wild outside of the species breeding season. Fish were presumed to be 1-year old adults. None were in reproductive state and we made no attempts to sex them. We did not quantify body condition, but none of the individuals captured were externally parasitised or looked to be in poor condition (indicated by thinness or the presence of injuries or abrasions). Hand-held nets were used to collect the fish. It is unknown whether this capture method is biased towards gathering individuals with particular characteristics. This species does not have any dominance-based social structure that we know of. Personality type was unknown at the time of collection, but

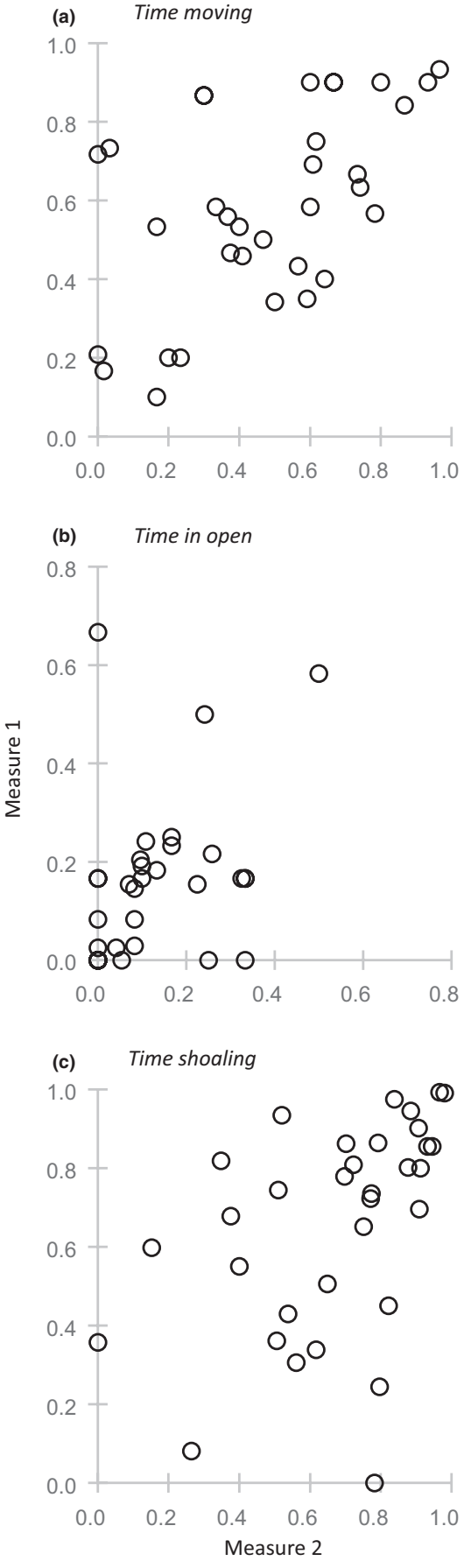

FIGURE 1 Scatter plots showing the proportion of trial time spent (a) moving, (b) in the open area of the arena and (c) shoaling for fish measured on two occasions. Measures were positively correlated in all cases (R^2 = .55, .39 and .46 respectively)

measures of personality were quantified as part of the experiment. Housing conditions in the laboratory provided social and physical enrichment. Individual behaviour may have been shaped by their experience in the wild, but no subjects had previous experience of the experimental approaches used in this study and none had previously taken part in any other experiment in our lab. (Fish from the 2018 set were released at the point of capture after testing, but given the large local population and short (typically < 2 years) lifespan of these fish, we think it unlikely that individual fish tested in 2018 were resampled in 2020.)

There was scope for individual differences in acclimation and habituation to the testing environment to affect test subject performance. The settling periods used in these experiments were long enough for most subjects to begin to move and explore, but two individuals were excluded because they were inactive in some of the trials (described above). Finally, we only tested subjects from one population, which should be considered when thinking about how our findings might apply more broadly.

Test subjects were tested individually, though other conspecifics were present to provide social stimuli in some treatments, as described above. All fish in the initial sample went through the full experimental schedule.

3 | RESULTS

We recorded two measures for each of three behaviours, time moving, time in open and time shoaling. The pairs of measures were positively correlated (Pearson's product-moment correlation: R^2 = .55, n = 33, p =.001; R^2 = .39, n = 33, p =.025; and R^2 = .46, n = 33, p =.007 respectively, Figure 1). A PCA (KMO 0.63, Bartlett's Test of Sphericity: X^2 = 33.0, df = 15, p =.005, see Table S1 for loadings) reduced these into two components, *Movement* (34.5% variance, consisting of both measures of movement and time in open) and *Sociability* (27.0%, containing the two shoaling measures).

Turning to trapping rates, as predicted we saw that subjects entered the traps sooner when these contained conspecifics than when they were empty (Cox regression: Wald X^2 = 28.22, df = 1, p <.001, Figure 2). There was no effect of year of testing (Wald X^2 = 0.12, df = 1, p =.79), nor any effect of testing order (Wald X^2 = 0.40, df = 1, p =.98). Also consistent with our predictions, we found that subjects' scores for *Movement* predicted trap entry in the treatment where the trap was empty, with less active individuals entering later, or not at all (Wald X^2 = 3.80, df = 1, p =.05). We saw no effect of *Sociability* upon trap entry times in this treatment (Wald X^2 = 0.10, df = 1, p =.75). *Movement* also predicted trap entry when the traps contained conspecifics, with more active individuals again being

captured sooner (Wald $X^2 = 15.04$, $df = 1$, $p < .001$). Here we also saw an effect of *Sociability* upon trap entry, but in contrast to our prediction we found that fish that spent more time shoaling actually took longer to enter the trap (Wald $X^2 = 10.28$, $df = 1$, $p = .001$). Hazard ratios are presented in Figure 3.

4 | DISCUSSION

The key findings from our experiment were first, that traps were more effective when they already contained trapped individuals, and second, that they were biased towards capturing individuals with particular behavioural or personality types. Subjects entered the traps sooner, and more were captured overall, when the traps already contained conspecifics. This is likely accounted for by social attraction – sticklebacks are facultatively group-living, and readily approach conspecifics (e.g., Ward et al., 2017). Traps seeded with conspecifics may exploit the tendency of fish to approach shoals, drawing them towards the trap and increasing their likelihood of entering it. While we saw this strong social effect, perhaps surprisingly we did not see that the more social individuals, (i.e. those that spent the greatest proportion of time close to the stimulus group on conspecifics in the shoaling assay) were more likely to enter the trap when it already contained fish. In fact, we saw the opposite pattern: less-social test subjects entered the trap sooner than the more social ones. This was unexpected. One possibility is that a tendency to spend more time shoaling with others actually better reflects neophobia or sensitivity to predation threat, with fish spending more time shoaling not due to greater social attraction to others but because they are less inclined to move away into open areas. We cannot confirm this with the data we collected as part of this study, but in principle this could be tested. Finally, and as predicted, we saw subjects that scored higher for *Movement* were captured sooner in both trap conditions in our experiment. These findings are consistent with those of other studies, that certain sampling methods can be biased towards the capture of individuals with particular behavioural types (Biro & Dingemanse, 2009). Our principal component metric of *Movement* encompassed activity levels and time spent in open, and both of these measures may have contributed to trapping likelihood in our experiment. More active subjects may get trapped sooner because they simply have a higher probability of encountering the trap, while those that spent less time in the open may have been less likely to swim into the centre of the pool where the trap was located. This raises the possibility that trap location – whether close to or far from cover – may also influence trapping bias with respect to personality type, and is worthy of further investigation.

Finding that certain trapping methods are biased towards individuals with particular characteristics is problematic if those characteristics – or other traits that co-vary with them – are the response variables measured in experimental studies. For example, pumpkinseed sunfish that were captured using traps similar to the ones used in our experiment

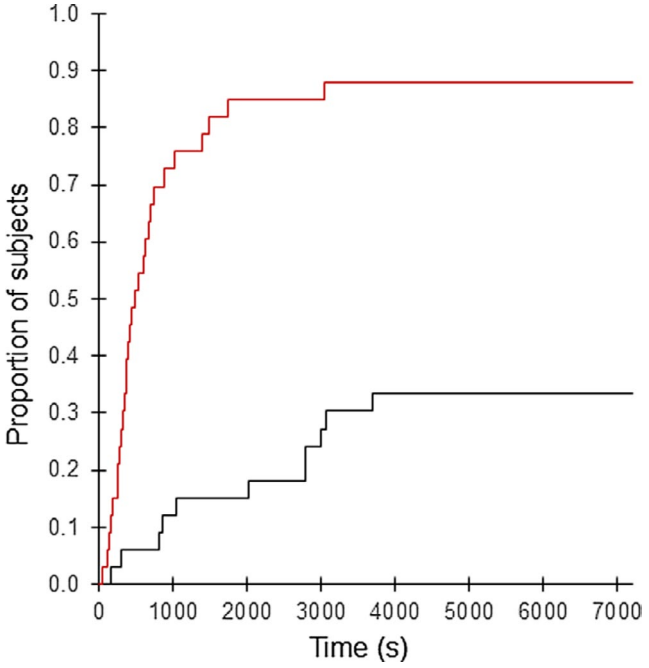

FIGURE 2 Survival plot (raw data) showing the rate and proportion of trapping events of subjects in trials where the trap contained four conspecifics (red line) and where the trap was empty (black line). Trapping rate differed significantly between the two treatments

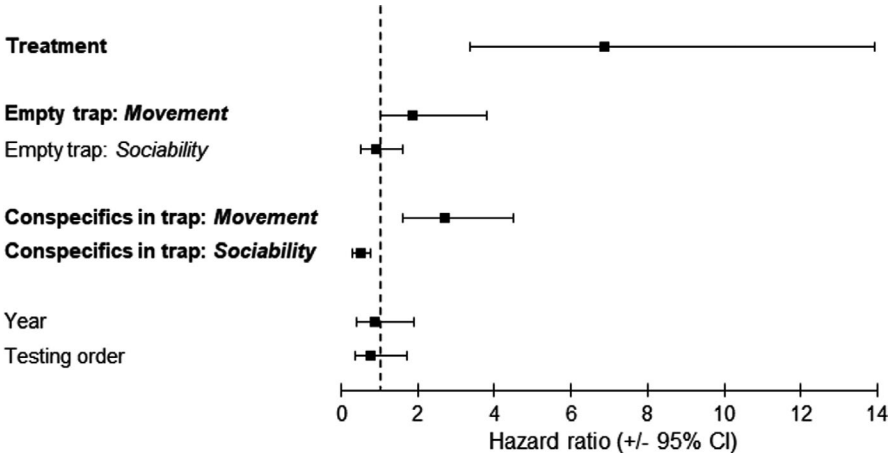

FIGURE 3 Hazard ratios for variables affecting trap entry times by test subjects. Hazard ratios > 1 (dashed line) indicate that a covariate is positively associated with time to enter the trap, while those < 1 indicate a negative relationship. Variables in bold had a significant effect. Treatment refers to conditions where the traps were either empty or contained conspecifics, with fish entering the trap sooner in the latter condition

started feeding sooner in captivity than did those that were captured in nets (Wilson et al., 1993). Time taken to begin feeding is not functionally related to tendency to enter traps. More likely, both behaviours reflect a more general response to risky, uncertain or novel stimuli or situations. Many seemingly different behaviours co-vary, perhaps because they are affected by common underlying physiological, perceptive or other processes (Biro & Stamps, 2008, 2010; Sih et al., 2004).

Sampling biases then have the potential to skew experimental findings even where the behaviours being quantified are not those we might immediately associate with likelihood of being trapped. Ultimately this can mean that the animals that we test, and the measures that we obtain from them, may not reflect the greater populations from which they are derived. This becomes a problem if it hinders our ability to use experiments to make accurate predictions about the behaviour of animals in the wild or to draw inferences about the ecological or evolutionary implications of the behaviours we measure. Similarly, such biases limit the extent to which we can make meaningful comparisons between populations or species, or even between different studies that use the same population – how much variation is explained by the sampling methods used to obtain the pools of subjects and how much by 'true' behavioural differences between the two wider populations?

In interpreting the findings of our experiment, we must be mindful of certain caveats (Webster & Rutz, 2020). First, we only tested one population of sticklebacks; if mean population measures for behavioural traits (Wright el al. 2003; Magnhagen et al., 2012) or the correlations between them vary substantially within species (Dingemanse et al., 2007; Evans et al., 2010) then some populations may be more susceptible to the kind of sampling bias inferred here than others. Second, our experiment was performed in the laboratory, not in the wild where sampling usually occurs. Other studies have found such effects in the field, however (Wilson et al., 1993), and we consider it realistic that our findings should apply under natural conditions too. Third, we measured behavioural consistency over a period of several days. If individual behaviour is more variable over longer periods this will have implications for the strength of the relationship between behavioural measures and trappability. Fourth, we tested our subjects individually. Sticklebacks are facultatively group-living, and group behaviour is shaped by the interplay between individual personality traits and social influences (Harcourt et al., 2009; Jolles et al., 2017; Ward & Webster, 2016; Webster & Ward, 2011), which may have implications for collective movement and trappability. Finally, we used dipnets to collect our subjects from the wild. This means that in effect, we sampled the population twice, first when collecting our subjects, without estimating bias, and then again as part of the study, where estimating the effects of bias was the main objective of the study. We assumed that active sampling (dip-netting) was less selective in terms of the range of individuals with different behavioural types, compared to passive sampling (using traps), as was found for active sampling using seine netting (Wilson et al., 1993), but this has not been explicitly demonstrated here, and may not actually be the case.

As in other fields, more researchers working in ecology and evolution are beginning to recognise and think about the issues surrounding replication (Kelly, 2019). While a major concern is that formal replications are seldom practised at all (Kelly, 2006), more subtle effects may be widespread and underappreciated (Webster & Rutz, 2020). Such effects include the sampling biases discussed here – but these can be detected and mitigated against. A seemingly straightforward approach is to identify and use collection methods that are as indiscriminate as possible. While determining the most effective sampling methods will likely require further experimental investigation, the findings of such work could be illuminating and valuable if it enables us to develop less biased protocols. It may well turn out that for some species or locations, the least biased options are problematic in other ways – they may be too impractical, expensive or labour-intensive, for example. Here a more pragmatic approach is required: one that allows researchers to collect the subjects necessary for their research, but which makes explicit any scope for sampling bias. We suggest that when reporting their findings researchers should clearly state how their samples were collected and include concise but thorough appraisal of the potential for artefacts arising from sampling methods to impact upon their results and the generality of their key findings (Webster & Rutz, 2020).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data produced from this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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