Environ Biol Fish (2026) 109:24
https://doi.org/10.1007/s10641-025-01795-4

Movement propensity differs in two morphs of the plainfin midshipman, *Porichthys notatus*

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Received: 17 December 2024 / Accepted: 1 December 2025

Abstract Alternative reproductive tactics occur when there is within-sex variation in how individuals achieve reproduction. Although these discrete alternative tactics have been well studied in a reproductive context, little is known about non-reproductive behavioural and cognitive differences between reproductive types. Using the plainfin midshipman fish, *Porichthys notatus*, a species with two distinct male reproductive tactics, we investigated whether individuals employing different tactics vary in movement propensity and spatial navigation ability. In this toadfish species, guarders (Type I males) build nests, acoustically court females, and provide parental care, while sneakers (Type II males) use stealth to enter nests and steal fertilizations. We hypothesized that because sneakers are thought to find multiple nests over the reproductive season, they would be better navigators. We tested guarders and sneakers in a T-maze and found that although sneakers swam faster on average, guarders unexpectedly completed the maze more frequently and more directly, taking a shorter path to the end than sneakers. Guarders also made fewer mistakes over time, entering the incorrect arm of the maze less frequently across subsequent trials within a day, whereas sneakers entered the incorrect arm more frequently over subsequent trials. We discuss how differences in motivation and the saliency of sensory cues could explain these findings. Our results demonstrate that in the plainfin midshipman, the two male reproductive morphs differ in spatial task completion and movement propensity, extending our knowledge of behavioural differences in alternative reproductive tactics to a non-reproductive context.

Keywords Male morph · Maze behaviour · Movement difference · Swimming velocity · Toadfish

Introduction

In a wide variety of animal species, two or more competing male reproductive tactics co-exist, with each male type maximizing its reproduction using a different discrete tactic (Oliveira et al. 2008). Typically, these alternative tactics are associated with different behavioural, morphological, physiological,

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10641-025-01795-4.

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and neurobiological traits (Gross 1996). The coexistence of such alternative reproductive tactics has long puzzled evolutionary and ecological biologists who seek to understand why selection favours the evolution of these discontinuous traits and how such alternatives can be maintained (Charnov 1982; Gross 1996; Engqvist and Taborsky 2016; Kustra and Alonzo 2020). Although differences in courtship and mating behaviour between tactics are well documented, to date, little focus has been placed on variation in non-reproductive behaviours like locomotion or feeding (Brockmann 2001). However, certain behavioural traits such as the tendency to explore and move through complex environments may be more beneficial for one particular reproductive tactic over the other (Smith et al. 2015; Synyshyn et al. 2021). For example, navigation or maze learning ability is predicted to be more important for the reproductive success of fish acting in a sneaker role than for individuals acting in a guarder role, as seen in the rose bitterling fish, *Rhodeus ocellatus* (Kner, 1866) (Smith et al. 2015). Thus, spatial navigation ability may be an important trait that contributes to the relative fitness of particular reproductive tactics.

Here, we tested the hypothesis that navigation ability has been more strongly selected for in one tactic using the plainfin midshipman, *Porichthys notatus* Girard, 1854, a species with two male reproductive morphs (Bass 1992). Each year in late spring to early summer, reproductive adults of this species undergo a vertical migration from deep water to rocky intertidal beaches to breed (Arora 1948). The larger guarders (Type I males) physically compete for nest sites consisting of an excavated cavity under a rock, acoustically court females, and perform parental care for months in the intertidal zone (Bass and Marchaterre 1989; Brantley and Bass 1994; Cogliati et al. 2014; Bose et al. 2018). In contrast, the smaller sneakers (Type II males) use stealth to enter numerous nests and steal fertilization from guarders (Fitzpatrick et al. 2016; Miller et al. 2019). Sneakers compete for fertilization by having comparatively larger testes that are filled with dense, fast-moving sperm (Fitzpatrick et al. 2016; Miller et al. 2019). These two reproductive morphs are largely assumed to be fixed, with differentiation between guarders and sneakers occurring early in development (Bass et al. 1996), but this topic remains an active area of research. Given that guarders typically remain in one nest over the breeding season, while sneakers are thought to locate and move between as many active nests as possible (Cogliati et al. 2013; Bose et al. 2018), we predicted that sneakers (as in the rose bitterling; Smith et al. 2015) would have better spatial navigation abilities and be more likely to move and explore. Using a T-maze design, we compared the spatial navigation and swimming speeds between males of the two alternative reproductive tactics.

Methods

Collection and housing

Six guarder male and seven sneaker male plainfin midshipman fish were collected from the intertidal zone in Ladysmith, British Columbia, Canada (48°59′27.7″ N 123°48′27.3″ W) at low tide during May and June 2021. Fish collection was severely limited by a number of factors beyond our control: (1) COVID-19 restrictions on travel, (2) a heat dome event in 2021, and (3) a relatively short breeding period when fish are present in the intertidal. Fish were transported to the University of Victoria in opaque aerated bins and were housed in reproductive-tactic-specific 400 L outdoor holding tanks prior to experimentation. Guarders ranged from 18 to 24.5 cm standard length, and sneakers ranged from 10.5 to 16.3 cm standard length. Fish were visually monitored each day and were offered krill once per week. Fish showed little interest in food, consistent with previous observations that plainfin midshipman do not actively forage during the summer breeding season (Cogliati et al. 2015), and all uneaten food was subsequently removed from the tank.

Experimental design

Fish were tested in a T-maze (100 cm × 100 cm) over a 4-day period. The maze was T-shaped with a barrier inserted at the top middle of the T creating a separate right and left lane in the main part of the maze (Fig. 1). Each lane led to either the right or left arms of the maze (Fig. 1). Two distinct artificial aquarium plants were placed at the end of each lane to provide additional visual cues to distinguish the right and left maze arms. A start chamber (28 cm × 33 cm) was attached to the start of the maze,

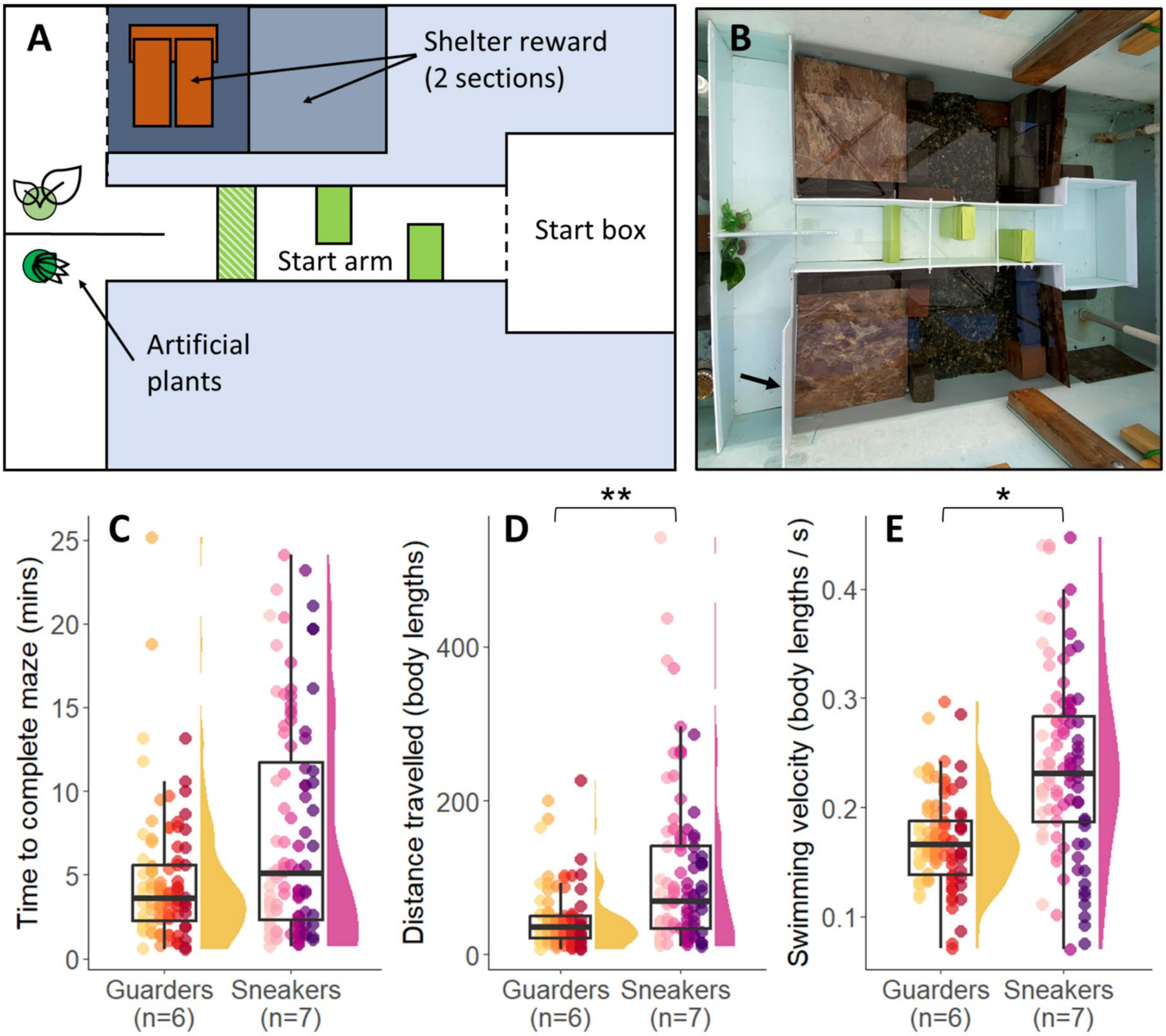

Fig. 1 **a**, **b** Maze design and experimental tank set-up with three green runway barriers (left, right, and bottom swim-over) in place. Left and right barriers are shown in solid green and the swim-over barrier in hatched green. The reward zone is separated into a covered section with sand substrate (dark blue in diagram) and uncovered section with pebble substrate (medium-dark blue in diagram). The barrier providing access to the reward zone is visible in the open position at bottom right of photo (denoted by a black arrow). During the 15-min acclimation period before each trial, the start box was separated from the rest of the maze by another removable barrier. **c**–**e** Differences in navigation between guarder male ($n = 6$, in shades of gold–red) and sneaker male ($n = 7$, in shades of pink–purple) plainfin midshipman, including maze completion time (minutes), distance travelled (m), and average fish velocity (cm/s) during each successfully completed trial of a 4-day trial sequence. Four trials were run each day for a total of 16 trials per individual. Points of the same colour indicate observations made on the same individual. Asterisk(s) represent statistically significant differences between male types (* $p<0.05$, ** $p<0.01$).

separated by a removable barrier (Fig. 1). The arm containing the reward for maze completion alternated between fish (Fig. 1a). A total of seven fish had the maze reward on the left-hand (L) side and six fish had the maze reward on the right-hand (R) side (sneakers: 4 L, 3 R; guarders: 3 L, 3 R). The reward was access to a compartment containing a dark shelter with sand substrate, as plainfin midshipman fish commonly bury themselves in substrate and prefer to be under a rock or shelter during the day (Cogliati et al. 2015; Bose et al. 2016). The reward box also included an uncovered area with pebble substrate, while the rest of the maze was devoid of substrate. To minimize external visual stimuli and direct sunlight during trials, the tanks were covered by a white tent and surrounded by white blinds. Tanks were continuously supplied with sea water (~ 12 °C), with inflow positioned near the start box and outflow near the top of the maze "T." However, the maze was placed inside the tank, so there was no direct connection to the inflow or outflow within the maze itself, and there was no apparent water flow within the maze. As mentioned above, trials were run in a 4-day sequence. On the first day, the maze did not contain any obstacles to encourage the fish to swim through the maze. Then, during the 2nd, 3rd, and 4th days, three green plastic barriers were added to the maze to explore how navigation metrics might differ in a higher complexity environment that is more ecologically relevant due to its similarity to the benthic rocky habitat of this species. The three barriers were a left-side barrier, a right-side barrier, and a bottom swim-over barrier (Fig. 1a).

We ran four trials per fish per day between 9:30 and 18:30. The day before experimentation began, we moved each fish into the maze and gave the fish an overnight acclimation period of at least 12 h in the reward section of the tank. During this acclimation period, the fish did not have access to the maze. Prior to the start of each trial, we moved each fish into the start chamber at the bottom of the T-maze and provided an additional 15-min acclimation period in this start chamber (Fig. 1a). A barrier separating the start chamber from the maze was then opened remotely, and the fish was given 30 min to enter and navigate through the maze. If the fish did not complete the maze after 30 min, it was removed from the maze. All fish were given 45 min to rest in the reward compartment before the next trial began. The fish were also left overnight in the reward chamber between trial days. Prior to beginning of each trial, we recorded whether the fish was positioned in the uncovered portion of the reward compartment or was fully under the shelter. The water inside the maze was thoroughly mixed between trials to prevent fish from being able to follow any scent trails. Trials were recorded using a video camera (Logitech Mevo Start) mounted above the maze.

Analysis

We used six metrics to assess tactic differences in spatial navigation abilities: (1) proportion of trials where fish successfully completed the maze, (2) time taken to complete the maze, (3) whether a fish entered the incorrect arm of the maze while completing the maze, (4) distance travelled in the maze, (5) average fish velocity, and (6) frequency of resting behaviour. The first three metrics were manually scored from video recordings using BORIS software (Friard and Gamba 2016). Supervised automatic tracking in TRex (Walter and Couzin 2021) was used to calculate the total distance each fish travelled. Average velocity was then calculated as the total distance travelled divided by the time to complete the maze, including time spent at rest. Average fish velocity and distance travelled were then scaled to individual body size (standard length). For a subset of trials (one randomly selected trial with successful maze completion per fish per day), we also manually recorded whether fish were actively swimming or at rest. Rest was defined as a motionless period of ≥ 5 s. The proportion of time fish spent at rest during each trial was calculated as the total resting duration divided by the maze completion time.

All statistical analyses were conducted in R (v.4.2.2; R Core Team 2024). Model diagnostic plots from the 'DHARMa' package were used to check model assumptions (Hartig 2022). Dependent variables were log-transformed when necessary to meet model assumptions. Unless otherwise specified, likelihood ratio tests were used to test for statistical significance of terms, and profile likelihood confidence intervals are reported. Plots containing model estimates and 95% confidence intervals were generated using the 'ggeffects' package (Fig. 2; Lüdecke 2018).

To analyze maze completion in each trial, we fit a bias-reduced binomial generalized linear model (GLMM; 'glmmTMB' package; Brooks et al. 2017). Bias adjustment was used to account for complete separation of the data (Clark et al. 2023), which occurred because guarders completed the maze during every trial. Linear mixed models were fit for maze completion time, distance covered in maze, and average fish velocity ('lme4' package; Bates et al. 2015). Binomial GLMMs were used to model the presence of an incorrect maze-arm entry and the presence of resting behaviour ('glmmTMB' package; Brooks

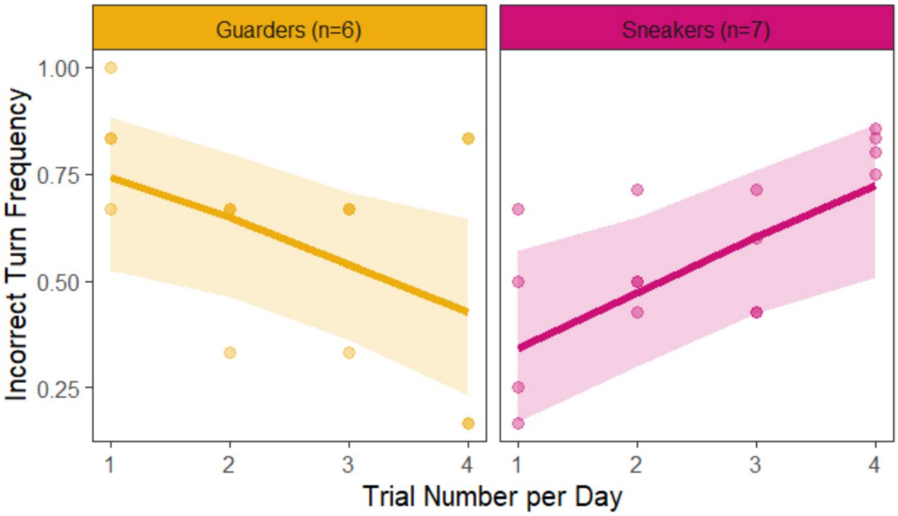

Fig. 2 Proportion of guarder ($n=6$) and sneaker ($n=7$) male plainfin midshipman that entered the incorrect arm of a T-maze during successful trials each day. Each fish completed four trials per day over 4 consecutive days (16 total trials). Points show the mean proportion of individuals making one or more incorrect turn across each trial number, male type, and trial day. Lines show model estimates with 95% Wald confidence intervals.

et al. 2017). A beta GLMM was used to model the proportion of time fish spent at rest during each trial (‘glmmTMB’ package; Brooks et al. 2017). Except for the maze completion model, all models above included data from successfully completed trials only (i.e., trials where the fish reached the shelter reward in less than 30 min).

All models above included male reproductive tactic, trial number within a day, and presence/absence of maze barriers as fixed effects, and subject identity as a random intercept. For the binomial model with incorrect maze-arm entry as a response variable, we also included an interaction effect between male type and trial number. We fit these models using trial number within each day rather than cumulative trial number across days to account for potential behavioural effects of the overnight gap between trials (see the supplementary materials for plots of maze completion metrics across trial days).

Maze completion time was further separated into time spent in the start box and time spent in the maze after exiting the start box. For these models, we took the median time per individual for each day, as the more complex models for each trial had poor fit even following log-transformation. We included male reproductive tactics and the presence or absence of maze barriers as fixed effects, and subject identity as a random intercept. We also fit a linear model to determine whether fish preferred the covered or uncovered area of the reward box, with male type and trial number within a day as fixed effects, and subject identity as a random effect.

To assess whether fish displayed any behavioural lateralization or a side bias, (i.e., a preference for one arm of the maze), we compared the frequency at which each fish first entered the left versus right arm of the maze for every trial. We analyzed the data with a binomial GLMM, where entering the right arm of the maze was considered a ‘success’, and the null hypothesis was that the proportion of successes is equal to 0.5 (no side bias). We included male type as a fixed effect, and subject identity as a random intercept. A Wald test was used to test statistical significance of terms.

To assess the potential relationship between body size and average fish velocity, we fit two separate linear mixed models for each reproductive tactic. Only successfully completed trials where fish reached the reward before the end of the trial were analyzed. We included fish standard length (cm) as a fixed effect, and subject identity as a random intercept.

Results

Guarders completed the maze more frequently than sneakers (likelihood ratio test [LRT]: $\chi_1^2=4.66$, $p=0.03$). All guarders successfully completed the maze in every trial, while sneakers only completed 86% of trials overall. Sneakers swam 2.0 times further (95% CI 1.3, 3.3; LRT: $\chi_1^2=7.33$, $p=0.007$; Fig. 1d) and had a 1.3 times faster average fish velocity (95% CI 1.1, 1.7; LRT: $\chi_1^2=5.41$, $p=0.02$; Fig. 1e) while navigating the maze when scaled for body size. We

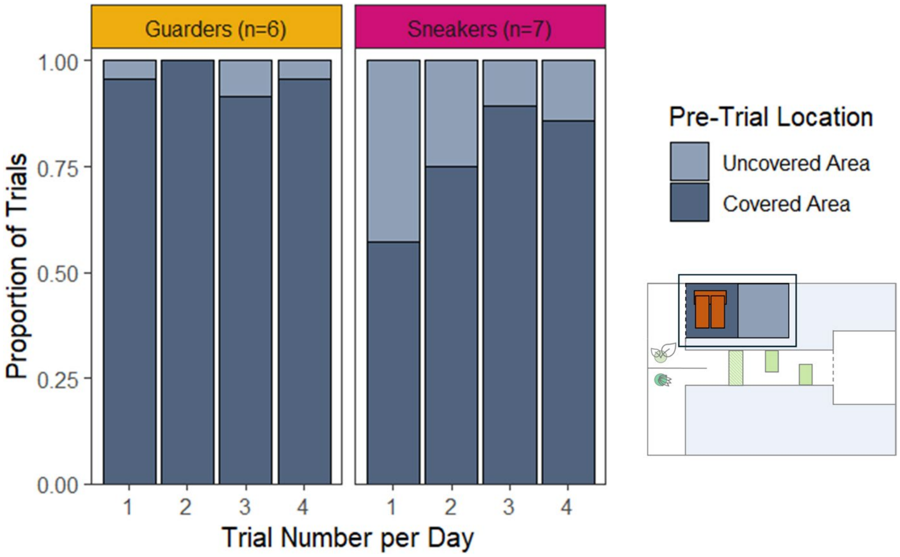

Fig. 3 Proportion of guarder ($n=6$) and sneaker ($n=7$) male plainfin midshipman fish selecting the uncovered and covered areas of a reward zone prior to a maze trial across all trial days. The covered area of the reward zone consisted of a dark shelter with sand substrate, whereas the uncovered area had pebble substrate and no shelter. Four maze trials were run each day for a total of 16 observations per individual.

did not find evidence for a relationship between body size and mean absolute velocity for guarders (Fig. S1; LRT: $\chi_1^2=0.32$, $p=0.57$) or for sneakers (Fig. S1; LRT: $\chi_1^2=0.22$, $p=0.64$). There was a significant interaction between male type and trial number on the likelihood of fish making an incorrect turn in the maze (LRT: $\chi_1^2=12.42$; $p<0.001$). During the first trial, sneakers were less likely to make an incorrect turn than guarders (log-odds −1.71; 95% CI −2.90, −0.63). However, while guarders made fewer incorrect turns over subsequent trials within a day (log-odds −0.45; 95% CI −0.86, −0.07), sneakers showed the opposite pattern, with their error rates increasing over time per day (interaction log-odds 0.99; 95% CI 0.43, 1.58; Fig. 2). We did not find any evidence that fish preferred the right or left arm of the maze (Fig. S2; Wald test: $z=-0.20$, $p=0.84$) or that guarder or sneaker males differed in this respect (Fig. S2; Wald test: $z=0.41$, $p=0.68$). Overall, the fish took a median time of 4.0 min to complete the maze (IQR [2.2, 7.9]), but sneakers took 1.5 times as long to complete compared to guarders (95% CI 0.9, 2.4; LRT: $\chi_1^2=3.05$, $p=0.08$; Fig. 1c). Sneakers spent longer in the start box (0.7 min; 95% CI 0.1, 1.3; LRT: $\chi_1^2=4.85$, $p=0.03$), but not in the maze after exiting the start box (1.5 times; 95% CI 0.9, 2.7; LRT: $\chi_1^2=2.15$, $p=0.14$).

Of the subset of trials scored for resting behaviour, fish were observed to be resting during 35% of trials, and rest periods had a median duration of 26 s. There was no difference in the occurrence of resting (LRT: $\chi_1^2=0.20$, $p=0.66$) or duration of resting (LRT: $\chi_1^2=1.09$, $p=0.30$) between male types. Both male types preferred the covered area of the reward compartment, but sneakers were more frequently found in the uncovered portion (LRT: $\chi_1^2=10.6$, $p=0.001$; Fig. 3).

The addition of maze barriers increased the time taken by fish to complete the maze by 1.7 times (95% CI 1.3, 2.2; LRT: $\chi_1^2=18.0$, $p<0.001$) and decreased average fish velocity by 28% (95% CI 23, 33; LRT: $\chi_1^2=71.4$, $p<0.001$). Average fish velocity also decreased across trials within each day by 7% per trial (95% CI 4.2, 9.4; LRT: $\chi_1^2=23.8$, $p<0.001$), suggesting that the fish may have become less motivated to reach the reward and/or explore the maze with each subsequent trial within a day. Fish were more likely to exhibit resting behaviour when barriers were in place (LRT: $\chi_1^2=8.59$, $p=0.003$), but barriers had no significant effect on rest duration (LRT: $\chi_1^2=1.47$, $p=0.23$). Resting behaviour occurred at similar frequencies (LRT: $\chi_1^2=0.45$, $p=0.50$) and durations (LRT: $\chi_1^2=1.75$, $p=0.19$) across subsequent trials on the same day. Fish were more frequently found in the covered area of the reward zone later in the day (LRT: $\chi_1^2=5.88$, $p=0.02$; Fig. 3). Fish did not complete the maze more frequently (LRT: $\chi_1^2=0$, $p=1$), or quickly (LRT: $\chi_1^2=0.13$, $p=0.72$), or directly (LRT: $\chi_1^2=1.11$, $p=0.29$) over sequential trials within a day.

Discussion

Navigation ability and propensity to move are important factors that can influence survival and reproductive success (Morand-Ferron and Quinn 2015; Blake et al. 2018). In some species, individuals of the same sex that adopt alternative reproductive tactics also differ in these activity traits (Corlatti et al. 2013; Rochais et al. 2021). These differences provide an opportunity to examine how movement ecology and navigation ability vary with life history and reproductive tactic (Morand-Ferron and Quinn 2015; Smith et al. 2015).

To our knowledge, this study is the first to examine spatial ability in the plainfin midshipman, a deep-water toadfish that migrates each year to the shallow intertidal zone. Our study therefore contributes to the limited body of research on spatial navigation in the context of alternative reproductive tactics (Smith et al. 2015; Griebling et al. 2020; Rochais et al. 2021). Despite our study's small sample sizes, we found that navigation strategy varied between male tactics. Guarders completed the T-maze more frequently and more directly, covering less distance than sneakers when controlling for body size differences. Guarders also made fewer errors across trials within a day, decreasing their frequency of entering the incorrect arm of the maze over time. In contrast, sneakers entered the incorrect arm more frequently as trials progressed each day and had higher average velocity relative to body size. These results support our initial hypothesis that sneakers would have higher motivation to move, as this tactic attempts to visit as many active nests as possible over the breeding season (Smith et al. 2015; Bose et al. 2018), but contradict the hypothesis that sneakers would have better spatial task completion. Several factors may help explain the differences in navigation observed, including variation in exploratory tendencies, sensory capabilities, and motivation (Nathan et al. 2008; Fagan et al. 2013).

Male alternative reproductive tactics are associated with a variety of morphological and neurobiological traits in plainfin midshipman, including variation in body size (Brantley and Bass 1994). Guarder males are the larger of the two reproductive tactics, potentially providing an advantage in aggressive competitions for nest sites (Bose et al. 2018). Across fishes, larger body size tends to be associated with faster swimming speed, with critical swimming speed serving as a common swim metric (Plaut 2001; Cano-Barbacil et al. 2020).

We accounted for the body size difference between guarder and sneaker males by scaling fish velocity and distance covered to individual body length. After this correction, we found that sneakers in fact exhibited a higher mean fish swimming velocity and covered more distance while navigating the maze. This difference did not appear to be driven by periods of rest. In the subset of trials scored for resting behaviour (one trial per fish per day), there were no significant differences in either the frequency or duration of resting between male types. The elevated activity of sneakers may allow individuals of that morph to locate more nests with actively spawning females over the breeding season, potentially increasing their reproductive success. However, such a strategy is likely to have an energetic cost (Metcalfe et al. 2016; Rimbach et al. 2019). This trade-off may be less advantageous for guarders, who remain at a single nest and already have substantial energetic demands associated with parental care (Cogliati et al. 2013; Bose et al. 2016). Our findings align with previous research on the round goby, *Neogobius melanostomus* (Pallas, 1814), that found sneaker males were more active and exploratory than guarder males (Synyshyn et al. 2021). However, despite demonstrating higher activity levels, we found that sneakers still completed the maze less frequently than guarders. This unexpected result suggests that increased activity does not necessarily translate to enhanced spatial task completion. We discuss possible explanations for this pattern below, but future studies should examine whether higher activity levels are indeed linked with greater reproductive success in sneaker male plainfin midshipman.

In terms of sensory capabilities, sneaker males are highly sensitive to the courtship hum of guarders during the breeding season and possess tactic-specific swim bladder morphology, which is predicted to allow greater overall sound pressure sensitivity compared to guarders (Mohr et al. 2017; Bhandiwad et al. 2017). It is possible that sneakers preferentially use sound to localize active nests to spawn in, while guarders might use self-centered (egocentric) references to create a map of their environment and likely use physical information to select a high-quality nest site. If this is the case, the higher spatial task completion rate observed for guarders, when placed in an environment without social cues, could potentially be attributed to their familiarity with using these environmental factors to navigate.

Guarders and sneakers may also have had differing levels of motivation to reach a shelter reward. As sneakers are reliant on stealing fertilizations from active nest sites (Brantley and Bass 1994), an empty shelter would have reduced reproductive value for this male type compared to guarders, who must take primary ownership of a nest site (DeMartini 1988; Brown et al. 2021). Guarders may also be more motivated to return to an existing nest site, as they provide continual parental care to their young and defend their territory, whereas sneakers can continue spawning in new nests (Brantley and Bass 1994; Brown et al. 2021). If guarders fail to relocate their nest, they are likely to suffer reduced fitness resulting from increased egg mortality (Bose et al. 2016; Pepler et al. 2021). Additionally, as there are a limited number of high quality nest sites available in the intertidal (Bose et al. 2018; Brown et al. 2021), guarders who navigate quickly to the breeding grounds will have the first selection of these nesting sites. This motivation would be relevant for the reproductive individuals in our study, as migration and initial nest establishment typically occurs in late spring (Arora 1948), a few weeks prior to our maze testing period.

Supporting the hypothesis that guarders had a higher motivation to reach the shelter reward, we found that guarders completed the maze more frequently and spent less time in the start box than sneakers on average. Both male types preferred the covered area of the reward zone, but sneakers were more often found outside of the shelter in the uncovered area, suggesting a lower motivation to occupy the shelter in the absence of social cues. Guarders also entered the non-rewarded arm less frequently over successive trials within a day, whereas sneakers entered the non-rewarded arm more often with each subsequent trial. This demonstrates that, while both male types adjusted their exploration patterns with experience, guarders prioritized direct movement towards the shelter, whereas sneakers engaged in a strategy of consistent broad exploration.

Our results emphasize the importance of considering non-reproductive behavioural differences when assessing the viability and fitness of alternative reproductive tactics. Despite our study's small sample sizes, we observed that sneaker and guarder male plainfin midshipman exhibited distinct navigation strategies. Guarder males completed the T-maze more frequently and directly, whereas sneaker males swam faster, covered greater distances, and explored the non-rewarded arm of the maze more consistently over time. These findings suggest that navigation traits could play a role in shaping the mating system of this fish. An important next step in understanding this system would be to examine whether navigation ability predicts reproductive success or shows heritable variance.

While our results may or may not be broadly generalizable to other species, they do provide important insight into the rarely studied non-reproductive behavioural differences between alternative reproductive tactics (Brockmann 2001). Future work should focus on exploring how the two male morphs make use of sound versus landmarks to navigate when moving through space (Mohr et al. 2017; Bhandiwad et al. 2017) and on examining alternative paradigms, such as open field tests, novel object interactions, or scototaxis assays with larger sample sizes to explore which behavioural traits might explain the differences in navigation observed in this study. Field-based movement studies with marked fish would also help determine the applicability of our findings to real-world navigation patterns and assess potential fitness consequences.

Acknowledgements Collection, animal housing, and experimental procedures were approved by the University of Victoria Animal Care Committee (Animal Use Protocol: Juanes 2021-012). We would like to thank Bridget Maher and the University of Victoria Aquatics staff for their assistance with lab work and equipment set-up. We also thank Ben Bolker and Ian Dworkin for their invaluable statistical support and guidance. We are grateful to the editor and the anonymous reviewers for their constructive feedback that significantly strengthened this manuscript.

Author contribution Madeleine G. Thomson: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, and writing—original draft. Mackenzie B. Woods: conceptualization, funding acquisition, investigation, methodology, supervision, and writing—review and editing. Sigal Balshine: conceptualization, supervision, funding acquisition, and writing—review and editing. Francis Juanes: conceptualization, supervision, funding acquisition, and writing—review and editing.

Funding This research was funded by Natural Sciences and Engineering Research Council of Canada (NSERC) Undergraduate Student Research Award to MGT, Mitacs Accelerate fellowships to MBW, and NSERC Discovery grants to SB and FJ.

Declarations

Conflict of interest The authors declare no competing interests.

References

Arora HL (1948) Observations on the habits and early life history of the batrachoid fish, *Porichthys notatus* Girard. Copeia 1948:89–93. https://doi.org/10.2307/1438409

Bass A (1992) Dimorphic male brains and alternative reproductive tactics in a vocalizing fish. Trends Neurosci 15:139–145. https://doi.org/10.1016/0166-2236(92)90356-D

Bass AH, Marchaterre MA (1989) Sound-generating (sonic) motor system in a teleost fish (*Porichthys notatus*): sexual polymorphism in the ultrastructure of myofibrils. J Comp Neurol 286:141–153. https://doi.org/10.1002/cne.902860202

Bass AH, Horvath BJ, Brothers EB (1996) Nonsequential developmental trajectories lead to dimorphic vocal circuitry for males with alternative reproductive tactics. J Neurobiol 30:493–504. https://doi.org/10.1002/(SICI)1097-4695(199608)30:4<493::AID-NEU5>3.0.CO;2-Z

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Bhandiwad AA, Whitchurch EA, Colleye O et al (2017) Seasonal plasticity of auditory saccular sensitivity in "sneaker" type II male plainfin midshipman fish, *Porichthys notatus*. J Comp Physiol A 203:211–222. https://doi.org/10.1007/s00359-017-1157-9

Blake CA, Andersson ML, Hulthén K et al (2018) Conspecific boldness and predator species determine predation-risk consequences of prey personality. Behav Ecol Sociobiol 72:133. https://doi.org/10.1007/s00265-018-2544-0

Bose APH, McClelland GB, Balshine S (2016) Cannibalism, competition, and costly care in the plainfin midshipman fish, *Porichthys notatus*. Behav Ecol 27:628–636. https://doi.org/10.1093/beheco/arv203

Bose APH, Cogliati KM, Luymes N et al (2018) Phenotypic traits and resource quality as factors affecting male reproductive success in a toadfish. Behav Ecol 29:496–507. https://doi.org/10.1093/beheco/ary002

Brantley RK, Bass AH (1994) Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae). Ethology 96:213–232. https://doi.org/10.1111/j.1439-0310.1994.tb01011.x

Brockmann HJ (2001) The evolution of alternative strategies and tactics. Adv Study Behav 30:1–51. https://doi.org/10.1016/S0065-3454(01)80004-8

Brooks ME, Kristensen K, van Benthem KJ et al (2017) GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Brown NAW, Houpt NSB, Yee NL et al (2021) Consequences of nest site selection vary along a tidal gradient. J Anim Ecol 90:528–541. https://doi.org/10.1111/1365-2656.13385

Cano-Barbacil C, Radinger J, Argudo M et al (2020) Key factors explaining critical swimming speed in freshwater fish: a review and statistical analysis for Iberian species. Sci Rep 10:18947. https://doi.org/10.1038/s41598-020-75974-x

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton, NJ

Clark RG, Blanchard W, Hui FKC et al (2023) Dealing with complete separation and quasi-complete separation in logistic regression for linguistic data. Res Methods Appl Linguist 2:100044. https://doi.org/10.1016/j.rmal.2023.100044

Cogliati KM, Neff BD, Balshine S (2013) High degree of paternity loss in a species with alternative reproductive tactics. Behav Ecol Sociobiol 67:399–408. https://doi.org/10.1007/s00265-012-1460-y

Cogliati KM, Balshine S, Neff BD (2014) Competition and cuckoldry: estimating fitness of alternative reproductive tactics in plainfin midshipman. Behaviour 151:1209–1227

Cogliati KM, Danukarjanto C, Pereira AC et al (2015) Diet and cannibalism in plainfin midshipman *Porichthys notatus*. J Fish Biol 86:1396–1415. https://doi.org/10.1111/jfb.12649

Corlatti L, Bassano B, Valencak TG, Lovari S (2013) Foraging strategies associated with alternative reproductive tactics in a large mammal. J Zool 291:111–118. https://doi.org/10.1111/jzo.12049

DeMartini EE (1988) Spawning success of the male plainfin midshipman. I. Influences of male body size and area of spawning site. J Exp Mar Biol Ecol 121:177–192. https://doi.org/10.1016/0022-0981(88)90254-7

Engqvist L, Taborsky M (2016) The evolution of genetic and conditional alternative reproductive tactics. Proc R Soc B 283:20152945. https://doi.org/10.1098/rspb.2015.2945

Fagan WF, Lewis MA, Auger-Méthé M et al (2013) Spatial memory and animal movement. Ecol Lett 16:1316–1329. https://doi.org/10.1111/ele.12165

Fitzpatrick JL, Earn DJD, Bucking C et al (2016) Postcopulatory consequences of female mate choice in a fish with alternative reproductive tactics. Behav Ecol 27:312–320. https://doi.org/10.1093/beheco/arv159

Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol 7:1325–1330. https://doi.org/10.1111/2041-210X.12584

Griebling HJ, Rios-Cardenas O, Abbott J, Morris MR (2020) A study of tactical and sexual dimorphism in cognition with insights for sexual conflict. Anim Behav 170:43–50. https://doi.org/10.1016/j.anbehav.2020.10.006

Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol Evol 11:92–98. https://doi.org/10.1016/0169-5347(96)81050-0

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Kustra MC, Alonzo SH (2020) Sperm and alternative reproductive tactics: a review of existing theory and empirical data. Philos Trans R Soc Lond B Biol Sci 375:20200075. https://doi.org/10.1098/rstb.2020.0075

Lüdecke D (2018) Ggeffects: tidy data frames of marginal effects from regression models. J Open Source Softw 3:772. https://doi.org/10.21105/joss.00772

Metcalfe NB, Van Leeuwen TE, Killen SS (2016) Does individual variation in metabolic phenotype predict fish behaviour and performance? J Fish Biol 88:298–321

Miller JS, Bose APH, Fitzpatrick JL, Balshine S (2019) Sperm maturation and male tactic-specific differences in ejaculates in the plainfin midshipman fish *Porichthys notatus*. J Fish Biol 94:434–445. https://doi.org/10.1111/jfb.13912

Mohr RA, Whitchurch EA, Anderson RD et al (2017) Intra- and intersexual swim bladder dimorphisms in the plainfin midshipman fish (*Porichthys notatus*): implications of swim bladder proximity to the inner ear for sound pressure detection. J Morphol 278:1458–1468. https://doi.org/10.1002/jmor.20724

Morand-Ferron J, Quinn JL (2015) The evolution of cognition in natural populations. Trends Cogn Sci 19:235–237. https://doi.org/10.1016/j.tics.2015.03.005

Nathan R, Getz WM, Revilla E et al (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci U S A 105:19052–19059. https://doi.org/10.1073/pnas.0800375105

Oliveira R, Taborsky M, Brockmann H (2008) Alternative reproductive tactics—an integrative approach. Cambridge University Press, Cambridge

Pepler MA, Hindra MJS et al (2021) Tactic-specific antimicrobial activity suggests a parental care function for accessory glands in a marine toadfish. Proc R Soc B 288:20202873. https://doi.org/10.1098/rspb.2020.2873

Plaut I (2001) Critical swimming speed: its ecological relevance. Comp Biochem Physiol A Mol Integr Physiol 131:41–50. https://doi.org/10.1016/S1095-6433(01)00462-7

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rimbach R, Blanc S, Zahariev A et al (2019) Daily energy expenditure of males following alternative reproductive tactics: solitary roamers spend more energy than group-living males. Physiol Behav 199:359–365. https://doi.org/10.1016/j.physbeh.2018.12.003

Rochais C, Pillay N, Schradin C (2021) Do alternative reproductive tactics predict problem-solving performance in African striped mice? Anim Cogn 24:703–716. https://doi.org/10.1007/s10071-020-01459-z

Smith C, Philips A, Reichard M (2015) Cognitive ability is heritable and predicts the success of an alternative mating tactic. Proc R Soc B 282:20151046. https://doi.org/10.1098/rspb.2015.1046

Synyshyn C, Green-Pucella AE, Balshine S (2021) Nonmating behavioural differences between male tactics in the invasive round goby. Anim Behav 182:227–237. https://doi.org/10.1016/j.anbehav.2021.09.007

Walter T, Couzin ID (2021) TRex, a fast multi-animal tracking system with markerless identification, and 2D estimation of posture and visual fields. Elife 10:e64000. https://doi.org/10.7554/eLife.64000