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Spatial learning and lateralization in lizards

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Spatial memory is a fundamental cognitive process that allows animals to navigate and interact with their environment effectively. While extensively studied in mammals and birds, the mechanisms underlying spatial cognition in reptiles remain less understood. In this study, we investigated spatial learning and the influence of behavioural lateralization in the common wall lizard (*Podarcis muralis*). We examined whether lizards could develop short-term spatial memory and whether lateralization affected their navigation in a complex maze. Experimental lizards received 3 days of training without reinforcement, while control lizards had no prior experience. We found that trained lizards learnt to navigate the maze rapidly, reaching a goal shelter faster and more reliably than controls. Additionally, strongly lateralized individuals took longer to reach the goal during training, but this did not impair escape performance once the route had been learned. Our study reports novel evidence on the role of lateralization during spatial exploration in lizards. Lateralization is hypothesized to enhance information processing, but our data suggest no benefit or cost of lateralization after a route was learnt. Our study contributes to a broader understanding of cognitive evolution across vertebrates and emphasizes the importance of reptiles as models for comparative cognition research.

1. Introduction

Spatial memory and place learning are fundamental cognitive processes that enable animals to navigate, recognize and remember their environment through mental representations such as cognitive maps [1]. These abilities are essential for behaviours critical to survival and reproduction, including foraging, predator avoidance, mate finding and habitat selection [2–4].

Animals exhibit individual differences in their cognitive skill but how these differences emerge (through genetic differences or due to the influence of environmental factors) is still unclear [5–7]. Cerebral lateralization, the functional specialization of the left and right brain hemisphere leading to asymmetric control of cognitive and behavioural processes [8], might impact motor efficiency, for instance by producing a turning bias that affects how effectively animals move through their environment and discover resources [9]. Because such biases reflect the same hemispheric division of labour that governs spatial processing, lateralization can enhance behavioural efficiency, for example by allowing one hemisphere to maintain motor routines while the other processes spatial cues, thereby stabilizing navigation during movement [8,10–12]. However, it may also constrain movement flexibility and impair performance in certain maze tasks [13,14]. Therefore, the advantages of strong versus weak lateralization might be dependent on the context [8,10,15].

Despite spatial memory and place learning playing such a central role in the life of animals [16–19], research in reptiles and amphibians remains underexplored compared to mammals and birds (e.g. hippocampal

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navigation in rats or food-caching in corvids [20,21]). Yet, some studies suggest that spatial cognition in ectothermic vertebrates may be more sophisticated than previously assumed [22–25]. Reptiles are particularly relevant for comparative cognition, as they represent an important outgroup within amniotes. Consequently, investigating their cognitive abilities and the effect of lateralization may reveal ancestral developmental processes shared among vertebrates [26]. Nevertheless, studies remain limited [27,28], and the mechanisms underlying reptile spatial navigation are poorly understood [29].

Here, we used a maze-based approach to test short-term spatial memory in the common wall lizard (*Podarcis muralis*), assessing its relationship with lateralization through a turning bias. During training, a shelter was available without reinforcement; in the test phase, a predatory stimulus rendered the shelter ecologically relevant. Given the link between lateralization and asymmetric neural processing, we hypothesized that individuals with stronger turning bias would outperform weakly lateralized individuals in their ability to learn and navigate the maze [8,10–12]. Alternatively, as some studies show that lateralization can negatively affect spatial learning [13,14], we might expect the exact opposite that weakly lateralized individuals outperform strongly lateralized individuals.

2. Methods

(a) Animals and housing

Forty adult, wild-caught, male lizards participated in this study. At the laboratory, lizards were kept in individual enclosures (35.6 × 23.4 × 22.8 cm), pre-arranged in cabinets and equipped with heat lamps, paper substrate, a water and food dish and a terracotta tile shelter. The animals were housed in the laboratory for four weeks before the experimental tests began and were released back at the capture site once the research was completed (for more details see electronic supplementary material).

(b) Experimental design

We tested spatial learning, memory and behavioural lateralization in three temporal batches between 4 April and 9 June 2023. Twenty treatment lizards were given three training trials in a maze (one per day, see below), a test trial the following day after the last training trial as well as 15 trials across 5 days in a T-maze thereafter (see below). Twenty control lizards received only the test trial.

(i) Spatial learning and memory

Lizards were randomly assigned to either (i) an experimental group (n = 20) or (ii) a control group (n = 20). Lizards were tested in a 'stag maze' (figure 1A,B), developed considering the ethology and ecology of lizards [30–32] (for details on maze construction see electronic supplementary material). The maze consisted of a holding area (separated from the maze with a gate that could be raised remotely via a tripod) from which lizards would start each trial and a complex assembly of arms with two possible ends one of which contained a shelter (terracotta tile). Each lizard was randomly assigned a fixed position for the shelter (either arm 3 or arm 4, figure 1C), which remained consistent for the duration of the experiment. Two transparent plexiglass panels were placed over the maze to prevent lizards from escaping. All trials were recorded from above with the maze evenly illumined using LED strips. The order in which animals were tested within a day was randomized.

During training (days 1–3), experimental lizards were placed in the holding area for 60 s, after which the gate was raised remotely to allow 20 min of exploration. Thereafter, individuals were returned to their enclosure. Control lizards did not receive any previous experience with the maze. On day 4, all 40 lizards were tested. At the start of a trial, animals were placed in the waiting area for 30 s, after which the gate was raised remotely and a predatory stimulus was introduced. This stimulus consisted of the experimenter tapping their fingernails on the walls of the waiting room with a rotating movement and continued until the lizard reached the first decision point in the maze. The trial ended when the animal either reached the shelter or after 5 min. To minimize bias, the experimenter was blind to group identity, preventing any unintentional influence on behaviour.

For each lizard we recorded: (i) the latency to reach the shelter on each of the three training days, measured from the opening of the door until the whole body was inside the shelter, (ii) whether the lizard reached the artificial shelter during the test day (binary variable), and (iii) the latency to reach the shelter during the test day. Lizards that did not reach the shelter were given a censored latency of 1200 s (training) and 300 s (test). In addition to latency, we recorded for each trial: (iv) the choice made at the first fork (correct vs. incorrect, relative to the shelter position) and (v) the total number of arm entries and the number of entries into arms located on the same side as the shelter. These variables were used to quantify exploratory patterns across trials (see electronic supplementary material, table S1 for details).

(ii) Lateralization

After testing spatial learning and memory, the 20 experimental lizards were tested for their behavioural lateralization in a T-maze (figure 1C,D, for details on maze construction see electronic supplementary material). Each lizard underwent 15 trials (three trials per day over 5 days). First, a lizard was placed in the holding area for 30 s, after which the gate was raised remotely and simultaneously, the animal was exposed to a predatory stimulus. The experimenter simulated a threat by moving their hand above the lizard, and touching the maze walls to generate noise leading to the lizard fleeing towards the maze fork and

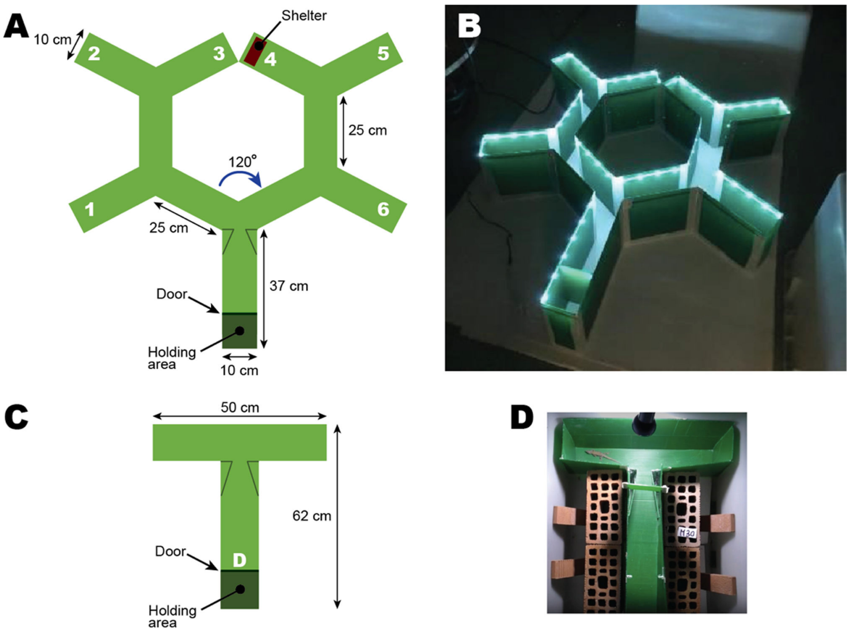

Figure 1. Schematics and pictures of the mazes used for the spatial learning and memory (A,B) and laterality test (C,D). (A) Schematic of the 'stag maze' used to test spatial memory. The maze included six arms of which one provided a shelter (either in arm 3 or 4) as the goal for lizards in the experimental group. Animals were held in a holding area at the start of the experiment and could enter the maze after a door was lifted. (B) Picture of the 'stag maze' with the door closed. LEDs covered the entire perimeter of the structure to achieve even illumination of the whole maze. (C) Schematic of the T-maze used to test behavioural lateralization in male *P. muralis*. Each animal was held in a holding area at the start of the experiment and could enter the maze after a door was lifted. (D) Picture of the T-maze with a male *P. muralis* in the left arm. The maze was illuminated from the top with a single light bulb.

turning either left or right. The same experimenter simulated the predatory stimulus for all trials. All trials were filmed from above (Canon Legria camera) with the maze illumined evenly by a light source. The direction of the turn was recorded as the primary variable of interest. The order in which animals were tested within a day was randomized.

(c) Data analysis

All statistical analyses were run in R v. 4.4.2 [33]. We provide Bayes factors (BF, from marginal likelihoods) to evaluate the results using the package *brms* (for more details see electronic supplementary material). Bayes factors below 1 indicate no difference while above 1, BF indicate support for a difference [34].

(i) Spatial memory, learning and laterality

To evaluate if lizards that experienced training learnt to navigate the maze, we ran a Bayesian generalized linear model (BGLM) with Bernoulli distribution using whether the lizard reached the shelter (= 1) or not (= 0) as the response variable and the treatment group (experimental and control group) as the fixed effect. No random effect was used as animals only received one test trial. Similarly, we compared the time taken to reach the shelter (response variable) between the experimental and control group (fixed effect) using a censored BGLM with log-normal distribution and no random effect was included. Finally, in the experimental group, we evaluated learning and the effect of lateralization by running a BGLMM (mixed model) on the time taken to reach the shelter across all four test days. As fixed effects, we used trial (to investigate learning), the strength of laterality and their interactions. We calculated the strength of lateralization as $\left|\frac{R-L}{R+L}\times 100\right|$, where R and L are the number of choices towards the right and left directions in the T-maze. We included the strength rather than the relative laterality index because few animals showed lateralized behaviour to either the left or right side in the laterality test (see below). We included a random effect of animal identity to account for repeated testing.

(ii) Lateralization

To assess the degree of lateralization in each individual, we employed a BGLMM with Bernoulli distribution and logit link function. The binary side choice (right = 1, left = 0) for each trial was used as the response variable; the model did not include fixed effects (null model), while the individual lizard was included as the random effect, accounting for repeated measurements within individuals. A lizard was deemed to have a side preference if the 95% credible intervals of its estimated effect (random intercept) did not cross 0.

(d) Ethics and permits

We applied non-invasive methods following the guidelines by the Association for the Study of Animal Behaviour/Animal Behaviour Society [35]. The method used to capture the lizards (noosing) is commonly employed due to its effectiveness and because it does not cause harm to the animals [36]. At the end of the experiments, lizards were returned to their original capture sites. Animal collection, husbandry and testing were approved by the Ministry of Ecological Transition (ISPRA Prot. 0010736/2022, 01/03/2022).

3. Results

We found a higher probability and lower latency to reach the shelter during the test trial in lizards from the experimental group compared to the control group (probability: BGLM, estimate = 1.721, CI_{low} = 0.551, CI_{up} = 2.948, BF = 36.6, figure 2; latency: estimate = −1.632, CI_{low} = −2.530, CI_{up} = −0.721, BF = 131.78; figure 2).

In the lateralization test, 10 individuals preferred the right direction, while the remaining 10 chose the left direction more often (figure 2). However, we found a significant preference in only seven individuals (35%), of which three preferred the right and four the left direction (figure 2). Overall, the group average did not reveal a significant group-level bias in lateralization (BGLMM, estimate = −0.006, CI_{low} = −0.646, CI_{up} = 0.673; figure 2).

We found no support for an effect of an interaction between trial and the strength of lateralization (BGLMM, estimate = 0.360, CI_{low} = −0.483, CI_{up} = 1.176, BF = 0.59) on the latency to reach the shelter during training; the interaction was subsequently removed. The simpler model found a decrease in the latency to reach the shelter across trials (BGLMM, estimate = −0.488, CI_{low} = −0.815, CI_{up} = −0.149) and a positive relationship between the latency and the strength of lateralization (BGLMM, estimate = 1.493, CI_{low} = 0.348, CI_{up} = 2.586, BF = 256), showing that more strongly lateralized individuals took longer to reach the shelter during the initial learning trials (figure 3). To visualize how the relationship between latency and lateralization varied across trials, we extracted estimates from the model including the lateralization × trial interaction. The slope for lateralization was significant (CI not crossing 0) and positive in both Trial 1 (β = 1.29, CI_{low} = 0.13, CI_{up} = 2.41) and Trial 2 (β = 1.59, CI_{low} = 0.01, CI_{up} = 3.18), and still positive but not significant in Trial 3 (β = 1.24, CI_{low} = –0.33, CI_{up} = 2.78), but absent in the test trial (β = 0.07, CI_{low} = –1.54, CI_{up} = 1.64). Exploratory measures based on arm entries were consistent with these patterns. During training, strongly lateralized individuals made a lower proportion of entries on the correct side of the maze in the first trial, whereas no clear relationship with lateralization was detected in Trials 2 and 3 (see electronic supplementary material, table S1). The probability of choosing the correct path at the first fork did not differ clearly from chance at any given trial, whereas in the final test, trained lizards chose the correct path on their first turn in around 70% of cases (see electronic supplementary material, Results).

4. Discussion

The fast acquisition of spatial information is crucial for animals to navigate their environment successfully. Our findings were somewhat consistent with our second prediction: turning biases influenced how lizards initially explored the unfamiliar maze, and strongly lateralized individuals showed longer latencies during the early familiarization phase. This pattern indicates that turning biases affected the initial exploratory trajectories in the maze, leading strongly lateralized individuals to take longer paths to reach the shelter during early trials (but also see [37]). This interpretation is supported by the arm-entry data, where strongly lateralized individuals entered proportionally fewer arms on the correct side during the first trial, thus indicating initial directional constraints in exploration behaviour. However, this early pattern cannot be taken as evidence for differences in learning rate. Trial 1 reflects only naive exploration, and although a latency difference persisted in Trial 2, it disappeared thereafter and did not affect performance in the final test. This temporal pattern shows that lateralization shaped how individuals initially sampled the maze but did not provide clear support for differences in the acquisition of spatial information and should be interpreted cautiously. At the same time, because exploratory behaviour and information gathering often overlap in the early stages of the tasks, our data do not allow us to exclude the possibility that exploration strategies influenced how quickly individuals formed spatial representations. Previous studies have often reported cognitive benefits of strong lateralization in certain tasks [38]. In our study, however, the effect of lateralization emerged only during initial exploration, suggesting that such advantages may be context-dependent and may not extend to early familiarization in a complex spatial environment. Similar patterns have been reported in goldbelly topminnow (*Girardinus falcatus*), where strongly lateralized individuals made more errors during early exploration of a multichoice task [39]. This aligns with the idea that lateralization can influence how animals initially sample and inspect unfamiliar environments, even when ultimate performance converges. It is possible that strongly lateralized lizards followed more constrained or less flexible exploratory trajectories during familiarization, yet finally showed similar escape performance once the path was available to memory. This suggests that strongly and weakly lateralized lizards might use different strategies that are similarly efficient in learning an escape route. For example, in European eels (*Anguilla anguilla*) strongly lateralized fish that were less exploratory and bold used a climbing strategy during migration, while weakly lateralized eels that were more exploratory and bolder were more likely to swim against a current. Both are successful migration strategies [40].

Finally, contrary to the training, during tests in both the T-maze and the complex maze, a predator stimulus was applied. A range of studies show that strongly lateralized individuals outperform less lateralized individuals only under certain conditions. This may help explain why lateralization differences observed during familiarization were not detectable during the escape test, when motivation and behavioural context changed markedly. For example, strongly lateralized chicks (*Gallus gallus domesticus*) remain proficient in a foraging task under predation pressure compared to weakly lateralized individuals [10]. It is possible that under pressure more strongly lateralized lizards performed better than without pressure resulting in

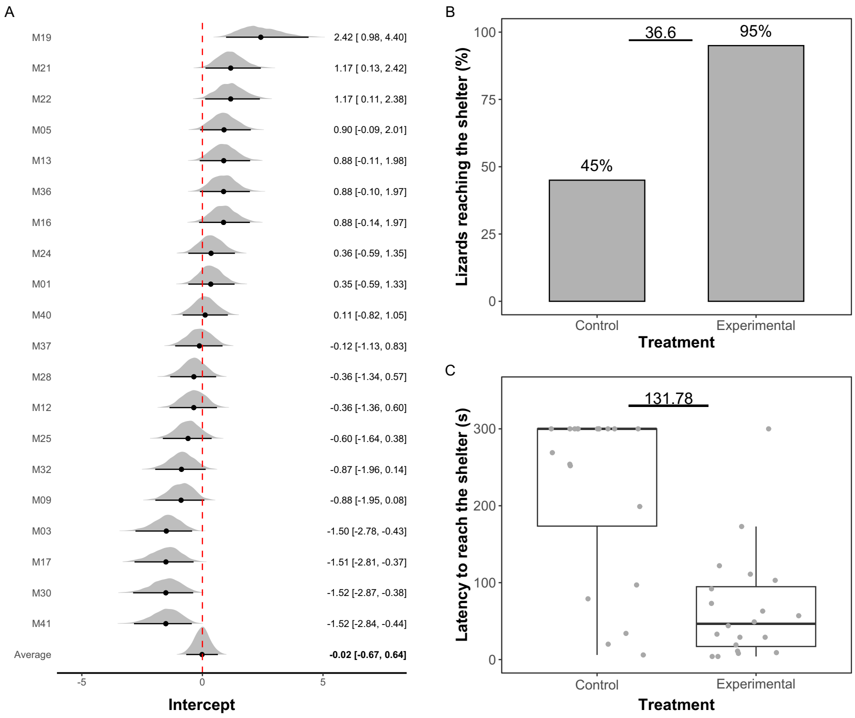

Figure 2. Results of the Bayesian analysis of logistic regression on lizard escape direction choice in the laterality test (experimental group: $n = 20$). (A) Each point represents the estimated random effect for individual lizards (log-odds), and horizontal black bold lines indicate the 95% credible intervals. The vertical red dashed line represents neutrality (log-odds = 0), where there is no preference for a specific escape direction (right or left). Density curves in the background (grey) represent the distribution of escape direction choices recorded for each individual across 15 tests. Points whose credible intervals do not intersect the dashed line indicate individuals with a significant preference for either the right or left direction. (B) Boxplot of the probability to reach the shelter in control lizards (no training; $n = 20$) and experimental lizards (trained in the maze; $n = 20$). (C) Boxplot of the latency to reach the shelter (s) for the same two groups. In panels (B) and (C), the bold line within the boxes represents the median, the box edges represent the upper and lower quartiles and the whiskers indicate the minimum and maximum. Grey dots indicate individual lizards' performance. Lizards that did not reach the shelter within 5 min (300 s) were assigned a censored latency of 300 s. Numbers above the black horizontal lines indicate Bayes factors.

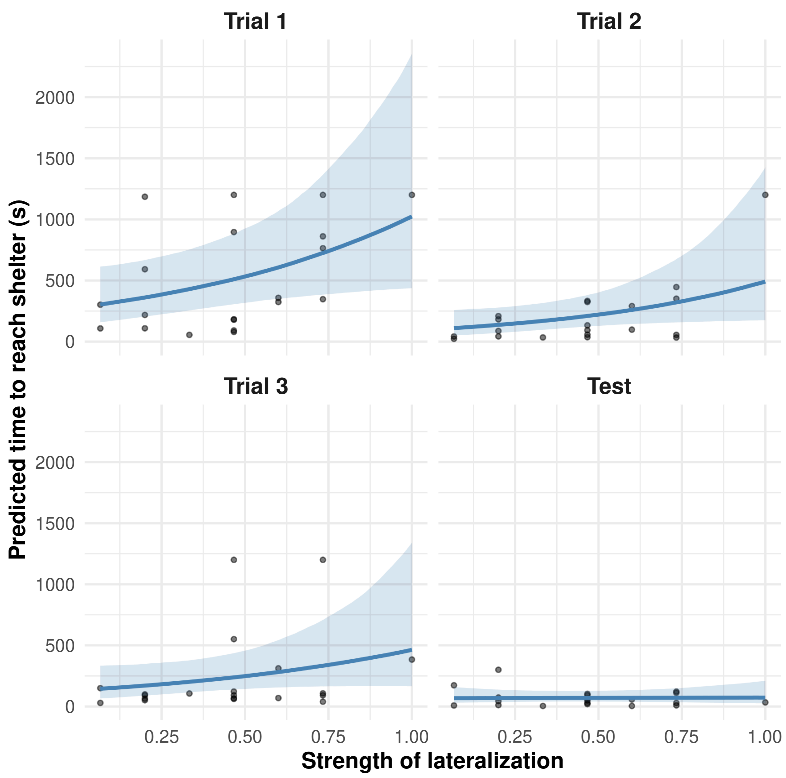

Figure 3. Predicted relationship between lateralization strength and the latency to reach the shelter across the four experimental trials ($n = 20$). Each panel displays a separate trial (training trials and the test). Grey points represent individual observations. The blue lines show predicted values from the Bayesian regression model, and the shaded areas correspond to 95% credible intervals. A positive association between lateralization strength and shelter latency is evident in the early trials, but this effect weakens in Trial 3 and is no longer present in the test phase.

similar performance to the weakly lateralized lizards. Alternatively, lizards might be able to overcome their innate side bias under pressure. Importantly, lateralized turning behaviour might only interfere with performance under certain conditions. For example, water skinks (*Eulamprus quoyii*) innate side preference interfered with learning a two-choice discrimination task but did not affect performance in a detour task in which they had to walk around an obstacle [41]. Nevertheless, further studies are needed to better understand how lateralization might affect information collection such as during learning and how differences in exploration caused by lateralization might affect fitness in the wild.

The comparison to naive lizards as well as our analysis regarding the change in performance across trials confirm that our experimental group learnt to navigate a maze fast and with minimal experience, one trial each for 3 days. Reptiles, such as lizards, are often regarded as slow and sluggish and mostly driven by innate behaviour and less so by cognitive processes [42,43]. Over the last few decades, however, research has accumulated showing that this is not the case [27]. As an outgroup in the vertebrate lineage, research on the cognitive abilities in lizards can shed new light on the evolution of cognition and due to their large diversity [44], lizards are excellent models for comparative cognition research. Our results support the use of lizards and demonstrate fast and proficient spatial learning in *P. muralis*.

Finally, similar to previous work across a wide range of taxa, we found that within our sample of wild lizards, most animals were not strongly lateralized [45]. Our lizards originated from the wild, and therefore, this pattern might demonstrate natural variation in turning behaviour if our subsample is representative of the male population of origin. Other studies in the same species seem to confirm this pattern [46,47].

In summary, strongly lateralized lizards initially showed longer latencies while exploring an unfamiliar maze, yet this early difference did not translate into any disadvantage during the final escape test. To the best of our knowledge, this is the first time that lateralized turning behaviour was linked to maze learning in a reptile species. Remarkably, just three training trials were sufficient for lizards to acquire the information needed to escape a simulated predator attack, demonstrating that they can learn to navigate a maze with minimal training. Our findings open new avenues for research on the role of brain lateralization in spatial learning across reptiles inhabiting different ecological contexts.

Ethics. We applied non-invasive methods following the guidelines by the Association for the Study of Animal Behaviour/Animal Behaviour Society. The method used to capture the lizards (noosing) is commonly employed due to its effectiveness and because it does not cause harm to the animals. At the end of the experiments, lizards were returned to their original capture sites. Animal collection, husbandry and testing were approved by the Ministry of Ecological Transition (ISPRA Prot. 0010736/2022, 01/03/2022).

Data accessibility. Data generated during this study as well as all code generated to analyse the collected data are available to download from the OSF [48].

Supplementary material is available online [49].

Declaration of AI use. During the preparation of this work, the author(s) used ChatGPT version 5 (in September 2025) in order to help with writing the abstract. After using ChatGPT, the author(s) reviewed and edited the content as needed and take full responsibility for the content of the publication.

Authors' contributions. D.P.-R.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, writing—original draft, writing—review and editing; B.S.: data curation, formal analysis, funding acquisition, validation, visualization, writing—original draft, writing—review and editing; A.G.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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