Animal Behaviour 239 (2026) 123692

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Ethologically informed enrichment improves behavioural and physiological indicators of welfare in a captive lizard

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A R T I C L E I N F O

Article history:
Received 23 September 2025
Initial acceptance 24 November 2025
Final acceptance 30 April 2026
Available online 20 August 2026
MS. number: 25-00569R

Keywords:
animal welfare
behavioural welfare assessment
environmental enrichment
faecal corticosterone metabolite
Podarcis muralis
reptile husbandry

Environmental enrichment has become an essential tool for maintaining captive animals and improving their welfare. The information necessary to implement enrichment practices is largely restricted to a few species, mainly mammals, while studies on reptiles lag behind. However, current research shows that reptiles, like other species, can benefit from well-designed enrichment. In this study, we evaluated the effects of three types of enrichment on welfare-related indicators in the European common wall lizard, *Podarcis muralis*, including behavioural measures and faecal corticosterone metabolites (FCMs). We used chemosensory (conspecific scents), thermal/structural (basking platforms) and nutritional (feeding device) enrichment designed to provide ethologically relevant challenges. All enrichment interventions yielded a significant decrease in abnormal behaviour (interacting with transparent boundaries) and a significant increase in exploration compared to baseline, indicating improved welfare. FCM levels increased with time spent in captivity, but less markedly when lizards were exposed to enrichment than when it was absent. Taken together, our results suggest positive effects of all three enrichment types and highlight the importance of using an ethologically informed approach to enrichment design. We discuss how, when grounded in species-specific knowledge, similar strategies can contribute to improving welfare in a broader range of captive reptiles.

Environmental enrichment is a widely used welfare tool in the management of captive animals. Its use has become widespread because of growing concern about animal welfare among the general public, legal institutions and the zoo and pet care sectors (Kagan et al., 2015; Whitham & Wielebnowski, 2013). The ultimate goal of enrichment is to improve the welfare of captive animals by promoting normal behaviour and positive use of space, reducing stress and abnormal or stereotypic behaviours and providing biologically relevant challenges (Burman et al., 2008; Young, 2003).

Successful design and implementation of enrichment relies on two key aspects. First, environmental enrichment must be evaluated empirically to determine its effectiveness. Behavioural measures are most commonly used for this purpose, but current welfare frameworks emphasize the importance of combining behavioural and physiological indicators (Dawkins, 2021; Mason & Mendl, 1993). Among physiological measures, noninvasive assessment of glucocorticoid activity (e.g. faecal cortisol/corticosterone metabolites: FCMs) provides an integrated measure of hypothalamic–pituitary–adrenal axis activity over time and is particularly suited to assessing chronic stress in captive animals (Palme, 2019). Second, environmental enrichment strategies need to be carefully designed and based on detailed knowledge of each species' behaviour and life history (Mellen & Sevenich MacPhee, 2001; Newberry, 1995; Shepherdson, 2003). Thus, evidence-based welfare methods require species-specific knowledge, which remains scarce for many taxa because of a marked taxonomic bias in enrichment and welfare research (Melfi, 2009; Mellor, 2015), which has led to a disproportionate focus on mammals and birds relative to other groups, such as reptiles (de Azevedo et al., 2007; Rose et al., 2019). For reptiles in particular, this lack of species-specific knowledge has important consequences, often resulting in captive environments with reduced

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https://doi.org/10.1016/j.anbehav.2026.123692
0003-3472/

environmental complexity, restricted behavioural opportunities and compromised welfare (Arena & C. Warwick, 2023; Whitehead, 2018). This lack of information, coupled with traditional notions regarding reptiles as stoic or low-maintenance animals (Burghardt, 2013; Font et al., 2023; Warwick, Steedman, et al., 2018), promotes husbandry practices that lack scientific validation (i.e. 'folklore husbandry': Arbuckle, 2010, 2013), highlighting the need to broaden the taxonomic scope of welfare research and adopt an evidence-based approach to reptile enrichment (Bartolomé et al., 2023; Riley & Rose, 2020; Tuite et al., 2022). With more than 12 000 recognized species (Uetz et al., 2025), reptiles are a highly diverse group. Research on reptile welfare and enrichment is particularly important given the diversity of species and the large number of individuals kept in captivity in zoos and private collections (Conde et al., 2013; Sparrow et al., 2024) and the widespread use of reptiles, particularly lizards, as model organisms in research (Hubrecht & Kirkwood, 2010). Their ectothermic physiology, distinctive morphology and behaviour imply that the requirements for captive reptiles may differ from those of endothermic animals (Mendyk & Augustine, 2023) and enrichment design requires an ethologically informed approach (Greenberg, 2023). For instance, as ectotherms, reptiles regulate their temperature mainly through behavioural means (e.g. basking, microhabitat selection and posture changes: Black et al., 2019; Vitt & Caldwell, 2014), so thermal enrichment should provide opportunities for behavioural thermoregulation by offering a range of temperatures and microhabitats. Nutritional enrichment, one of the most commonly used forms of enrichment along with structural changes to an animal's environment (Bartolomé et al., 2023; Eagan, 2019; Riley & Rose, 2020), can offer effective enrichment opportunities when it takes into account the lower metabolic rates and specific foraging behaviours of reptiles (Huey, 1982; Kuo et al., 2019; Vitt & Caldwell, 2014). Similarly, considering the sensory capabilities of reptiles is essential for good husbandry, although this has often been overlooked in captivity (Burghardt, 2013; Crowe-Riddell & Lillywhite, 2023). Despite reptiles possessing complex visual and chemosensory systems (Cooper, 1995; Fleishman & Font, 2019; Vitt & Caldwell, 2014), few studies have investigated the use of sensory stimuli as enrichment for these animals (Bannister et al., 2021; Bashaw et al., 2016; Londoño et al., 2018; Waterman et al., 2021).

Despite these challenges, the literature on environmental enrichment for reptiles has grown in recent years, leading to important advances in herpetological husbandry (Mendyk, 2018; Mendyk et al., 2016; Warwick et al., 2023). Although some studies have failed to find positive effects of enrichment on behavioural and physiological measures (in *Anolis carolinensis*: Borgmans et al., 2018; in *Sceloporus undulatus*: Rosier & Langkilde, 2011), most available evidence suggests that reptiles benefit from properly designed enrichment protocols. Enrichment increases activity, exploratory behaviour (Almli & Burghardt, 2006; Waterman et al., 2021) and behavioural diversity (Bashaw et al., 2016; Spain et al., 2020) and reduces aggressive behaviour, stereotypies and abnormal behaviour (Burghardt et al., 1996; Londoño et al., 2018; Rickman et al., 2025; Therrien et al., 2007). When given the opportunity to choose, reptiles prefer enriched, more complex environments (Case et al., 2005; Crisante et al., 2025; Hoehfurtner et al., 2021), and the positive effects of enrichment can improve reptiles' problem-solving and discrimination abilities (Almli & Burghardt, 2006; Nagabaskaran et al., 2021). Finally, physiological measures have rarely been validated as indicators of welfare in reptiles (Benn et al., 2019) and have only been used in a handful of studies (Carbajal et al., 2024), but there is evidence that enrichment may be linked to reduced levels of biochemical markers of stress (e.g. reduced heterophil to lymphocyte ratios in *Terrapene carolina*: Case et al., 2005). In this study, we evaluated the effects of different environmental enrichment types in the common wall lizard, *Podarcis muralis*. We employed three enrichment methods designed to provide ethologically relevant challenges: (1) chemosensory enrichment, using scents from conspecifics as a territorial challenge; (2) nutritional enrichment, using a device that allowed animals to search for food in drilled log holes simulating natural crevices where lizards typically forage in the wild; and (3) thermal/structural enrichment, expanding the temperature range within the enclosure and enabling animals to choose their preferred temperature. We conducted behavioural observations before, during and after each enrichment intervention for a group of treatment lizards in a counterbalanced single-subject design. We also measured faecal corticosterone metabolite (FCM) levels noninvasively to assess changes in stress-related adrenocortical activity, providing an integrated measure suitable for detecting potential effects of enrichment on chronic stress throughout the experiment. Finally, we included an external control group that was not exposed to enrichment for both behavioural and physiological measures.

METHODS

Study Species and Housing Conditions

The European common wall lizard is a small lacertid lizard that is widely distributed across Europe, with introduced populations in the U.S.A. and Canada. It is commonly used in research and kept in zoos and as a pet (Cooper, 2024). In September 2021, we captured 24 adult male lizards (mean snout–vent length, SVL $\pm$ SE = 66.12 $\pm$ 0.46 mm; mean weight $\pm$ SE = 7.57 $\pm$ 0.13 g) in the Cerdanya Valley, Eastern Pyrenees, Spain. Lizards were captured by noosing, using a pole with a slipknot that tightened around the lizard's neck. They were individually held in cloth bags and transported by car to our laboratory facilities on the day following capture.

Experimental/housing terraria measured 70 $\times$ 30 cm and 40 cm high. A 40 W Parabolica RP50 Radium lightbulb (Radium Lampenwerk, Wipperfürth, Germany, https://www.radium.de) was suspended on one side of the terrarium to create a thermal gradient, with mean temperature ($\pm$ SE) ranging from 23.5 $\pm$ 0.19 °C on the cold side of the enclosure to 32.43 $\pm$ 0.19 °C on the basking stones directly under the heat lamps, reflecting the preferred temperature gradient of this species (Avery, 1978; Braña, 1991; Trochet et al., 2018). Each terrarium was furnished with coconut husk substrate, two basking stones, three shelters along the thermal gradient, a piece of slate and a water dish. The terraria were housed in a room with a 12:12 h light:dark cycle, and the temperature (20 °C) and humidity (57%) were monitored daily. In addition, daylight/UV-enriched lamps (F30W 'Reptistar', colour temperature 6500 K; Sylvania Lighting, Budapest, Hungary, https://www.sylvania-lighting.com) were used. These lamps were positioned 25–35 cm above the enclosure floor and switched on for 2 h (1130–1330 hours) five times weekly. Every other day, lizards were fed mealworm larvae, *Tenebrio molitor*, or small crickets, *Acheta domesticus*, dusted with JBL Terravit vitamin and mineral powder (JBL, Neuhofen, Germany, https://www.jbl.de). All lizards (both enriched and control animals; see Experimental Design) were fed according to the same schedule and received the same total amount of prey. The difference between treatments lay in the mode of presentation: during the nutritional enrichment phase (see below), enriched animals received mealworms exclusively from the nutritional enrichment device. Water was available ad libitum.

Experimental Design

We used a single-subject design with 18 experimental lizards sequentially subjected to three types of enrichment, counterbalanced to minimize potential order-related effects (Fig. S1). Additionally, we included six animals that did not receive enrichment at any point during the experiment as an external control group. Upon arrival at the laboratory, lizards were housed and left in their enclosures for 10 days to acclimatize prior to the experiment, as described above. The experiment consisted of a baseline phase that lasted 12 days, three enrichment phases (E1, E2 and E3) lasting 9 days each and a post-treatment phase lasting 10 days (Fig. 1). The enrichment phases were separated by two resting periods (R1 and R2) lasting 8 days each to avoid carryover effects. During the enrichment phases, enrichment devices and/or stimuli were introduced into the terraria 2 h before lights were turned on and remained inside the enclosure for the duration of phase. The only enrichment items present in the enclosure were those assigned to each individual for that enrichment phase. The enrichment devices were removed on the final day of each enrichment phase after the lights were turned off to minimize disturbance to the animals.

Nutritional enrichment

For nutritional enrichment, we used a feeding trunk made from a cylindrical piece of wood drilled with six holes (2.5–3.5 cm deep) of two diameters (2 cm and 1.5 cm; Fig. 2a; Mendyk, 2012; Mendyk & Horn, 2011). We loaded three of the holes with mealworm larvae before placing the feeding trunk into the enclosures. The trunk allowed lizards to explore the holes and feed at their own pace in a naturalistic context, reflecting the natural foraging behaviour of this species, which actively explores holes and crevices in search of prey.

The feeding trunks provided prey every other day during each enrichment phase (i.e. on 4 of the 9 days). We lined the interior of the holes with thin plastic to prevent larvae from escaping, which also allowed us to record when and how many larvae each lizard consumed.

Thermal enrichment

Thermal/structural enrichment consisted of two platforms at different heights above the terrarium floor, each topped with a slate tile (higher platform: 13 × 10 cm and 14 cm high; lower platform: 10 × 7 cm and 9 cm high; Fig. 2b). The platforms allowed lizards to climb and approach the heat lamp, increasing the structural complexity and expanding the range of temperatures available within the terrarium. The mean temperature (± SE) was 41.0 ± 0.9 °C on the higher platform and 28.3 ± 0.8 °C on the lower platform.

Chemosensory enrichment

Chemosensory enrichment consisted of introducing 2 × 2 cm pieces of paper previously exposed to other males to simulate encounters with conspecific scents in the wild (Londoño et al., 2018; Fig. 2c). To implement the enrichment, we placed four 2.5 × 2.5 cm tiles in the corners of the enclosure to provide a surface for the scent-marked papers and facilitate their removal for cleaning. Each enclosure had its own tiles, which were present

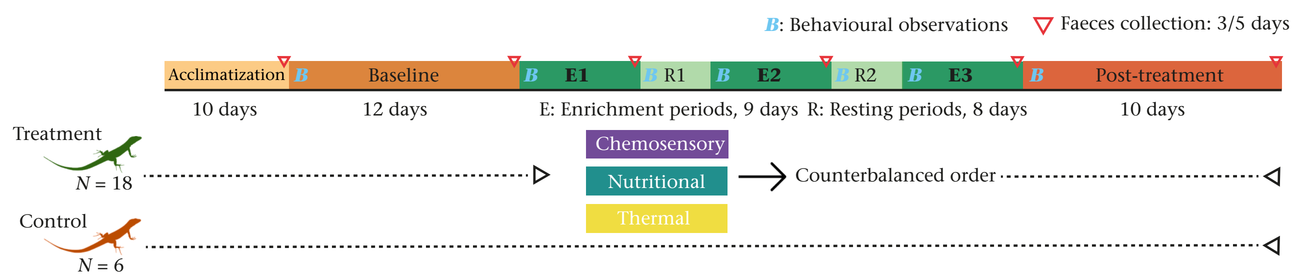

Figure 1. Overview of the experimental schedule and timeline. The experiment consisted of an acclimatization period, a baseline phase, three enrichment phases (E1, E2 and E3) separated by two resting periods (R1 and R2) and a post-treatment phase. Behavioural observations were made during all phases except the acclimatization period. Faecal samples were collected during all phases except the resting periods.

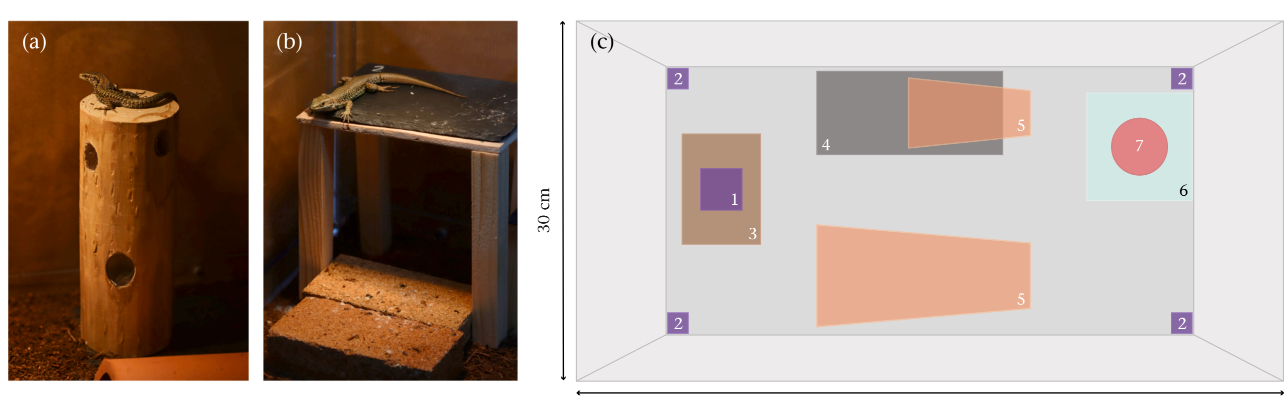

Figure 2. (a) Feeding device used for the nutritional enrichment. (b) A lizard basking on the higher of the two platforms used for thermal/structural enrichment. (c) Diagram of the terrarium with the chemosensory enrichment (modified from Londoño et al., 2018). Numbers indicate the contents of the terrarium: (1) a clean 4 × 4 cm piece of paper used to collect the scent of donor males; (2) 2 × 2 cm pieces of paper containing donor scent; (3) basking stone; (4) slate tile; (5) clay tiles; (6) shelter; and (7) water dish.

only during the chemosensory enrichment phase. Every day, we used small pieces of adhesive putty to attach a 4 × 4 cm piece of clean filter paper to each male's basking stone. After 24 h, we replaced these papers with clean ones and cut the scent-marked papers into four 2 × 2 cm pieces, which were then introduced into the terraria of lizards undergoing chemosensory enrichment. All lizards in the enriched group were exposed daily to the scents of two different donors, with two pieces from each donor placed on opposite sides of the terrarium. To ensure a variety of chemical stimuli, we changed the scent donors for each lizard every 2 days during the enrichment phase. We randomly assigned scent donors so that each lizard served as a donor.

Behavioural Observations

We performed behavioural observations during all phases of the experiment except the acclimatization phase. Relative to the total duration of each phase (see Fig. 1 and Experimental Design), behavioural observations were conducted on 11 days during the baseline phase, 8 days during each enrichment phase, 4 days during each resting period and 8 days during the post-treatment phase, resulting in a total of 51 observation days. We recorded the behaviours described in a partial ethogram (Table 1) compiled from the published literature on this species (Abalos et al., 2020; Avery, 1978; Braña, 1991; Font, Carazo, et al., 2012) and our own observations. The ethogram included the behaviours most commonly observed in this species in the wild and in captivity, excluding social interactions. Every day, after the lights came on (0845 hours), we recorded the behaviour of all animals from behind a hide to avoid disturbance, using scan sampling with an instantaneous recording rule at 25 min intervals (from 0910 to 1320 hours). Between consecutive scan samples, we conducted 10 min focal sampling observations using a continuous recording rule (Bateson & Martin, 2021; Lehner, 1998). We used BORIS logging software (Friard & Gamba, 2016) to record behaviours live, measuring the duration of state behaviours and the total number of occurrences of events. Finally, we counted the number of tongue flicks using a hand-held tally counter during the first 60 s of each focal sampling to calculate tongue-flicking rate. To ensure that behavioural observations were evenly distributed across the observation period and were representative of each lizard, we implemented a schedule with a randomized order of observations and rotated this schedule throughout the experiment. In addition to the laboratory experiment, we conducted behavioural observations of free-ranging lizards in their natural habitat. Details of the methods and results of these field observations are provided in the Supplementary Material (Fig. S2 and Tables S1 and S2). Observations were always made by the same observer (A.B.).

Table 1
Partial ethogram of *Podarcis muralis* with empirical descriptions of the behaviours

Category	Behaviour	Description
Orientation and locomotion	Posture change*	Adjustment of body posture not associated with locomotion, (e.g. turning, tail twitching, head movement)
	Walking	Relatively slow displacement of the lizard resulting in a change in location
	Running	Fast-paced forward movement of the lizard resulting in a change in location
	Jumping*	Leaping into the air with all four feet leaving the substrate, either from the floor to an elevated position (and vice versa), or between elevated positions
General behaviour	Foraging	Chasing or lunging at prey from a stationary position, followed by biting or grasping prey with the jaws
	Drinking	Placing the snout into water, accompanied by tongue extension and retraction
	Defecating	Extrusion of faecal material
	Cloacal drag*	Slowly moving forward while keeping the cloaca in contact with the substrate
	Hiding	Not visible to the observer (i.e. inside a shelter or under the substrate)
	Head out	Motionless inside a shelter with the head fully or partially sticking out (not beyond the forelimbs)
	Basking	Motionless and immediately under the heat source, with the lizard's abdomen dorsoventrally flattened and oriented at right angles to the heat source
	High perching	Motionless (either fully exposed or with the body sticking out beyond the forelimbs from a shelter) in an elevated posture (i.e. head and body elevated with the forelegs partially or fully extended)
	Low perching	Motionless (either fully exposed or with the body sticking out beyond the forelimbs from a shelter), with ventral side fully in contact with the surface (i.e. the head either resting on the substrate or slightly elevated and parallel with the substrate)
	Burrowing	Digging in the substrate and/or crawling under the substrate
	Tongue flicking	Rapid extrusion and retraction of the tongue, either contacting the air (air licks) or directly contacting any surface of the enclosure (tongue touches), except when directed at chemical enrichment stimuli (see interaction with enrichment objects)
Abnormal behaviour	Interaction with transparent boundaries (ITB)	Stereotyped interaction of the lizard with the limits of the terrarium consisting of: (1) scratching or clawing the walls repeatedly with the forelegs (2) pressing the snout against or attempting to bite the walls of the terrarium
	Jumping against wall*	Leaping into the air with all four feet leaving the substrate, from an elevated position to the walls of the terrarium, usually followed by ITB
	Scratching	Scraping or clawing the surface of an object repeatedly with the forelegs and/or rubbing the snout against enclosure furniture
	Biting furniture*	Biting the surface of enclosure furniture, usually associated with scratching and/or ITB
Interaction with enrichment objects	Basking on platform	For thermal enrichment: Motionless on top of the basking platform, with the lizard's abdomen dorsoventrally flattened and oriented at right angles to the heat source
	Feeding from nutritional device (FND)	For nutritional enrichment: Inserting the head into a hole in the feeding trunk and pulling prey out
	Enrichment-directed tongue flicks	For chemical enrichment: tongue flicks directed at chemical stimuli, including air licks aimed at paper containing the stimulus (when the lizard's snout is within a distance no greater than the length of its head from the stimulus) and tongue touches (when the tongue directly contacts paper containing the stimulus)
	Other enrichment-directed interactions	For thermal, chemical and nutritional enrichment: Touching the object with any part of the body (climbing, moving on top or pawing the object)

Behaviours were classified as states or events. Asterisks indicate events.

Faecal Corticosterone Metabolites (FCMs)

We collected faeces during the last 3 days of the acclimatization, baseline and enrichment phases (Fig. 1) and during the last 5 days of the post-treatment phase. We checked the terraria three times on the morning of each collection day and collected only faeces voided that day (fresh samples), as degradation by intestinal bacteria can affect corticosterone metabolite concentrations, which also increase as samples become drier (Palme et al., 2005). Faeces were collected using tweezers cleaned with alcohol to avoid cross-contamination, placed in zip-sealed plastic bags and frozen at −20 °C immediately after collection.

We measured FCMs using two group-specific enzyme immunoassays (EIAs): 5α-pregnane-3β,11β,21-triol-20-one (hereafter referred to as 37e: Touma et al., 2003) and 11-oxoaetiocholanolone (hereafter referred to as 72T: Möstl et al., 2002). Both EIAs have been used to measure glucocorticoid in other reptile species (Borgmans et al., 2018; Ganswindt et al., 2014; Scheun et al., 2018) and have been validated for *P. muralis* (Bartolomé et al., 2025). Based on the validation experiments, both assays were expected to detect changes in FCMs: the 37e assay showed greater sensitivity to increases in FCMs in response to stress-inducing conditions, whereas the 72T assay yielded higher absolute metabolite concentrations (Bartolomé et al., 2025). We therefore included both EIAs to provide a more robust characterization of adrenocortical activity.

Statistical Analyses

We selected the following behaviours for analysis based on their frequency and relevance to welfare assessment: interaction with transparent boundaries (ITB), walking, hiding, head out, basking, high perching and tongue flicking. Basking included only observations in which lizards were on the basking stones (Table 1). Regarding enrichment-directed behaviours, we recorded the behaviour basking on platform, which referred to observations of lizards on the enrichment platforms during the thermal enrichment phase (Table 1; Video S1). We calculated total basking as the sum of the time spent basking on the stones and the time spent basking on the platforms. Other enrichment-directed behaviours included feeding from the nutritional device (FND), enrichment-directed tongue flicks and other enrichment-directed interactions (Table 1). The latter two enrichment-directed behavioural categories were grouped into the functional category exploration of enrichment objects (EEO; Video S1) for statistical analyses because locomotion and tongue flicking are associated with exploration (Burghardt et al., 1986; Gómez et al., 1993; Greenberg, 1993, 2002), and exploratory behaviours are important for animal welfare (Mench, 1998; Wood-Gush & Vestergaard, 1989). Behaviours that were rarely observed were not statistically analysed (behaviour frequencies are provided in Table S3). Model selection information and additional details of the statistical analyses and post hoc tests are provided in the Supplementary Material. All data were analysed using R version 4.2.2 (R Core Team, 2022).

Effect of enrichment on behaviour

To evaluate the effect of enrichment on behaviour, we used counts of behaviours recorded during daily scan observations, that is, the number of sampling points at which each behaviour of interest was scored. For tongue flicking, the analysed variable was the frequency of tongue flicks per min, hereafter referred to as tongue-flicking rate. First, to assess whether there was a difference in the occurrence of behaviours between treatment and control animals during the enrichment and no enrichment phases, we fitted generalized linear mixed models (GLMMs) with a Poisson distribution. We included the variables enrichment on/off, group (treatment or control) and their interaction as fixed effects, and lizard identity and experimental day as random effects to account for individual variation and repeated measurements. Enrichment on/off was coded as 0 during phases in which enrichment was not provided (baseline, resting and post-treatment phases) and as 1 during the enrichment phases (E1, E2 and E3).

To assess the impact of environmental enrichment on behavioural variables relative to baseline, we fitted GLMMs with a Poisson distribution, except for tongue-flicking rate, for which we fitted a GLMM with a zero-inflated negative binomial distribution because this distribution provided a more appropriate fit for the data (Hu et al., 2011). In both models, we included enrichment type (baseline, chemosensory, nutritional or thermal) as a fixed effect, and lizard identity and experimental day as random effects. Additionally, we analysed whether enrichment affected behaviour across all phases of the experiment. To do so, we fitted a model with phase (baseline, E1, R1, E2, R2, E3 and POST) as a fixed effect, and lizard identity and experimental day as random effects, separately for treatment and control animals.

Temporal dynamics of enrichment effects

We performed a temporal analysis to evaluate the effect of enrichment throughout the experiment using focal sampling data (over 80 h of observations; Table S3b), with the total number of seconds spent engaged in a specific behaviour during focal observations as the response variable. First, to analyse the effect of time across the experiment on enrichment-directed behaviours, we fitted a GLMM with a zero-inflated negative binomial distribution in which the response variable was the total number of seconds (recorded as integers) spent exploring enrichment objects (EEO). We assessed whether there was an effect of time both across and within enrichment phases. For the first model (across enrichment phases), we included enrichment type (chemosensory, nutritional and thermal), enrichment phase (a continuous integer covariate representing the three successive enrichment phases) and their interaction as fixed effects, and lizard identity as a random effect. For the second model (within enrichment phases), we created the variable enrichment day. This covariate ranged from 1 to 8, reflecting the order of days within each enrichment phase while combining data from all three enrichment types to account for counterbalancing. We included enrichment type, enrichment day and their interaction as fixed effects, and lizard identity as a random effect.

Second, we investigated whether the effects of enrichment on behaviour persisted after enrichment was removed. Our experimental design included three postenrichment periods: two resting phases (R1 and R2; Fig. 1) following the first (E1) and second (E2) enrichment phases, and one post-treatment phase following the final enrichment phase (E3). To analyse behavioural changes over time, we divided the experiment into 2-day intervals and created the variable subphase, which was used as a continuous covariate to assess temporal trends in behaviour. Each enrichment phase (8 observation days) was divided into four subphases (subphases 1–4: days 1–2, 3–4, 5–6 and 7–8, respectively). The resting phase (4 observation days) and the post-treatment phases (the first 4 observation days) were divided into two subphases (subphases 5–6: days 1–2 and 3–4, respectively). To evaluate the persistence of the effects of each enrichment intervention, we created another variable, enrichment, that assigned each individual the enrichment type (chemosensory, nutritional or thermal) experienced during the preceding phase for each postenrichment period (R1, R2 and post-treatment). This allowed us to assess behavioural changes across enrichment and postenrichment phases (i.e. after enrichment removal) for each enrichment type while incorporating data from all phases to account for counterbalancing. We fitted separate models for interaction with transparent boundaries (ITB), walking, high perching and tongue-flicking rate, including subphase as a continuous covariate, enrichment (chemosensory, nutritional and thermal) and their interaction as fixed effects, and lizard identity as a random effect.

Faecal corticosterone metabolites

For FCMs analysis we used linear mixed models (LMMs) with lizard identity as a random effect to deal with unbalanced design (because of missing data for some lizards on some days) and repeated measures from the same individuals (Crawley, 2013).

We first evaluated the effect of each phase and type of enrichment by fitting two separate models with phase (with six levels: acclimatization, baseline, E1, E2, E3 and post-treatment) and enrichment type (with six levels: acclimatization, baseline, chemosensory, nutritional, thermal and post-treatment) as fixed effects and lizard identity and experimental day as random effects. We also evaluated the effect of time across the experiment on FCM levels by fitting a model with the covariate day within phase (which referred to faeces sampling days), enrichment on/off (0 during the phases in which enrichment was not provided and 1 during enrichment phases) and their interaction as fixed effects, and lizard identity and experimental day as random effects. Control individuals were not included in this analysis because of low defaecation rates.

Ethical Note

Lizards were captured and housed in the laboratory under research permit number SF/024/21 issued by the Departament de Territori i Sostenibilitat, Direcció General de Polítiques Ambientals i Medi Natural, Generalitat de Catalunya, Spain. All research complied with the ASAB/ABS Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching (https://doi.org/10.1016/j.anbehav.2025.123421) and all applicable local (Decreto 13/2007), national (Real Decreto 53/2013) and European legislation (Directive 2010/63/EU). The University of Valencia Ethics Committee was consulted and confirmed that formal approval was not required because the study was observational. Nevertheless, we recognize that the capture and temporary confinement of wild reptiles can impose stress and affect their welfare, with potential short- and long-term consequences (Borgmans et al., 2021; Langkilde & Shine, 2006). To minimize these effects, we prioritized minimal and careful handling, avoided disturbance from human observers and closely monitored each individual in our care.

Aside from the initial handling required to measure the animals and place them in their enclosures, all procedures were noninvasive and consisted solely of behavioural observations. Capture by noosing is a selective method that does not harm lizards (Pérez i de Lanuza, Carazo, & Font, 2014). Upon arrival at the laboratory, lizards underwent mite treatment before the experiments. Lizards were sprayed with a doramectin suspension formulated for reptiles (Ophionol: doramectin 0.2 mg, Sera GmbH, Heinsberg, Germany, https://www.sera.de) according to the manufacturer's instructions, and were subsequently rinsed with tepid water (28−29 °C) to help remove any remaining mites, following the recommendations of Castro et al. (2019), Kaplan (2014) and Pasmans et al. (2008).

All lizards were housed individually to prevent co-occupant aggression. The enclosures were designed to meet the basic spatial and behavioural needs of the species, allowing lizards to thermoregulate across a temperature gradient. According to the 'size−diameter' formula by Warwick, Jessop, et al. (2018), 70 cm long enclosures are suitable for the temporary housing of *Podarcis* lizards and comply with European recommendations for minimum enclosure size (e.g. terrestrial lizards up to 20 cm in body length require at least 1600 cm^2: Ewert et al., 2004).

Throughout the experiment, we visually inspected the lizards daily to monitor their wellbeing (Warwick et al., 2013). We also monitored food intake to ensure appropriate feeding and prevent prey from accumulating in the terraria. Observations were conducted from behind a hide to reduce disturbance to the animals and minimize observer effects (Bateson & Martin, 2021; Lehner, 1998). Wooden enrichment devices were sterilized in an oven (120 °C for 2 h) before use. All devices (e.g. the plastic lining of feeding devices, platforms and tiles used for chemical stimuli) were cleaned with water between enrichment phases, and the terraria were cleaned only minimally (removal of faeces, uneaten prey and shed skin) throughout the experiment to maintain hygiene. Thorough cleaning during the experiment was avoided to minimize disturbance because excessive removal of familiar scents has been shown to induce stress and alter behaviour in reptiles (Chiszar et al., 1980; Mendyk & Augustine, 2023). No deaths or injuries occurred during the experiment. Snout−vent length and weight were measured before and after the experiment. On average, lizards gained weight during the experiment (mean initial weight ± SE = 7.57 ± 0.13 g; mean final weight = 7.73 ± 0.11 g). All lizards were released back at their georeferenced capture location after the experiment.

RESULTS

Effect of Enrichment on Behaviour

We found significant interactions between enrichment on/off (enrichment versus no enrichment phases) and group (control versus treatment) for ITB (GLMM: $\chi^2 = 43.62$, $P < 0.001$), walking ($\chi^2 = 9.12$, $P = 0.003$), high perching ($\chi^2 = 5.03$, $P = 0.025$), tongue-flicking rate ($\chi^2 = 35.76$, $P < 0.001$) and basking ($\chi^2 = 7.44$, $P = 0.006$), but not for total basking ($\chi^2 = 1.84$, $P = 0.175$; Table S4a). To further explore these interactions, we conducted posthoc pairwise comparisons separately for treatment and control groups. These comparisons showed that ITB, walking, tongue-flicking rate, basking and high perching changed significantly during enrichment periods in the treatment group but not in the control group (Table S4b). Within the treatment group, high perching (Fig. S3c), ITB (Fig. 3a) and basking (Fig. 3b) decreased, whereas walking (Fig. 3c) and tongue-flicking rate (Fig. 3d) increased during enrichment periods compared with no enrichment periods. Hiding and head out did not change significantly between enrichment and no enrichment periods in either the control or treatment groups (Fig. S3).

In the model evaluating the effect of enrichment type on behaviour (Table 2), we found a significant effect of enrichment type on ITB ($\chi^2 = 45.04$, $P < 0.001$), walking ($\chi^2 = 20.90$, $P < 0.001$), hiding ($\chi^2 = 16.07$, $P = 0.001$), basking ($\chi^2 = 195.24$, $P < 0.001$), high perching ($\chi^2 = 9.29$, $P = 0.026$) and tongue-flicking rate ($\chi^2 = 46.18$, $P < 0.001$). In contrast, no significant effect of enrichment type was found for head out ($\chi^2 = 2.95$, $P = 0.399$). Pairwise comparisons (Table S5) using Tukey's honest significant difference (HSD) test showed that all three enrichment interventions decreased ITB (chemosensory: $P = 0.021$; nutritional: $P < 0.001$; thermal: $P < 0.001$; Fig. 4a) and increased tongue-flicking rate relative to baseline (chemosensory: $P < 0.001$; nutritional: $P < 0.001$; thermal: $P < 0.001$). There was no difference in tongue-flicking rate between the three enrichment types (Fig. 4d). However, chemosensory enrichment resulted in a significantly smaller

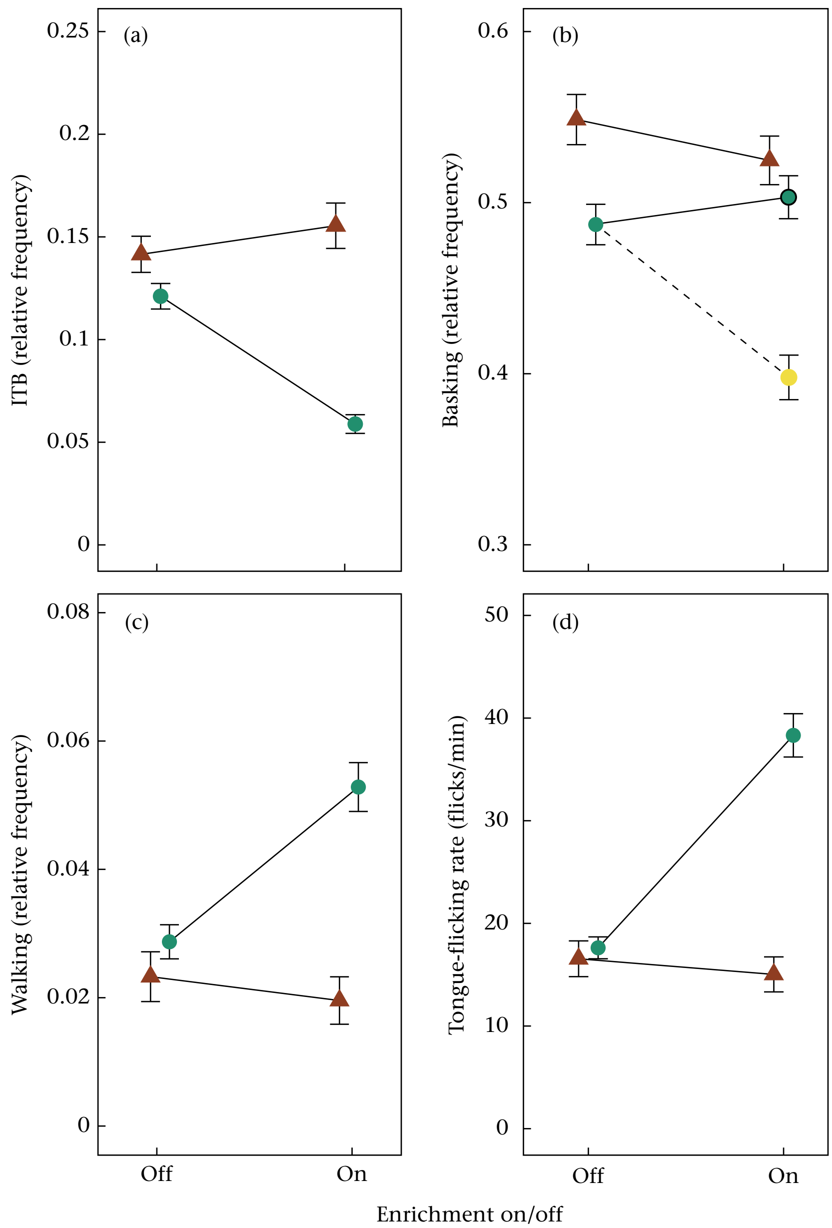

Figure 3. Mean relative frequency (± SE) for (a) interaction with transparent boundaries (ITB), (b) basking, (c) walking and (d) tongue-flicking rate according to whether enrichment was present (on) or absent (off). Brown triangles represent the control group ($N = 6$) and green circles represent the treatment group ($N = 18$). In (b), the dashed line and yellow data point indicate time spent basking on the basking stones, whereas the solid line and green data point with a black outline indicate total basking time.

Table 2
Results from generalized linear mixed models assessing the effect of enrichment type on the occurrence of behaviours in treatment animals ($N = 18$) during scan sampling

Behaviour	Model	χ^2	*df*	*P*
ITB	ITB ~ enrichment type	45.04	3	**<0.001**
Basking	Basking ~ enrichment type	195.24	3	**<0.001**
Total basking	Total basking ~ enrichment type	6.62	3	0.085
Walking	Walking ~ enrichment type	20.90	3	**<0.001**
Hiding	Hiding ~ enrichment type	16.07	3	**0.0011**
Head out	Head out ~ enrichment type	2.95	3	0.399
High perching	High perching ~ enrichment type	9.29	3	**0.026**
Tongue-flicking rate	Tongue-flicking rate ~ enrichment type	46.18	3	**<0.001**

Tukey's post hoc contrast tables can be found in Table S5, illustrating which enrichment types had a significant effect on behaviour relative to baseline. All models included an offset term, and lizard identity and experimental day as random effects. Significant effects ($P < 0.05$) are highlighted in bold. ITB = interaction with transparent boundaries; total basking = the sum of basking and basking on the platform.

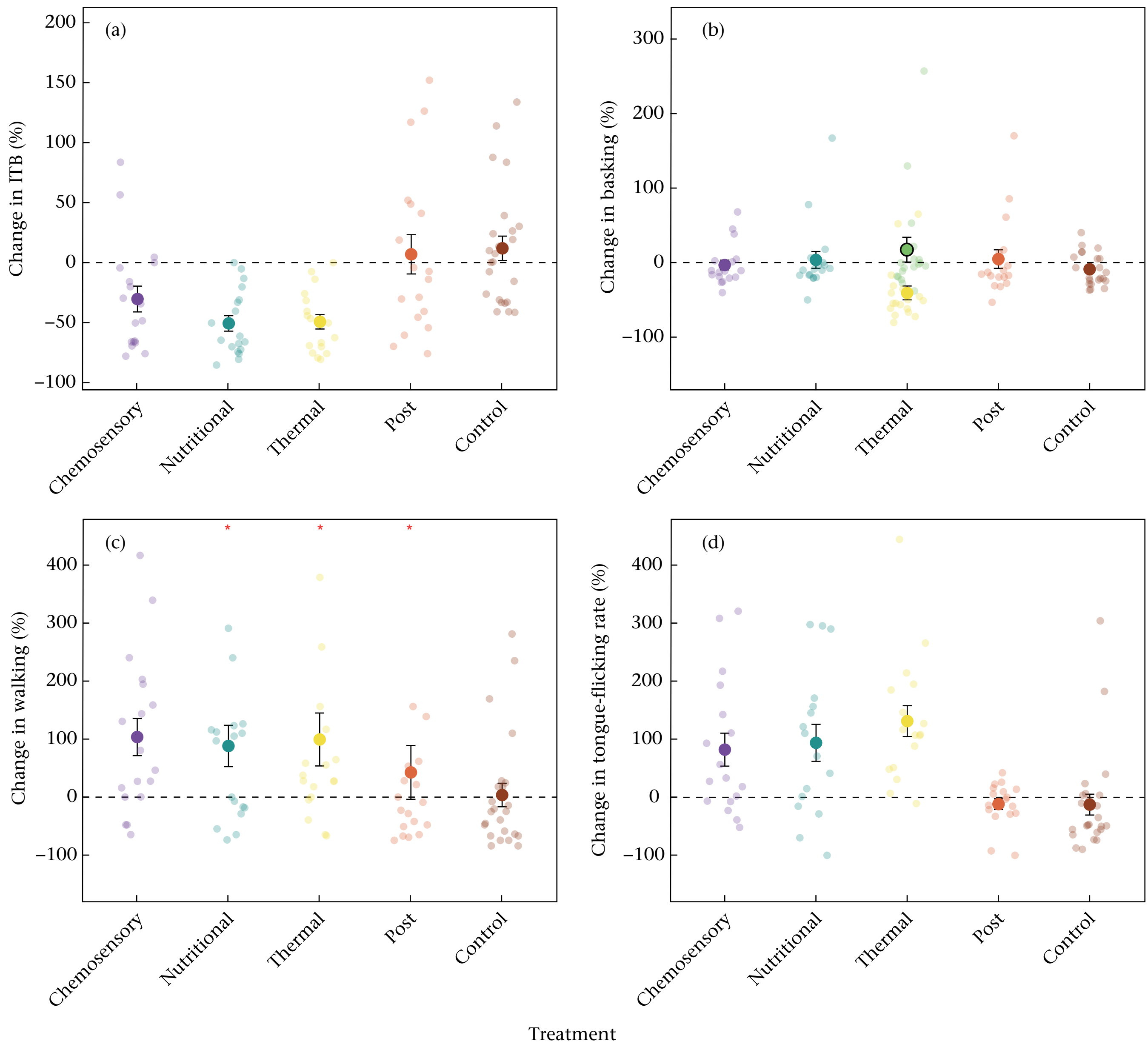

Figure 4. Mean percentage change (± SE) relative to baseline for (a) interaction with transparent boundaries (ITB), (b) basking, (c) walking and (d) tongue-flicking rate. Data were normalized relative to individual baseline values, with each animal acting as its own control. For each individual and day, we calculated behaviour rates (BR) and then computed relative changes from baseline as (BR during treatment − BR during baseline)/BR during baseline. We added a constant (pseudocount = 0.009) to all values to minimize visual distortions caused by zero baseline values. Values above the dashed line indicate increases relative to baseline, whereas values below the line indicate decreases. In (b), yellow points indicate basking on the basking stones, whereas green points with a black outline indicate total basking time. Red asterisks indicate outlying data points.

reduction in ITB relative to baseline (Fig. 4a). Similarly, the three enrichment interventions significantly increased hiding relative to baseline (chemosensory: $P = 0.004$; nutritional: $P = 0.014$; thermal: $P = 0.001$; Fig. S4a). Nevertheless, this effect may not be attributable to enrichment, as the analysis including phase as a factor showed that the increase was also significant in control lizards (control: $\chi^2 = 40.47$, $P < 0.001$; treatment: $\chi^2 = 40.87$, $P < 0.001$; Table S6). Post hoc analyses (Table S5) also showed that both chemosensory and thermal interventions led to a significant increase in walking (chemosensory: $P < 0.001$; thermal: $P = 0.021$; Fig. 4c), with thermal enrichment also decreasing high perching ($P = 0.045$) compared with baseline (Fig. S4c). Additionally, nutritional enrichment produced a marginally nonsignificant increase in walking ($P = 0.078$; Fig. 4c). Analyses of the effect of phase on the remaining behaviours can be found in the Supplementary Material (Fig. S5, Table S6). Percentages of activity budgets during baseline, post-treatment and the three enrichment interventions for both scan and focal data are presented in Table S3a and S3b, respectively. The occurrence of event behaviours for both scan and focal data is presented in Table S7.

Temporal Enrichment Effects

We did not find a significant interaction between enrichment type and phase in the model evaluating the effect of enrichment type across enrichment phases on EEO (GLMM: $\chi^2 = 2.34$, $P = 0.310$), although we found a significant main effect of enrichment type ($\chi^2 = 29.7$, $P < 0.001$; Fig. 5a, Table 3). Tukey's HSD tests

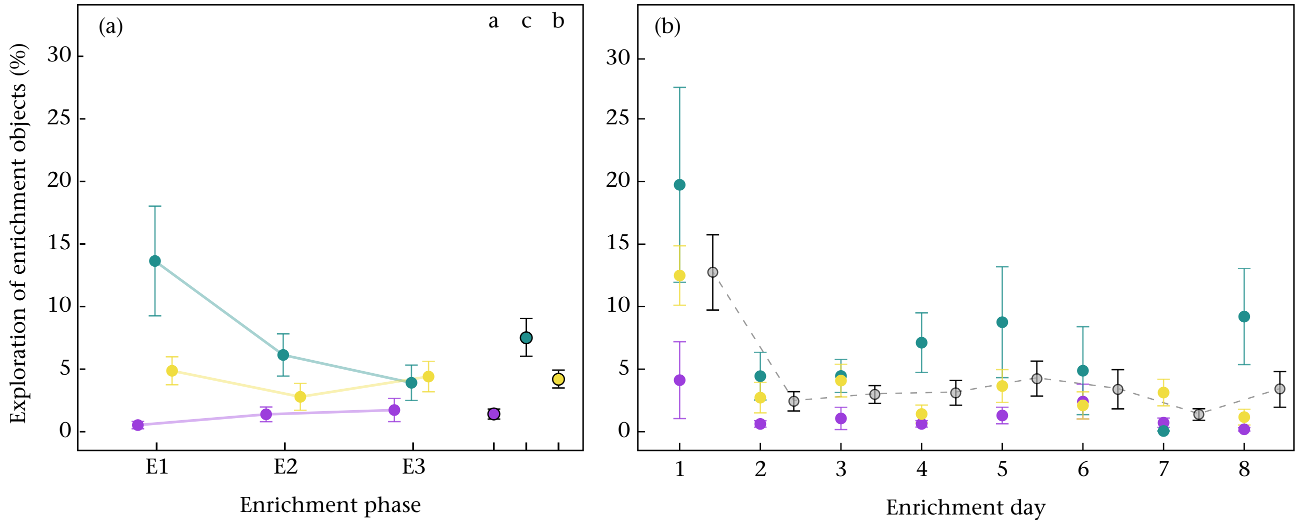

Figure 5. Mean percentage (± SE) of exploration of enrichment objects (EEO) (a) across enrichment phases and (b) within enrichment phases. (a) shows mean percentage of EEO during each phase (E1, E2 and E3) for each type of enrichment ($N = 6$, as the experiment was counterbalanced, with six lizards receiving a different type of enrichment in each phase). Coloured data points with a black outline show mean overall EEO for each enrichment type. Purple indicates chemosensory, blue indicates nutritional and yellow thermal enrichment. Letters indicate a compact letter display from post hoc pairwise comparisons. Means not sharing a letter differ significantly ($P < 0.05$) according to Tukey tests. (b) shows mean percentage of EEO within the enrichment phase ($N = 18$, with means calculated for each day across E1, E2 and E3). Open data points with a black outline show mean overall EEO for each day within each enrichment phase.

Table 3
Results from generalized linear models examining the effects of enrichment type and its interaction with enrichment phase and enrichment day on exploration of enrichment objects (EEO) in treatment animals ($N = 18$) during focal sampling

Behaviour	Model	Term	χ^2	*df*	*P*
EEO	EEO ~ enrichment type *enrichment phase	Enrichment type*enrichment phase	2.34	2	0.310
		Enrichment type	29.70	2	**<0.001**
		Enrichment phase	0.20	1	0.657
	EEO ~ enrichment type *enrichment day	Enrichment type*enrichment day	4.04	2	0.133
		Enrichment type	36.02	2	**<0.001**
		Enrichment day	15.38	1	**<0.001**

Models included an offset term and lizard identity as a random effect. Statistics for nonsignificant interactions are reported at the point of their removal from the model. Significant effects ($P < 0.05$) are highlighted in bold.

showed that the three enrichment types differed significantly from one another (chemosensory versus nutritional: $P < 0.001$; chemosensory versus thermal: $P = 0.008$; nutritional versus thermal: $P = 0.008$). Overall, lizards interacted most with the nutritional enrichment device (mean percentage of time ± SE = 7.39 ± 1.50%), followed by thermal enrichment (4.06 ± 0.66%) and the chemosensory enrichment (1.28 ± 0.40%; Table S3b). Other enrichment-directed behaviours included basking on the platforms, which was preferred by lizards during thermal enrichment (36.12 ± 3.60%) compared with basking on the basking stones (19.98 ± 3.63%) and feeding from the nutritional device, which was very infrequent (0.18 ± 0.13%; Table S3b). The device was used during a mean of 69.44% of the total enrichment periods across the experiment, with 36.56% of the larvae provided being consumed (Table S8). We did not find a significant interaction between enrichment type and enrichment day in the model evaluating the effect of enrichment type on EEO within enrichment phases (GLMM: $\chi^2 = 4.04$, $P = 0.133$). We found significant main effects of enrichment day ($\chi^2 = 15.38$, $P < 0.001$) and enrichment type ($\chi^2 = 36.02$, $P < 0.001$; Fig. 5b–Table 3).

We next assessed whether the effects of enrichment on behaviour persisted after removal. We did not detect a significant enrichment*subphase interaction for any of the behaviours analysed, although we found a marginally nonsignificant interaction for tongue-flicking rate (GLMM: $\chi^2 = 5.42$, $P = 0.067$). We detected a significant main effect of subphase for all behaviours (Fig. S6, Table S9). We conducted post hoc pairwise comparisons to identify between which subphases the most pronounced changes occurred. Table 4 presents the changes in behavioural duration (rate in the case of tongue flicking) between consecutive phases (ratios with 95% confidence intervals) for the behaviours analysed. We observed the largest decrease in walking, high perching and tongue flicking between subphases 4 and 5 (Fig. S6), that is, after enrichment removal (Table 4). In contrast, we observed an increase in ITB across phases (except between postenrichment subphases; Fig. S6a). This change was more pronounced between subphases 3 and 4, with a ratio of 1.84 (1.05–3.22), and was similar to the change after enrichment removal (between subphases 4 and 5), with a ratio of 1.83 (1.04–3.22); that is, between these subphases, the duration of ITB almost doubled (Table 4). Mean values per subphase for the behaviours analysed can be found in the Supplementary Material (Table S10).

FCMs

We found an effect of enrichment type on FCM levels in both the 37e assay (LMM: $\chi^2 = 19.59$, $P = 0.002$; Fig. 6a) and the 72T assay ($\chi^2 = 37.21$, $P < 0.001$; Fig. 6b). Post hoc pairwise comparisons showed a significant increase in FCM levels following chemosensory enrichment relative to acclimatization for both assays

Table 4
Changes between consecutive subphases expressed as ratios (95% confidence intervals) for the behaviours analysed in relation to the persistence of enrichment effects in treatment animals ($N = 18$)

Contrast	ITB	Walking	High perching	Tongue-flicking rate
E2/E1	0.99 (0.57–1.73)	0.94 (0.61–1.46)	0.70 (0.39–1.23)	0.82 (0.57–1.19)
E3/E2	0.74 (0.42–1.28)	1.08 (0.70–1.65)	1.19 (0.67–2.12)	0.97 (0.68–1.39)
E4/E3	**1.84** (1.05–3.22)	0.84 (0.54–1.29)	1.02 (0.56–1.85)	0.85 (0.60–1.22)
POST1/E4	1.83 (1.04–3.22)	**0.70** (0.45–1.07)	**0.68** (0.37–1.25)	**0.59** (0.41–0.85)
POST2/POST1	0.79 (0.44–1.43)	1.04 (0.66–1.64)	0.97 (0.51–1.83)	0.80 (0.54–1.18)

We were interested in identifying the consecutive subphases between which the most pronounced changes in the response variables occurred. Therefore, we examined contrasts exclusively between consecutive subphases. Values highlighted in bold represent the contrasts showing the greatest increase (ratios > 1) or decrease (ratios < 1) for each behaviour. ITB = interaction with transparent boundaries.

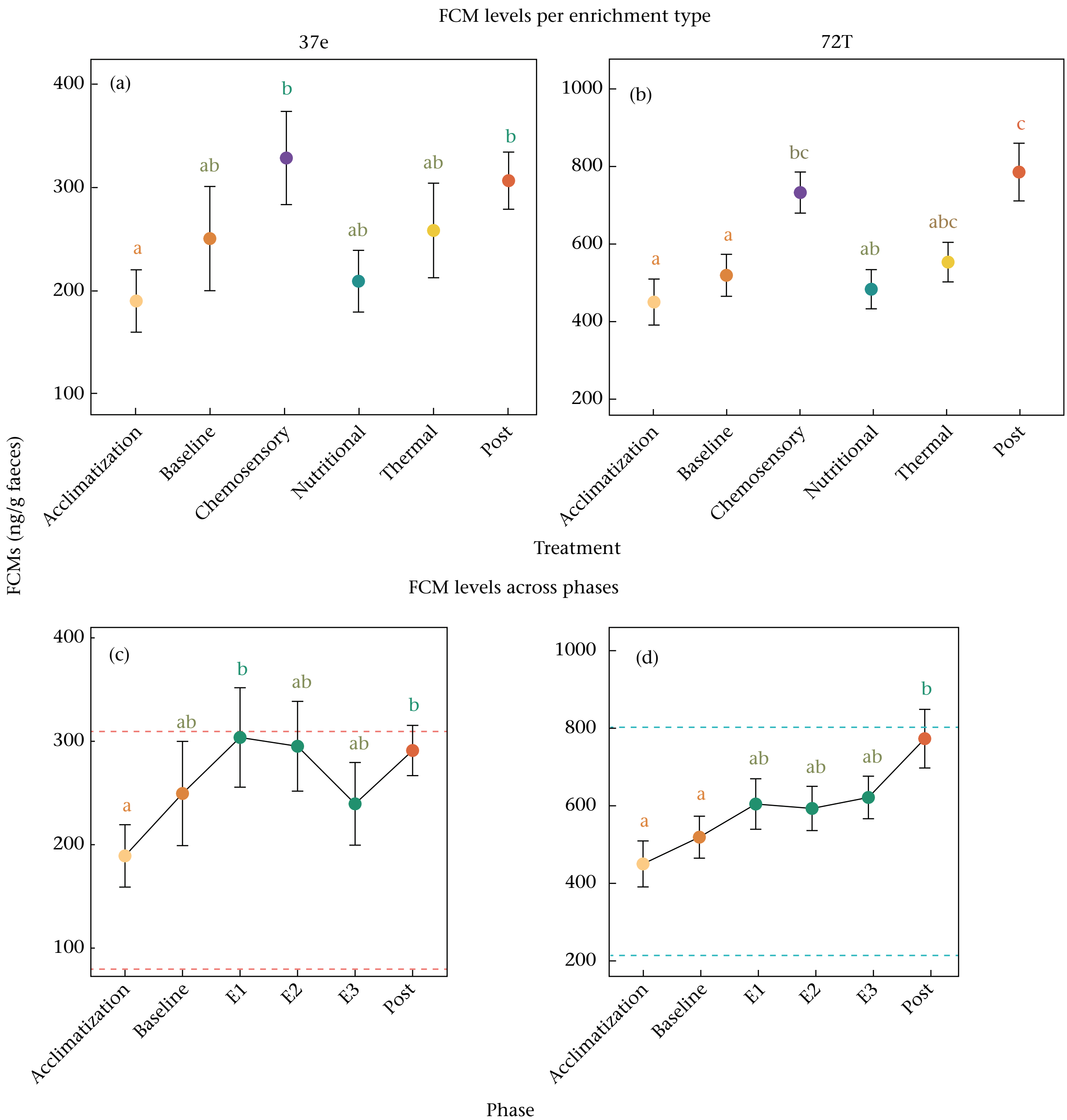

Figure 6. Mean faecal corticosterone metabolite (FCM) levels (ng/g ± SE) for lizards in the treatment group ($N = 18$), measured within each enrichment treatment using the (a) 37e and (b) 72T assays and across phases using the (c) 37e and (d) 72T assays. Dashed lines in (c) and (d) represent the range of individual FCM variation observed during the baseline period of the validation experiment for *Podarcis muralis* (Bartolomé et al., 2025). Purple data points indicate chemosensory, blue indicate nutritional and yellow thermal enrichment. Letters represent a compact letter display from post hoc pairwise comparisons (see Table S11). Means not sharing a letter differ significantly ($P < 0.05$) according to Tukey tests.

(Table S11a). Compared with baseline levels, we found a significant effect of chemosensory enrichment in the 72T assay and a marginally nonsignificant effect in the 37e assay (Table S11a). We found a significant overall effect of phase in both the 37e assay ($\chi^2 = 18.62$, $P = 0.006$; Fig. 6c) and the 72T assay ($\chi^2 = 31.01$, $P < 0.001$; Fig. 6d). The mean phase increase in FCM levels throughout the experiment was 3.55% and 10.98% for the 37e and 72T assays, respectively. Post hoc pairwise comparisons for the 37e showed a significant increase in FCM levels between the acclimatization and post-treatment periods (Table S11b). For the 72T assay, we also found increases in FCM levels from both the acclimatization and baseline phases to the post-treatment phase and a marginally nonsignificant increase from the acclimatization phase to the first enrichment period (Table S11b).

Finally, to evaluate whether changes in FCM concentration over the course of the experiment differed between enrichment and no enrichment phases (Table 5), we analysed the interaction between day within phase and enrichment on/off, which was significant for the 37e assay ($\chi^2 = 7.73$, $P = 0.005$) and marginally nonsignificant for the 72T assay ($\chi^2 = 3.43$, $P = 0.064$; Table 5, Fig. S7). This indicates that the increase in FCM levels differed between phases in which the treatment group received enrichment and the remaining phases. A summary of mean FCM levels for control and treatment groups is provided in the Supplementary Material (Table S12).

DISCUSSION

In this study, we tested three types of enrichment for *P. muralis* and evaluated their effects using behavioural and physiological indicators. All three enrichment interventions increased normal behaviours (exploration) and decreased an abnormal behaviour (ITB). The effects of enrichment on these behaviours tended to return to baseline levels once the enrichment was removed. Physiological data showed an increase in FCM levels over the course of the experiment, although this increase was less pronounced during enrichment phases. Overall, our results suggest that enrichment improved welfare, highlighting the importance of designing and evaluating enrichment that is informed by species-specific behaviour.

Effect of Enrichment on Behaviour: Welfare

Enrichment produced behavioural changes associated with improved welfare. We observed increases in walking and tongue-flicking rate during all enrichment types. Exploratory behaviours, such as locomotion and tongue flicking, are associated with positive welfare and are considered intrinsically reinforcing (Benn et al., 2019; Boissy et al., 2007; Mellor, 2015; Warwick et al., 2013). However, interpretation is not always straightforward. Tongue flicking, an indicator of chemical exploration (Burghardt et al., 1986), increases in novel environments or with novel objects (Greenberg, 1993; Moszuti et al., 2017) but may also reflect arousal due to stress or fear (Greenberg, 2002). More specifically, changes in the type of tongue-flicking behaviour (air licks versus tongue touches; see Table 1) have been shown to differ depending on novelty or stress-inducing conditions (e.g. *A. carolinensis*: Greenberg, 1985) and husbandry conditions, including enrichment (e.g. *Pogona vitticeps*: Crisante et al., 2025). These examples highlight the importance of considering taxon-specific differences and suggest that distinguishing between different tongue-flicking behaviours may provide additional insights into affective states in other species or contexts. Similarly, locomotion needs to be interpreted according to the behavioural context (Watters et al., 2021). In captivity, perimeter pacing is often associated with stereotypic behaviour (Warwick, 2023), making it crucial to distinguish between locomotion types. We defined walking as slow-paced locomotion (usually accompanied by tongue flicking: Greenberg, 1993; Warwick et al., 2013) and ITB as rapid pacing with scratching or snout rubbing (Divers, 1999; Warwick, 1990). ITB is one of the most frequent abnormal behaviours in captive reptiles and can cause physical damage, such as rostral abrasions (McCracken et al., 2017; Warwick et al., 2013). Our findings for *P. muralis* are consistent with previous studies. For example, conspecific scents in a closely related species, *Podarcis liolepis*, reduced ITB and facilitated habituation in exploration tests (Londoño et al., 2018). Similarly, structural enrichment increased activity and hiding opportunities in corn snakes, *Pantherophis guttatus* (Hoehfurtner et al., 2021), and chuckwallas, *Sauromalus ater* (Rose et al., 2014), as well as reducing abnormal behaviour in the latter.

In contrast to exploratory and abnormal behaviours, hiding appeared largely unaffected by enrichment. Providing sufficient shelters for reptiles is a crucial part of their husbandry (Arena & Warwick, 2023; Hennig & Dunlap, 1978). However, excessive hiding can be problematic if it impairs other behaviours such as feeding or thermoregulation (Warwick, 2023; Warwick et al., 2013). In reptiles in particular, abnormal hiding has been proposed to be specifically associated with behaviours such as persistent head hiding (Johnson, 2017; Warwick et al., 2013). In our study, hiding behaviour did not increase in response to enrichment and was not associated with suppression of other behaviours. Moreover, we did not observe head-hiding behaviour. Given that increases in hiding frequency occurred across all phases (including post-treatment) and in both control and treatment groups, this change may reflect a general trend associated with captivity. Therefore, prolonged increases in hiding could potentially interfere with normal behaviour and should be considered when interpreting behavioural responses in captive reptiles.

Finally, our results regarding the effects of enrichment on welfare-related behaviours must be interpreted within the broader context of reptile husbandry. Captive environments for

Table 5
Results from linear mixed models evaluating the effect of day within phase and its interaction with enrichment on/off on faecal corticosterone metabolite (FCM) levels in treatment lizards ($N = 18$) using two enzyme immunoassays (EIAs): 37e and 72T

EIA	Model	Term	χ^2	*df*	P
37e	LogFCM ~ day within phase*enrichment on/off	Day within phase *enrichment on/off	7.73	1	**0.005**
		Day within phase	0.64	1	0.422
		Enrichment on/off	8.10	1	**0.004**
72T	LogFCM ~ day within phase*enrichment on/off	Day within phase *enrichment on/off	3.43	1	*0.064*
		Day within phase	1.43	1	0.232
		Enrichment on/off	3.32	1	*0.069*

Day within phase refers to the days in which faecal samples were collected during each experimental phase, whereas enrichment on/off refers to phases in which enrichment was provided to the treatment group or to periods without enrichment. All models included lizard identity and experimental day as random effects. Statistics for nonsignificant interactions are reported at the point of their removal from the model. Significant effects ($P < 0.05$) are highlighted in bold. Marginally nonsignificant effects are noted in italics.

reptiles are often impoverished (Arena & Warwick, 2023; Burghardt, 1996; Warwick et al., 2019), and enrichment studies frequently use baseline conditions that do not meet the species' basic husbandry and behavioural requirements, or compare enrichment interventions with barren conditions (Borgmans et al., 2018; Nagabaskaran et al., 2021; Roe et al., 2015). In some cases, enrichment proposals are in fact basic husbandry rather than true enrichment (see Bartolomé et al., 2023; Mendyk & Augustine, 2023). What constitutes enrichment may also vary depending on context and specific management objectives (Meehan & Mench, 2007). In our study, we therefore focused on enrichment strategies that were easy to implement and relevant to laboratory-housed reptiles. Prior to enrichment, enclosures were designed to meet the species' basic needs, providing adequate space and a thermal gradient (Ewert et al., 2004; Warwick, Jessop, et al., 2018), substrate (Griffing et al., 2018; Wilkinson, 2015) and diverse shelters and textures following an ethologically informed approach (Greenberg, 2023).

Effect of Enrichment on Behaviour: Ethological Validity

Thermal enrichment

A thermal gradient that includes the species' preferred temperature should be considered a basic husbandry requirement for captive reptiles (Burghardt & Layne-Colon, 2023; Lillywhite, 2023). Thermal opportunities depend on spatial constraints and can thus be limited in captivity (Arena & Warwick, 2023). The inclusion of structural complexity can provide reptiles with a greater degree of control and choice over their environment (Rust et al., 2024), increasing thermal flexibility and climbing opportunities and promoting physical activity (Almli & Burghardt, 2006; Bashaw et al., 2016; Rose et al., 2014). In our study, we ensured that the enclosures provided a complex thermal gradient including the preferred temperature range for *P. muralis*, with enrichment basking platforms reaching temperatures above this range. In our experiment, thermoregulatory behaviour was largely unaffected by enrichment. The apparent decrease in basking during thermal enrichment is artefactual, as basking referred only to time on the basking stones, whereas total basking showed only a small increase. This suggests that lizards were not exposed to suboptimal thermal conditions prior to enrichment. Such conditions may otherwise induce compensatory behaviours such as hyperbasking, characterized by excessive basking due to an inability to reach preferred body temperatures (Warwick et al., 2013).

Nutritional enrichment

Enrichment that promotes naturalistic feeding has been shown to change behavioural profiles of different species, suggesting improved welfare (Fernandez & Timberlake, 2019; Hocking et al., 2015; Waterman et al., 2021; Whilde et al., 2021). In our study, we used a feeding trunk similar to those used in studies with monitor lizards (Mendyk & Horn, 2011), which allows active foragers such as *P. muralis* to express a range of natural foraging behaviours (e.g. climbing, jumping or exploring crevices). In our experiment, we were able to track device use and number of prey consumed, but observations of feeding from the log (i.e. feeding from nutritional device) were rare. However, lizards interacted with the feeding trunk in other ways, such as basking on its upper surface. The incidental use of the device is consistent with other studies showing that lizards use vertical and structurally complex elements of their environment (Abalos et al., 2020; Avery et al., 1993), even in primarily ground-dwelling species (Bashaw et al., 2016; Rose et al., 2014). Although we did not measure the temperature on top of the device, it is possible that the proximity to the lightbulb increased the temperature of the wood, making it attractive for thermoregulation. Therefore, the positive changes observed in behaviour could be partially due to the structural and/or thermal aspects of the device.

Our device could be modified into a puzzle feeder to increase its complexity (Leal & Powell, 2011; Manrod et al., 2008; Pérez i de Lanuza, Ábalos, Bartolomé, & Font, 2018). Provision of problem-solving opportunities that engage a species' cognitive processes may help maintain interest in enrichment and improve psychological wellbeing (Krebs & Watters, 2017; Watters, 2009). Given the growing evidence on reptiles' cognitive abilities, which challenges the traditional view of reptiles as limited and passive animals (Burghardt, 2020; Font, 2019, 2020; Font et al., 2023; LaDage et al., 2012), cognitive enrichment appears to be a promising avenue of research for this understudied group (Clark, 2017, 2020; Garcia-Pelegrin et al., 2022).

Chemosensory enrichment

Wall lizards rely on chemical stimuli in many contexts, including the assessment of conspecific familiarity and individual recognition (Carazo et al., 2007, 2008; Font & Desfilis, 2002). In our experiment, the choice of chemical stimuli was therefore grounded in the species' natural chemosensory behaviour, in which male wall lizards actively patrol their territories to gather information about neighbouring or intruding rivals and potential mates, exploring scent marks, especially new or displaced ones (Carazo et al., 2008; Font, Barbosa, et al., 2012). An increase in exploration rates in response to conspecific scents, as observed in the present study, was therefore expected. Frequent renewal of odours in our experimental design simulated a functional challenge that lizards naturally encounter in their environment, which could potentially make this intervention less prone to habituation than other stimuli (i.e. external reinforcers: Tarou & Bashaw, 2007). Two aspects should be considered regarding the ethological validity and future application of this type of enrichment.

First, although territorial behaviour dominates much of *P. muralis* and other territorial species' daily activity during the reproductive season (Edsman, 1989), responses to scent marks and exploratory behaviour vary seasonally (Baird et al., 2008; Carazo et al., 2007; Jenssen et al., 1995). Second, male and female *Podarcis* lizards differ in their chemosensory behaviour and use of chemical stimuli (Barbosa et al., 2006; Carazo et al., 2011; Font, Barbosa, et al., 2012). Responses to enrichment may therefore vary between sexes and seasons and this should be taken into account when using chemical stimuli as enrichment. Other chemosensory stimuli, such as snake scent or bedding from mammal exhibits, have been used in leopard geckos and monitor lizards (Bashaw et al., 2016; Waterman et al., 2021), producing similar increases in exploration to those observed in our study. Nevertheless, chemosensory enrichment remains relatively understudied in reptiles (Bartolomé et al., 2023) and other taxa, with most existing studies focusing on felids and primates (Clark & King, 2008).

Overall, all three enrichment interventions had similar effects on welfare-related behaviours. This may be because they all targeted basic, functionally relevant aspects of behaviour, eliciting intrinsically motivated responses such as scent exploration, a form of information gathering (Boissy et al., 2007). However, inspective exploration (i.e. exploration in response to change) typically declines as novelty fades (Veissier et al., 2024), so the temporal dynamics of enrichment should be considered when evaluating their impact.

Temporal Dynamics of Enrichment Effects

Lizards engaged with enrichment devices in all phases of the experiment, although enrichment-directed behaviours decreased within each phase, particularly after the first day. Similarly, Waterman et al. (2021) found that engagement with enrichment in monitor lizards waned significantly within sessions for both nutritional and sensory enrichment. It is important to note that our behavioural category exploration of enrichment objects (EEO) includes a behaviour exclusive to chemosensory enrichment (enrichment-directed tongue flicks; Table 1), so direct comparisons with the other two enrichments may not be appropriate. However, it provides insight into how lizards engaged with each type of enrichment. For chemosensory enrichment, we collected scents from the basking stones using filter paper, which may include faeces and other sources of semiochemicals, such as femoral secretions or skin lipids (Font, Barbosa, et al., 2012; Font & Desfilis, 2002). As we lack information on the active space of lizard scent marks, we probably underestimated the percentage of EEO during chemosensory enrichment, given our conservative description of this behavioural category (i.e. touch and/or tongue flicks directly on top of or within a distance no greater than the lizard's head length from the stimulus; Table 1).

We also evaluated whether behavioural changes persisted after enrichment removal. We found that behaviours affected by enrichment tended to return to baseline levels after enrichment withdrawal. Maintaining the efficacy of enrichment over time (i.e. avoiding enrichment protocols becoming ‘band-aid solutions’: Markowitz & Aday, 1998) has proven to be difficult (Mellen & Sevenich MacPhee, 2001). Enrichment can be kept ‘enriching’ (Kuczaj et al., 2002) by adopting strategies to avoid habituation or reinforce desired behaviours (see Tarou & Bashaw, 2007). Strategies such as alternating enrichment types, increasing unpredictability of enrichment presentation, avoiding prolonged use of the same enrichment and varying exposure time have all been shown to be effective (Bassett & Buchanan-Smith, 2007; Watters, 2009; Watters et al., 2011). However, some evidence suggests that continuous rather than intermittent exposure may yield longer-lasting effects, such as reduced stereotypies (Anderson et al., 2010). Other studies show that enrichment duration influences both impact and persistence, with longer periods associated with improved learning (Ahlbeck Bergendahl et al., 2016) and faster habituation to novelty (Amaral et al., 2008).

Effect of Enrichment on FCMs

We observed an overall increase in FCM concentration over time, although this increase was less marked during enrichment than during no enrichment phases. Captivity alone can impose restrictive and potentially aversive conditions (Carlstead & Shepherdson, 2000; Morgan & Tromborg, 2007) that can increase stress-related hormone levels (Martín et al., 2023; Sparkman et al., 2014). If these conditions are sustained, they can lead to chronic stress, impairing health and welfare (Dantzer et al., 2014; Sapolsky et al., 2000). Data from the validation study for FCM measurement in this species (Bartolomé et al., 2025) can help contextualize the observed changes in our experiment. Despite the overall increase in FCMs, levels remained below the upper range of variation during the baseline period of the validation, indicating that the increase did not fall within elevated levels for the animals and did not indicate chronic stress.

Prior studies on the effects of enrichment on glucocorticoid levels have reported mixed results (decrease: Boinski et al., 1999; increase: Marashi et al., 2003; no effect: de Almeida et al., 2018). Although information on reptiles is scarce (Borgmans et al., 2018; Case et al., 2005; Rosier & Langkilde, 2011), evidence from mammals and birds shows that enrichment can increase an animal's capacity to cope with sporadic stress-inducing situations, improving adaptation to captivity (Carlstead & Shepherdson, 2000), and that long-term exposure to enrichment may reduce levels of glucocorticoid metabolites even after an initial increase (Fairhurst et al., 2011), consistent with our observation that enrichment attenuated FCM elevation. A limitation of the present analysis is that FCM data from control animals could not be included due to the low number of samples obtained (Table S12). Low defaecation rates are a well-known constraint in reptiles and can limit the applicability of noninvasive glucocorticoid measurements (Bartolomé et al., 2025; Borgmans et al., 2018; Ganswindt et al., 2014). As a result, changes in FCM levels could not be directly compared between treatment and control groups. However, the experimental design followed a single-subject approach, allowing meaningful evaluation of within-individual changes in FCM levels in response to enrichment, which was the primary aim of the study.

We also observed a small increase in FCMs during chemosensory enrichment, which is to be expected after perception of conspecific scents (Barja et al., 2011; Watson et al., 1999). Short-term stress responses can have beneficial effects, influencing an animal's physiological and behavioural responses to overcome the stressor, and enhancing exploration, learning or immunity (Bassett & Buchanan-Smith, 2007; Carlstead & Shepherdson, 2000; Meehan & Mench, 2007). Additionally, an animal's perception of the stimulus and surrounding context influence the valence of the response to a stressful situation (Veissier & Boissy, 2007). In our experiment, lizards were exposed to other males' scents, but they never encountered the potential rival, thereby avoiding the costs of an agonistic encounter. Nevertheless, although short-term stress may not necessarily have a negative impact on welfare, it is important to manage it to prevent it becoming chronic (Moberg, 2000).

Although the present results should be considered preliminary, they provide a first empirical reference for FCM variation in *P. muralis* in captivity and under enrichment conditions. Future studies should consider that low defaecation rates may limit the application of noninvasive glucocorticoid measurements in reptiles and that physiological data should be interpreted within the framework of natural FCM variability and combined with complementary measures (e.g. behavioural indicators) to obtain an integrated assessment of welfare.

Conclusions

Our results show that environmental enrichment can promote normal behaviour and reduce indicators of poor welfare in *P. muralis*. Behavioural effects were consistent across enrichment types but did not persist after enrichment was removed. The attenuated rise in FCMs during enrichment suggests a potentially beneficial physiological response, although further research is needed given the limited knowledge of stress-related indicators in reptiles (Benn et al., 2019; Carbajal et al., 2024). We emphasize the need for an integrated approach to enrichment evaluation, incorporating multiple welfare indicators that have been carefully selected and previously validated. Our findings support the growing recognition that reptiles, like other vertebrates, benefit from enrichment strategies that consider species-specific traits and use an ethologically informed design (Greenberg, 2023). We propose that the strategies used here could be adapted for other reptile species, provided that species-specific and individual differences are considered and efficacy is continually assessed within an evidence-based framework.

Author Contributions

Alicia Bartolomé: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rupert Palme:** Writing – review & editing, Supervision, Resources. **Sabine Macho-Maschler:** Writing – review & editing, Investigation. **Pau Carazo:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Enrique Font:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization.

Data Availability

The complete data set and R code used for analyses are available as Supplementary Material.

Declaration of Interest

None.

Acknowledgments

We thank James Waterman and Luis M. Carrascal for their help with the statistical analysis of this study. We also thank Claudia Londoño and Javier Ábalos for their valuable statistical advice and support, and Carla Salcedo and Ferrán de la Cruz for their help during lizard capture. A.B. was supported by a Formación de Profesorado Universitario predoctoral fellowship from the Spanish Ministerio de Universidades (FPU18/04021). This project was funded in part by a grant from the Spanish Ministerio de Ciencia e Innovación (PID2019-104721GB-IOO).

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123692.

The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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