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Does post-natal parental care influence cognitive development in a social gecko?

Birgit Szabo [a, b] *, Eva Ringler [a]

[a] Division of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

[b] Centre for Research on Ecology, Cognition and Behaviour of Birds, University of Gent, Belgium

*Correspond to: Birgit Szabo, Division of Behavioural Ecology, University of Bern, 3032 Bern, Switzerland; email: birgit.szabo@gmx.at,

ORCID BS: 0000-0002-3226-8621

ORCID ER: 0000-0003-3273-6568

Abstract

How cognition evolved remains a debated “hot-topic” in the field of animal cognition. Current hypotheses link variation in sociality, ecology, and more generally, environmental challenges to differences in cognitive development, both between as well as within species. Research supporting the Social Intelligence Hypothesis, which states that cognition evolved to deal with social challenges, is largely focused on highly social mammal and bird species, limiting our ability to evaluate the general applicability of the hypothesis. Unfortunately, developmental studies which can reveal the causal link between early life experiences and cognitive development are scare. The aim of this study was to test the effect of the early post-natal social environment on the development of neophobia, exploration, food motivation, habituation and associative learning in a social lizard, the tokay gecko (*Gekko gecko*). We did not find evidence that the early social rearing environment influenced object neophobia. However, our results show that the early social environment influenced the time taken to enter a novel space and the variation in associative learning. We discuss our findings in the light of the Social Intelligence Hypothesis taking into account the facultative sociality nature of our study system. Our study provides new insight into how cognitive benefits associated with group living might have promoted the evolution of more complex social structures in animals.

Keywords: behaviour, cognition, developmental plasticity, fearfulness, squamate, reptile

Background

Cognition is a general term for all neural processes by which individuals collect, retain, process and use information gathered from their environment through the use of exploration, exploitation, or evasion, leading to changes in behaviour that increase survival and fitness (Shettleworth 2009; Lyon 2020). How cognition evolves, what causes differences in cognition and what are the consequences of these differences are still some of the most intensely debated topics in the field. A number of hypotheses have been proposed connecting sociality (Social Intelligence Hypothesis, Humphrey, 1976; Jolly, 1966; Chance and Mead, 1953; Machiavellian Intelligence Hypothesis, Byrne and Whiten, 1988; Social Brain Hypothesis, Dunbar, 1998), ecology (Ecological Intelligence Hypothesis, Rosati, 2017) or more generally challenges in the environment (Cognitive Buffer Hypothesis, Sol et al., 2021) with enhanced cognition. A recent meta-analysis has found general support for the Social Intelligence Hypothesis across inter-, intra- as well as developmental studies (Speechley et al., 2024). This Hypothesis links the demands of leading a social life, such as resource competition, tracking of individual, their status and relationships, or parasite transmission, to the development of enhanced cognitive ability to deal with these challenges (Humphrey, 1976; Jolly, 1966; Chance and Mead, 1953). However, research is still biased towards mammals and birds substantially limiting our ability to generalise the existence of this link across taxonomic groups (Speechley et al., 2024). Therefore, an increase in taxonomic breadth is urgently needed to develop a broad concept of the factors influencing the evolution of cognition.

Research aiming to understand how sociality influences cognitive ability has taken three broad directions: (1) large projects comparing cognitive abilities across species with varying degrees of sociality (e.g. Borrego and Gaines, 2016; Devaine et al., 2017; MacLean et al., 2013; 2014), (2) intraspecific studies that compare cognition across individuals living in differently sized groups or groups with varying social complexity in the wild (e.g. Berhane and Gazes, 2020; Ashton et al., 2018; Wascher, 2015) and (3) controlled developmental studies. Developmental studies utilise developmental plasticity, the development of variation in phenotypic traits resulting from different environmental conditions that are linked to differences in survival and reproductive success (Eastwood et al., 2023; Holloway, 2002; Lee et al., 2013; Lindström, 1999; Uller, 2008). Developmental studies are a powerful tool as they can uncover the causal link between the early social environment (pre- and post-natal) and the development of cognition (e.g. Chapman et al., 2008; Meagher et al., 2015; Schrijver et al., 2002; Toyoshima et al., 2018) and can provide insights into if social challenges select or facilitate the development of cognitive abilities. However, only some of the developmental studies found an early life effect on cognition mostly showing a negative effect of social deprivation (i.e. social isolation or parental deprivation; e.g. Meagher et al., 2015; Toyoshima et al., 2018; but see e.g. Lévy et al., 2003; Riley et al., 2017; 2018). A potential reason for the mixed results might be a weak effect of social interventions (e.g. social isolation or group density; Lambert and Guillette, 2021). The existence and direction of the early life effects might depend on the social system of the tested species as well as the cognition tested (Lambert and Guillette, 2021; Lévy et al., 2003; Speechley et al., 2024). Consequently, it is necessary to investigate the effects of the early social environment on the development of a large range of cognitive abilities as well as in a large range of species expressing diverse sociality to gain a comparative evolutionary perspective (Ward and Webster, 2016).

Various forms of group living (e.g. eusociality, cooperative breeding, fission fusion societies, long- and short-term family groups) have evolved across all major vertebrate groups as well as in invertebrates (Rubenstein and Abbot, 2017), however, research on the Social Intelligence Hypothesis has traditionally focused on primates, rodents and passerine birds (Speechley et al., 2024). Especially studies in reptiles are lacking hampering not just our understanding of the general applicability of the Social Intelligence Hypothesis but also or understanding of what environmental factors influence reptile cognition. For instance, De Meester and colleagues (2019) found evidence that solitary squamates (lizards, snakes and worm lizards) had larger brains, a frequently used proxy for cognitive ability (e.g. Benson-Amram et al., 2016; Lefebvre et al., 2004), compared to social species contradicting the Social Intelligence hypothesis. To the best of our knowledge, no intraspecific studies have been done in reptiles so far, but three studies have looked at how the early social life influences cognition in two species of lizards. Tree skinks (*Egernia striolata*), a group living species, showed similar social and spatial learning ability regardless of if they were reared alone or with a conspecific (age matched social partner; Riley et al., 2017; 2018). While in the White's skink (*Liopholis whitti*), a closely related group living species with a similar social structure, offspring raised with their mother performed better in a learning task (Munch et al., 2018). Consequently, due to the limited number of studies, a large gap is still present as to how different expressions of sociality might affect cognition and what types of cognitive processes are affected. Facultative social species, such as reptiles, provide a powerful comparative model and a chance to look into the benefits of cognition as they might have occurred in early forms of group living.

Therefore, the aim of this study was to test the effect of the early post-natal social environment on the expression of cognition and behaviour in the Tokay gecko (*Gekko gecko*). Behavioural measures were included to ensure that effects on cognition are mainly caused by early-life effects not indirect effects of the early life on personality and motivation (Dougherty and Guillette, 2018; van Horik and Madden, 2016; Völter et al., 2018). More specifically, we investigated how individuals reared in social isolation (without competition from conspecifics) express object and space neophobia (the hesitation to approach or total avoidance of a novel stimulus; Crane et al., 2020), exploration, food motivation, habituation and associative learning as compared to individuals reared in a family group (with competition from conspecifics, i.e. the parents and siblings). Tokay geckos are a social lizard species that form pairs and family groups with biparental care (Grossmann 2007). Adults provide care to their eggs as well as offspring after hatching. Offspring stay with their parents until sexual maturity (7-12 months after hatching) at which point, they are evicted from the territory (Grossmann 2007). Tokay gecko females lay up to two eggs every approximately 30 days. Therefore, family groups usually include offspring from multiple clutches (Grossmann 2007). Tokay geckos are an excellent model to study the effects of the early social life on cognition because offspring can be easily separated and raised alone after hatching or left with their parents to grow up in a family group. Furthermore, tokay geckos are part of the Gekkonidae family, as opposed to tree skinks and White's skinks that are part of the Scincidae family (Pyron et al., 2013), and consequently, the results of this study provide important new insights from a boarder phylogenetic perspective within lizards. Based on previous work (e.g. Bannier et al., 2017; Janetsian-Fritz et al., 2018; Munch et al., 2018), we expected individuals raised in social isolation to express lower cognitive ability (decreased ability to in the neophobia tests, less habituation and lower associative learning ability) due to experiencing fewer social challenges during early life (Humphrey, 1976; Jolly, 1966). Furthermore, we expected behaviours often associated with performance in cognitive tasks (exploration and food motivation) to be affected if they correlate with cognition.

Methods

Animals, breeding setup and rearing conditions

20 captive bred Tokay geckos (*Gekko gecko*), 14 females and 6 males, were included in this study. Sexes were determined by looking at the presence (for males) or absence (for females) of femoral glands (Grossmann 2007). All animals originated from 10 breeding pairs (see details below) and hatched between May 2022 and March 2023.

We established 10 breeding pairs from our captive population of 22 adult, captive bred geckos. All adults were purchased from different breeders and were between 3 and 8 years old. Adults were paired in January 2022 and stayed in pairs until January 2023. Females produced their first clutches in February 2022 and continued to produce clutches approximately every 30 days. All eggs and their location were recorded upon discovery of a clutch. Across breeding pairs, ten offspring hatched from a first clutch, four from a second clutch, one from a fourth clutch, two from a sixth clutch, two from a seventh clutch, and one each from an eighth, tenth and eleventh clutch. The distribution of individuals across clutches was based on hatching success (some eggs did not develop and were removed by females). All clutches incubated within the home enclosure of the parents.

From around 90 days of incubation, we started checking for hatchlings daily. Offspring started hatching after 78 to 138 days (range) of incubation. After hatching, offspring were allocated to either stay within the home enclosure to be raised with their parents or were removed immediately to be raised alone without adults or siblings. Offspring that stayed with their parents either had no siblings or had one or two siblings. Therefore, group sizes rained from 1 (isolation, N = 7 offspring), 3 (adult parents only, N = 5 offspring), 4 (adult parents plus one sibling, N = 2 offspring) and 5 (adult parents and two siblings, N = 6 offspring) individuals. Offspring were raised with parents until they were six month of age and then moved to be housed alone in the same room as hatchlings raised in isolation for one month before the start of testing (Figure 1). This ensured that immediate housing conditions were equally influencing behaviour across treatment groups and that potential effects on cognition and behaviour were due to long-term effects of the early social environment (e.g. Bannier et al., 2017; Brandão et al., 2015; Ferreira et al., 2024).

Captive condition and husbandry

Single housing

Animals were housed in terraria of the size 30 L × 45 B × 45 H cm, made of rigid foam plates with a mesh top and glass front doors. Terraria are fitted with a compressed cork wall fixed to the back, cork branches cut in half hooked on the back (functioning as shelters), cork branches allowing lizards to climb, and life plants as enrichment. Each terrarium has a drainage layer of expanded clay, separated by a mosquito mesh from the soil placed on top (organic tropical forest soil; Dragon BIO-Ground). We spread sphagnum moss and autoclaved red oak leaves on the soil as shelter and food for the isopods that decompose the faecal material of the lizards. Terraria are organized on shelves in three layers. To simulate natural environmental conditions, the room environment is controlled by an automatic system. Animals are exposed to a reversed 12h:12h photo period (i.e. light from 6 pm to 6 am, dark from 6 am to 6 pm). The system imitates sunrise and sunset, which are accompanied by changes in temperature reaching approximately 25 °C during night and 31°C during day. In addition, an UVB light (Exo Terra Reptile UVB 100, 13 W) is provided on top of the terraria during the day. A red light

(PHILIPS TL-D 36W/15 RED) invisible to geckos (Loew 1994) is kept on for 24h so as to enable experimenters to work with the lizards. Furthermore, lizards can thermoregulate to their optimal body temperature at any time due to a heat mat (TropicShop) attached to the right outer wall of each enclosure, which locally increases the temperature by 4-5 °C. Humidity is kept at 50 %, but every 12 hours, at 5pm and 4am, 30 seconds of rainfall (with reverse osmotic water) briefly increases humidity to 100%.

Group housing

Terraria for group housing are 90 L × 45 B × 100 H cm in size. Except for their size, they are set up exactly the same as the terraria isolated offspring were raised in. Additionally, large enclosures included a larger number of branches and shelters on the back wall, larger plants a larger heat mat that allowed basking of multiple individuals at the same time as well as larger water bowls. To prevent small offspring to drown in these water bowls, we added a large stone to ensure easy escape of small individuals.

Husbandry

Offspring were fed five times per week, with 10-15, small to medium sized house crickets (*Acheta domesticus*) using scatter feeding. The size of the crickets was adjusted to the changing head size while growing. Offspring at about 3-4 month of age and adult geckos are fed 3-5, adult house crickets using 25 cm long forceps in order to control food intake. To provide optimal nutrition to our animals (vitamin D and calcium), the insects are fed with high protein dry cat food (various brands), cricket mix (reptile planet LDT), and fresh carrots. Fresh water is supplied ad libitum in water bowls. Moreover, adult geckos are weighted (± 1g) every month and measured (SVL - snout vent length, ±0.5 cm) approximately every three months, to track their body condition. Offspring were measured (SVL - snout vent length, ±0.5 cm) evert two weeks until they reached 6 months of age after which they were put on the same monitoring schedule as adults.

Behavioural experiments

Testing started one month after individuals were put into single housing (approximately at 7 month of age). All individuals were tested at the same age. Therefore, the whole data collection lasted from the 19th of December 2022 until the 7th of November 2023 and all trials were conducted between 8:00 and 15:00.

Object neophobia was tested on Mondays to coincide with a feeding day after lizards had not received food for two days over the weekend (Figure 1). Space neophobia was tested the following Tuesday (which was a non-feeding day; Figure 1). Habituation was tested between the second and third object/ space neophobia session, while associative learning was tested between the third and fourth object/ space neophobia session (Figure 1; except for four individuals [G039, G040, G041, G042] which were tested for habituation and associative learning after object/ space neophobia testing had finished due to logistic reasons). The order of tests was chosen due to logistical reasons and minimize the testing period. If possible, test were conducted within the home enclosure of animals to reduce stress of handling and exposure to new environments (except for the space neophobia test which was a test to measure responses to novel space; Langkilde and Shine, 2006).

Object neophobia

Neophobia is the hesitation to approach or total avoidance of a novel stimulus and the result of the cognitive process that allows individuals to distinguish familiar from unfamiliar stimuli (Crane et al., 2020; Szabo and Ringler, 2023). We expected individuals that are poor at distinguishing novel from familiar to feed faster near a novel object. Therefore, individuals that are raised in social isolation and express lower cognitive abilities should show lower object neophobia compared to individuals raised in a group.

To reduce stress of handling (Langkilde and Shine, 2006) and ensure strong neophobic responses (Greenberg and Mettke-Hofmann, 2001), lizards were tested within their home enclosures. At the start of a session, we first placed a dim white light (LED, SPYLUX® LEDVANCE 3000K, 0.3 W, 17 lm) on top of the tank mesh lid (lizards expected food when this light was used). Next, a focal individual was located within its enclosure and if behind a shelter, the shelter was gently removed to expose the lizard for video recording. Thereafter, we presented a cricket in 25 cm long forceps in front of the lizard's snout at a distance of approximately 4-5 cm (optimal attack distance; personal observation) for a maximum of one minute.

Each individual received four sessions of two trials each (test and control) with an inter-session interval of 14 days (Figure 1) to be able to investigate individual repeatability. In control trials, a single cricket was presented with forceps (same as during regular feeding) while in test trials, the experimenter attached a novel object (toilet paper roll - 9.5 cm L and 4 cm diameter; egg carton - 9.5 cm L x 4.5 cm H x 4 cm W; fine, blue, high sponge - 11.2 cm L x 4.2 cm H x 3.4 cm W; course, blue, thin sponge - 10 cm L x 2 cm H x 3.8 cm W; Figure 2) to the forceps next to the cricket. Each object was only used once. The order of presenting test and control trials was randomised but counterbalanced so as to ensure that each individual received the test/ control first in two sessions. Furthermore, we randomised the order in which novel objects were presented (in a counterbalanced fashion) as well as the order in which lizards were tested each session to randomise the effects of temperature on behaviour. Trials were recoded using a Samsung S20 smartphone (108 Megapixel, 8K-FUHD). We measured the time from when the lizard first noticed a cricket (by either moving their head or eyes) until the first strike regardless of if the food was successfully captured or not.

Space neophobia and exploration

Compared to object neophobia which tests the discrimination of novel and familiar stimuli in a foraging context, space neophobia test the hesitation to enter a novel environment in a non-food related context.

Lizards were tested in an empty glass terrarium (i.e. testing tank, 45 L x 45 B x 60 H cm, ExoTerra). We used one testing tank which was placed on top of a table at approximately 100 cm distance facing (with the front transparent doors) a wall within the animal room. To make the sides and bottom opaque, they were wrapped in black plastic on the outside. To be able to measure exploration, a white grid was drawn onto the outside of the testing tank (grid: 11.25 cm x 15 cm long sides; 11.25 cm x 11.25 cm lid and bottom; Figure 3B). To enable video recording in sufficient quality to score animal behaviour, we placed a dim white light (LED, SPYLUX® LEDVANCE 3000K, 0.3 W, 17 lm) in the top right corner of the testing tank mesh lid. A GoPro (Hero 8; linear mode, 1080 resolution, 24 FPS) was mounted on a tripod in a way that enable recording from above (40 cm from the tank lid; Figure 3C).

To test space neophobia, we first captured a focal lizard by hand and placed it gently in an opaque, plastic box (white opaque bottom of the size 24 cm L x 18 cm W x 7.5 cm H; lid covered in black isolation tape with 6 air holes; Figure 3A). Next, the lizard (within the box) was carefully placed inside the bottom centre of the testing tank with the closed box exit facing the back wall (Figure 3C). After 5 minutes of acclimation, the experimenter started the video recording, opened 1/3 of the box lid carefully and secured it to the back of the box with a wire to allow the lizard to exit into the testing tank (Figure 3A). Thereafter, the experimenter closed and locked the testing tank door and left the room. Each individual was left undisturbed for 20 minutes. At the end of the trial, the individual was recaptured by hand and carefully released back into its home enclosure.

After each trial, the testing tank and box were thoroughly cleaned with 70% ethanol to remove chemical cues left by each lizard and left for a minimum of 10 minutes for the alcohol to vanish. Each individual received four trials of space neophobia to investigate individual repeatability.

Habituation and food motivation

Habituation is a short-term reduction in the response to a stimulus that at least partially reverts back to its original state after a certain period of time with no stimulation (Thorpe 1963; Rankin et al. 2009). We tested habituation in a foraging context and expected individuals raised in social isolation to habituate less or not at all to a novel stimulus compared to individuals raised in a group that had adult demonstrators present during development.

For five days (Monday to Friday), we presented each individual with a cue card (4 x 4 cm, either depicting a white triangle on a grey background or a black and white stripe pattern, evenly spread across individuals) next to a cricket by attaching the card to 15 cm long forceps using adhesive putty (UHU® Patafix) on the back. On a given test day, we first placed a dim white light on top of the enclosure mesh lid. Thereafter, we located the lizard and carefully removed its refuge to expose the lizard for testing if needed. To quantify this change in response, we recorded if a lizard attacked a cricket presented next to the cue card (1 = yes, 0 = no) across six trials each day (total of 5 x 6 trials = 30 trials). Furthermore, to quantify food motivation, we recorded the number of crickets attacked across all trials. Trials were not recorded on video.

Associative learning

Similar to habituation, we investigated associative learning in a foraging context and expected individuals raised in social isolation to show lower associative learning ability compared to individuals raised in a group.

In this test, we aimed to train lizards to touch a cue card to receive a reward. Similar to the habituation test, lizards received six trials a day for five days (Monday to Friday). We followed the same procedure as for the habituation test. During the first day, we performed six trials of habituation to ensure that lizards remembered the cue cards after the one week break. Thereafter, we presented crickets first in full view of the lizard to draw their attention and next, hid the cricket behind the cue card. We recorded a trial as correct (= 1) if the lizard attacked the cue card. After the attack we removed the cue card and the lizard received the cricket. If the lizard did not immediately respond we presented the cricket again before hiding it behind the card. If a lizard attacked the cricket but not the card, the trial was scored as incorrect (= 0). Associative learning was tested after habituation to ensure that lizards had acclimated to the testing procedure and were familiar with the cards. Trials were not recorded on video.

Video analysis

We scored videos of object neophobia using the free behavioural coding software BORIS (Friard and Gamba, 2016) and measured latencies to an accuracy of 0.001 seconds. To this end, videos were slowed down to half their speed. If no attack occurred, we recoded occurrence as 0 and assigned this data point a censored latency of 60 seconds.

From the video of space neophobia, we scored the time taken to exit (exit latency, in seconds) into the novel space (testing tank) starting from when the experimenter locked the testing tank door to when a lizard exited the opaque box by lifting its' tail base over the rim of the box (= exiting with their whole body not counting the tail). If a lizard did not exit the box, we recoded occurrence as 0 and assigned it a censored latency of 1200 seconds (= 20 minutes). Furthermore, we also counted the time it took an individual to lift its head out of the box (chin above the rim of the box) before exiting fully. To gain a measure that was comparable across individuals and sessions, we divided the number of head lifts by the exit latency (as this latency differed across individuals and sessions). To measure exploration, we counted the number of line crossings after a lizard had exited the box (one line crossing was recorded for exiting the box). If a lizard crossed in a grid corner, we counted two line crossings. To accurately estimate each individuals' exploration score we divided the total number of line crossings by the time left for exploration after the opaque box was exited. Because videos could not be scored blind as to test and animal identity, 40 % of videos were scored by an observer that was unaware of the objectives of the study and we recorded high inter-observer reliability (occurrence: Kohens kappa = 1; latency: Spearman rank correlation, S = 857.53, p

< 0.001, $r_s = 0.9784056$; relative crosses: Spearman rank correlation, $S = 197.34$, $p < 0.001$, $r_s = 0.9602133$).

Ethical statement

The experimental procedure applied in this study was strictly non-invasive and followed the guidelines provided by the Association for the Study of Animal Behaviour/ Animal Behaviour Society for the treatment of animals in behavioural research and Teaching (ASAB Ethical Committee and ABS Animal Care Committee, 2023). Experiments were approved by the Suisse Federal Food Safety and Veterinary Office (National No. 33232, Cantonal No. BE144/2020). Captive conditions were approved by the Suisse Federal Food Safety and Veterinary Office (Laboratory animal husbandry license: No. BE4/11). Two offspring died (pathology was inconclusive) during the course of this study. One around 16 weeks and another around six weeks after hatching. During pair formation, we monitored adults closely for 12h to prevent harm. If any aggression occurred within the first hour of pairing, we immediately separated the male and female to avoid injury. Males were then paired with a different female (N = 7 attempted pairings total) until we established stable pairs that did not show any aggression towards each other. Similarly, after hatching, we monitored hatchlings that stayed with their parents closely and removed one hatchling (G033) due to concerns of insufficient parental care.

Statistical analyses

All statistical analyses were run in R version 4.2.2 (R Core Team, 2022). We ran Bayesian linear mixed (LMM) and generalised linear mixed models (GLMM) using the package *brms* (Bürkner 2017, 2018, 2021) all including a random effect of animal identity as well as parent identity (to account for relatedness). We used a generic weakly informative normal prior with a mean of 0 and a standard deviation of 1 and ran 4 chains per model of 5000 iterations each and a thinning interval of 1 (default settings). We made sure that model Rhat was 1, that the

ESS was above 2000 and checked the density plots and correlation plots to ensure that the models had sampled appropriately. To investigate differences across variable levels (e.g. stimulus) and the results of interactions, we applied estimated marginal means (EMM) *post hoc* tests using the function *emmeans* or *emtrends* from the package *emmeans* (Lenth, 2023). We used a test for practical equivalence to determine whether to accept or reject a "null hypothesis", formulated as “not difference” or “no relationship”, for each fixed effect in a model using the *equivalence_test* function from the package *bayestestR* (Makowski et al., 2019). We report results in which the null hypothesis was accepted (100% within the Region of Practical Equivalence – ROPE) or was undecided as no evidence and results in which the null hypothesis was rejected (0% within the ROPE) as evidence. Additionally, we provide Bayes factors (BF) to further evaluate the results by determining Bayes Factors from marginal likelihoods using the package *brms*. Bayes factors below 1 indicate no difference while above 1, BF indicate support for a difference (Schmalz et al., 2023). We report cases in which the equivalence test produced “undecided” results but Bayes factors were above 1 as evidence. To investigate differences in variance across rearing treatments, we use a two-tailed F-test using the *var.test* function from base stats. To calculate individual repeatability of behaviour, we used the *rptGaussian* function from the package *rptR* (Stoffel et al. 2017). Finally, we used the *corr.test* function from the package *corrplot* (Wei and Simko, 2021) to investigate correlations across test. Due to small sample sizes and imbalanced design (breeding pair identity) we pooled all individuals that were raised socially into a single group regardless of rearing group size. Data generated during this study and the analysis code are available for download from the Open Science Framework (OSF, link for review purposes: https://osf.io/6sp8b/?view_only=08bdb8d4916842a1a242144dd223bd7b).

Object neophobia

First, we subtracted the latency measured in the control trials from the latency measures in the test trial to gain a measure of neophobia (negative values indicate longer control latency, while positive values indicate longer test latencies). This differences was then used as the response variable in a Gaussian model with the fixed effects of care (1 – raised socially, 0 – raised in isolation), stimulus (toilet paper roll, egg carton, low sponge, high sponge), session (1 - 4), sex (male or female), body condition (SMI – scaled mass index; Peig and Green, 2009) and temperature (enclosure temperature measured automatically every 15 minutes). We then analysed differences across stimuli using a *post hoc* EMM test. Furthermore, we compared the variance across rearing treatments based on the average neophobia per individual and calculated agreement repeatability.

Space neophobia

To investigate space neophobia, we used two different measures: (1) the censored latency to exit as well as (2) the relative number of times geckos lifted their heads out of the box before exiting as a measure of information gathering. To analyse the exit latency (response variable), we ran a censored log-normal model including the fixed effects of care, session, sex, body condition and temperature. Because we were interested if the change in latency across session differed across rearing treatments, we also included the interaction between care and session as a fixed effect. Thereafter, we investigated the result of the interaction using a *post hoc* EMM test. Furthermore, we compared the variance across rearing treatments using the average latency for each individual. Finally, we calculated adjusted repeatability accounting for session.

To analyse the relative number of times geckos lifted their head over the rim, we ran a Gaussian model with the same fixed effects as the model for latency. We also used a *post hoc* EMM test to investigate the result of the interaction, compared the variance across rearing treatments using the average relative number of head lifts per individual and calculated agreement repeatability.

Exploration

To analyse the effects of care, session, sex, body condition and temperature (fixed effects) on the tendency to explore a novel space, we used the relative number of line crossings as the response variable in a Gaussian model. Again, we were interested if the change in exploration across sessions differed across rearing treatments by including the interaction between care and session as a fixed effect. We investigated the result of the interaction using a *post hoc* EMM test and compared the variance across rearing treatments using the average relative number of crosses for each individual. Finally, we calculated adjusted repeatability accounting for session.

Habituation and food motivation

To investigate if lizards habituated to a cue card presented while feeding, we used the occurrence of feeding (1 – ate the cricket, 0 – did not eat the cricket) as the response variable in a Binomial model. We included care, trial (1 to 30), sex, body condition and temperature as the fixed effects. We were also interested if habituation across time differed across rearing treatments by including the interaction between care and trial as an additional fixed effect and investigated the result of the interaction using a *post hoc* EMM test.

To analyse food motivation, we first summed up the trials in which each individual ate a cricket (out of a total of 30 possible trials). We then used this value as the response variable in a Poisson model and included care, sex and body condition as fixed effects. We did not include temperature in this model because we considered all instances of feeding across a whole week of testing. Additionally, as individuals were tested in a different order each day, we assumed that temperature effects would be evenly distributed across days. In addition, we compared the variance across rearing treatments using the number of times a cricket was eaten for each individual.

Associative learning

To analyse associative learning, we focused on the number of trials in which a lizard showed the desired behaviour of first touching the cue card before receiving food. We ran a Poisson model with the number of trials as the response variable and included the fixed effects of care, sex, body condition and temperature. Thereafter, we compared the variance across rearing treatments using the number of times the behaviour occurred for each individual.

Association between test performances

To understand if performance across test was related within individuals, we performed pairwise Spearman rank correlations with a Holm correction for multiple testing. From the object neophobia test, we including the average difference in attack latency for each individual. From the space neophobia test, we included the average latency, average relative number of head lifts, the difference in latency to exit from the first to the last session (as a measure of habituation), and the average number of relative crosses for each individual (for exploration). Finally, from the habituation test, we included the difference in the number of attacks from session one to five (as another measure of habituation), and the number of crickets eaten, and from the associative learning test, we included the number of correct trials for each individual.

Results

Object neophobia

Object neophobia was highly repeatable across all individuals with R = 0.405 (CI_{low} = 0.125, CI_{up} = 0.619). However, we found no evidence that the early social environment (BF = 0.983; Figure 4A), stimulus (BF = 0.966), session (BF = 0.963), sex (BF = 0.993), body condition (BF = 0.996) or temperature (BF = 1.038) had an effect on object neophobia. Furthermore, neophobic responses did not differ across objects used (Appendix Table A1). The variance in neophobic responses did not differ across rearing treatments (F = 0.946, p = 0.997; Figure 4A).

Space neophobia

The time taken to exit into a novel environment was repeatable at R = 0.292 (CI_{low} = 0.031, CI_{up} = 0.514). We found no evidence that the change in the time taken to exit into a novel environment (habituation) differed across rearing treatments (EMM, estimate = 0.133, CI_{low} = -0.232, CI_{up} = 0.485, 34.34% inside ROPE). Therefore, we removed the interaction. Based on this simpler model, we found evidence that the time taken to exit into a novel environment decreased across sessions (BF = 3504.076; Figure 4B) and found weak evidence that lizards receiving care after hatching took longer to enter novel space compared to individuals that were raised in isolation (BF = 1.249; Figure 4B). We also found evidence that males took longer to exit into the novel environment compared to females (BF = 2.698). We found no evidence that body condition (BF = 0.216) or temperature (BF = 1.028) were related to the time taken to exit (Appendix Table A2). The variance in the time taken to exit into a novel environment did not differ across rearing treatments (F = 1.543, p = 0.492).

Similarly, the relative number of head lifts before exit was repeatable at R = 0.298 (CI_{low} = 0.042, CI_{up} = 0.510). We found no evidence that the change in relative number of head lifts differed across rearing treatments (EMM, estimate = 0.0002, CI_{low} = -0.0009, CI_{up} = 0.0013, 100% inside ROPE). Therefore, we removed the interaction. This simpler model produced no evidence of an effect of rearing treatment (BF = 0.006; Figure 4C), session (BF = 0.012; Figure 4C), sex (BF = 0.033), body condition (BF = 0.004), or temperature (BF = 0.031) on the relative number of head lifts before exiting (Appendix Table A2). The variance in the relative number of head lifts before exit did not differ across rearing treatments (F = 2.307, p = 0.205).

Exploration

The relative number of crosses was highly repeatable at R = 0.680 (CI_{low} = 0.429, CI_{up} = 0.818). We found no evidence that the change in the relative number of line crossings differed across rearing treatments (EMM, estimate = -0.001, CI_{low} = -0.011, CI_{up} = 0.009, 100% inside ROPE). Therefore, we removed the interaction. This simpler model showed evidence that exploratory behaviour increased across sessions (BF = 5.361; Figure 5A), while we found no evidence that rearing treatment (BF = 0.023; Figure 5A), sex (BF = 0.022), body condition (BF = 0.001) nor temperature (BF = 0.005) were associated with exploratory behaviour (Appendix Table A3). We found no evidence that the variance in the relative number of crosses differed across rearing treatments (F = 2.963, p = 0.103).

Habituation and food motivation

We found no evidence that the change in the likelihood to eat next to a cue card (i.e. habituation) differed across rearing treatments (EMM, estimate = 0.037, CI_{low} = -0.036, CI_{up} = 0.107, 97.89% inside ROPE). Therefore, we removed the interaction. This simpler model revealed no evidence that habituation occurred across trials (BF = 0.036; Figure 5B). Furthermore, we found no evidence that rearing treatment (BF = 0.687; Figure 5B), sex (BF = 1.060), body condition (BF = 0.106) nor temperature (BF = 1.053) were associated with habituation (Appendix Table A4).

Similarly, we found no evidence that rearing treatment (BF = 0.374; Figure 5C), sex (BF = 0.496) or body condition (BF = 0.026) influenced how many crickets lizards ate during the habituation test (Appendix Table A5). We found no evidence that the variance in the relative crickets eaten differed across rearing treatments (F = 0.699, p = 0.689).

Associative learning

We found evidence that the variance in the number of correct trials did differ across rearing treatments (F = 0.055, p = 0.002; Figure 6); with a higher variance in animals raised with parents. However, there was no evidence that the rearing treatment (BF = 0.753; Figure 6), sex (BF = 0.835), body condition (BF = 0.062), or temperature (BF = 0.938) influenced the number of correct trials (Appendix Table A6).

Association between test performances

Spearman rank correlations showed that the latency to exit was negatively correlated with the number of head lifts (r_s = -0.89; Figure 7A), which indicates that more neophobic individuals that take longer to exit into the novel environment lift their heads less often before exiting. Furthermore, exploration was negatively correlated with the latency to exit (r_s = -0.68; Figure 7B) and positively correlated with the number of head lifts (r_s = 0.58; Figure 7C). This indicates that more neophobic individuals were less exploratory. We also found that object neophobia was positively correlated with the number of head lifts (r_s = 0.61; Figure 7B) and negatively correlated with the latency to exit into a novel environment (r_s = -0.78; Figure 7E) demonstrating that individuals that were more neophobic towards novel space were less neophobic towards novel objects. Finally, object neophobia was positively correlated with exploration (r_s = 0.69; Figure 7F); individuals with lower object neophobia explored less. No other measures were correlated above a coefficient of 0.5 (Appendix Table A7).

Discussion

Overall, we found that individuals that were raised in a social group showed higher space neophobia measured as the time taken to enter a novel space and expressed a larger variation in associative learning ability compared to individuals raised in social isolation. However, the average associative learning ability across social rearing treatments did not differ statistically. We also found a sex effect on the time to enter a novel space, with males taking longer to exit the opaque box, as well as habituation to novel space shown by a decrease of the latency to enter the novel space and increase in exploration across sessions. Both object neophobia and exploration were more repeatable (R = 0.405 and R = 0.680, respectively) than the measures relating to space neophobia ($R_{latency} = 0.292$ and $R_{head\ lifts} = 0.298$). Finally, we found that measures obtained from the same test were correlated (latency to enter a novel space, head lifts and exploration), but found that object and space neophobia were negatively correlated indicating that they do not measure the same trait. In no case was food motivation and body condition associated with any cognitive measure taken in our experiment.

We found that the early social environment influenced only some but not all of our cognitive measures. Lizards raised in social isolation showed lower space neophobia and entered a novel environment faster compared to lizards raised in a family group. Higher space neophobia could provide advantages when it comes to delaying dispersal. An unwillingness to enter novel space as shown by the social treatment group might be a direct result of parental care to prolong the benefits of protection until forced to disperse by the parents especially in males (for which we find longer exit latencies) as female offspring are often tolerated for longer (Groothuis and Maestripieri, 2013; Grossmann 2007; Roulin et al., 2010). Alternatively, being raised in a deprived environment might have increased isolated individuals' novelty seeking behaviour. However, this seems unlikely, because we found no differences in object neophobia based on the early social environment, even though the measures of object and space neophobia were inversely correlated.

We also found larger variation in associative learning by individuals from the social rearing treatment but no average difference between the groups. Some individuals from the social rearing treatment far outperformed others within both rearing treatments. Such enhanced learning ability might give these individuals a competitive advantage over others. For example, enhanced learning ability is related to increased reproductive success (e.g. Ashton et al., 2018; Smith et al., 2015; White et al., 2022) and survival (e.g. Dayananda and Webb, 2017; Madden et al., 2018) although this relationship might dependent on other factors (e.g. mating tactic, incubation temperature, or body condition) and not all studies find such a relationship between cognition and fitness measures (e.g. Huebner et al., 2018). Furthermore, better learning ability in the context of foraging might help them to occupy different social niches and avoid competition for resources later in life (Humphrey, 1976; Montiglio et al., 2013). However, as our experiment was performed in captivity we do not know if these "smarter" individuals would fare better as predicted by the Social Intelligence Hypothesis. Studies linking cognition and survival are still scare (Rochais et al., 2022) but important to understand how the link between sociality and cognition might play out on an evolutionary scale. More generally, our sample size was low, and therefore, our power to detect differences was also diminished. We might have only been able to detect the strongest effects while other, more subtle influences were masked by individual variation. Furthermore, even though geckos were raised in differently sized family groups, we were unable to analyse performance separately for these different groups due to the low number of replicates (e.g. one family with two offspring and two families with three offspring). To gain a better understanding of the subtle influence of early social experiences on the development of cognition, future studies should include larger samples sizes across a broader range of social environmental treatments.

Previous studies in lizards have shown mixed results as to the influence of the early social environment on cognition potentially due to the large variation in social environments tested (e.g. siblings versus parents). Tree skinks (*Egernia striolata*) raised with an age matched, unrelated partner did not differ in their spatial learning ability in a vertical maze compared to individuals raised alone (Riley et al., 2017). Furthermore, both socially reared and isolated individuals learnt a discrimination and reversal task with individuals from both groups similarly likely to use social information from a demonstrator (Riley et al., 2018). Contrary, White's skinks (*Liopholis whitii*) reared with their mother showed better learning to escape a simulated predator attack by decreasing errors across trials compared to skinks raised in social isolation that did not decrease errors (Munch et al., 2018). In the present study, we find differences in space neophobia and associative learning across rearing treatments. One striking variation across these and our study is that when offspring were raised with adults (mother or both parents) we find an influence on cognitive development, while when they are raised with age matched conspecifics there is no effect. Similarly, a study in the cooperatively breeding cichlid fish, *Neolamprologus pulcher*, found that the presence of older group members during the early life decreased object neophobia (Bannier et al., 2017). It is possible that, depending on the social expression of a species, the presence of certain conspecifics such as the parents exerts a stronger influence than other individuals (e.g. siblings). Future studies in the tokay gecko should, therefore, compare the effects of parents compared to age matched social partners.

Our study and many others investigating how sociality is linked to the development of cognition often test general cognitive abilities such as associative learning, discrimination and reversal learning, spatial learning or neophobia (e.g. Brandão et al., 2015; Meagher et al., 2015; Riley et al., 2017). Even though some studies have found an effect of sociality on non-social cognitive abilities (e.g. Ashton et al., 2018), arguably, we would expect the most pronounced effect to occur in the social domain such as during social learning or when using social information to make decisions. Indeed, a study across six lemur species demonstrated that groups size predicted cognitive performance only in social (perspective taking) but not non-social cognitive tests (inhibitory control; MacLean et al., 2013). Furthermore, a recent study in the cichlid fish, *N. pulcher*, showed an effect of the early social environment on behavioural flexibility only in social contexts but not in non-social contexts (Ferreira et al., 2024). In contrast, tree skinks were similarly unlikely to use social information during social learning, regardless of the social environment during rearing (Riley et al., 2018). In the current study, we were unable to include social cognitive tests due to time constraints. To gain a truly comprehensive understanding of how sociality influence cognition, future studies should test a wide range of cognitive abilities, both social and non-social.

Object and space neophobia as well as exploration are commonly investigated animal personality traits (animal personality is defined as consistent individual differences across time and/ or contexts; Carere and Locurto, 2011) and personality has been linked to cognition (Carere and Locurto, 2011) and can be influenced by early social life experiences (e.g. Edenbrow and Croft, 2013; Haller et al., 2014; Liedtke et al., 2015). Object neophobia, both measures of space neophobia and exploration were repeatable in our study less so, however, to previous studies collected from the adult parents of the cohort used in the current study

($R_{object} = 0.124$; $R_{exploration} = 0.538$; $R_{space} = 0.044$; Szabo and Ringler 2022; 2023). On average, studies on novel object tests find repeatability of 0.47 (Takola et al., 2021) while studies on behaviour find on average a repeatability of 0.37 (Bell et al., 2009). Therefore, the values we find in the current study are within the range of what would be expected. What is more interesting is the increased repeatability in the individuals tested in the current study which might have a number of causes. First, for space neophobia and exploration, we might have been able to estimate repeatability more reliably in the current study, because we used four instead of two repetitions. However, this explanation cannot account for the increased repeatability in object neophobia because we used four repetitions previously. Second, animals in our study were between seven and nine months old, whereas adults were between two to six years old. Age might, therefore, be a factor influencing repeatability. Contrary to our results, a study in turtles (*Terrapene carolina*) showed no difference in the magnitude of repeatability in boldness between adults and juveniles which was stable across years (Carlson and Tetzlaff, 2020). Similarly, a study in zebra finches (*Taeniopygia guttata*) showed that activity, aggression and exploration were repeatable across life stages, boldness was not (Wuerz and Krüger, 2015). Interestingly, the early social life lizards experienced did not influence the development of behaviour even though such effects were shown in mammals (e.g. Haller et al., 2014), fish (e.g. Edenbrow and Croft, 2013) and spiders (e.g. Liedtke et al., 2015). Either, early life effects are present but vanished before we tested behaviour (e.g. Płaskonka et al., 2024) or personality has a strong genetic basis in tokay geckos. Overall, we still have an incomplete understanding about how personality develops and is maintained across an individuals' lifetime, a gap that future research needs to fill (Cabrera et al., 2021).

We also found correlations across measures from different tests. However, in most cases, measures collected in the same test were correlated suggesting that they are not independent. For example, the latency to exit into a novel environment was negatively correlated with the relative number of head lifts before exiting, suggesting that individuals that lift their head less often before exiting are more neophobic and consequently are better at recognising novelty and need to sample information less frequently before making a decision.

Nonetheless, all measures collected from the space neophobia test were correlated with the results from the object neophobia test. In all cases, individuals that were more neophobic towards objects, were less neophobic towards novel space but explored more. This suggest that the measures obtained in these two test represent different traits as opposed to a general neophobia/ boldness trait. Previously, we found no correlation between object and space neophobia in the adult parents (Szabo and Ringler 2022; 2023). It is, therefore, possible that this syndrome (a correlation between two or more personality traits; Sih et al., 2004) is only present in young geckos. In other species, such as the Chimango Caracara (*Milvago chimango*), exploration was not correlated with object neophobia, neither in adults nor in juveniles (Biondi et al., 2010). Alternatively, the syndrome we found might only be present in the current cohort, and consequently, should be confirmed in additional tests in the future. Importantly, we find that food motivation was not correlated with any of our measures demonstrating that despite most of our tests involving food, body condition, and in extension hunger level, did not influence performance.

Conclusions

We provide evidence that the early social environment experienced after hatching influenced the development of some non-social cognitive abilities (space neophobia and associative learning) in a facultatively social gecko. Geckos, and more generally lizards, provide exciting albeit underutilised models to investigate the relationship between sociality and cognition especially considering that they are facultative social with independent offspring. Consequently, by testing different species expressing a range of social complexity, we might gain a unique perspective into which cognitive abilities could have been selected for during the early stages in the evolution of sociality and provided an adaptive advantage to mitigate the challenges of group living.

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Figure Legends

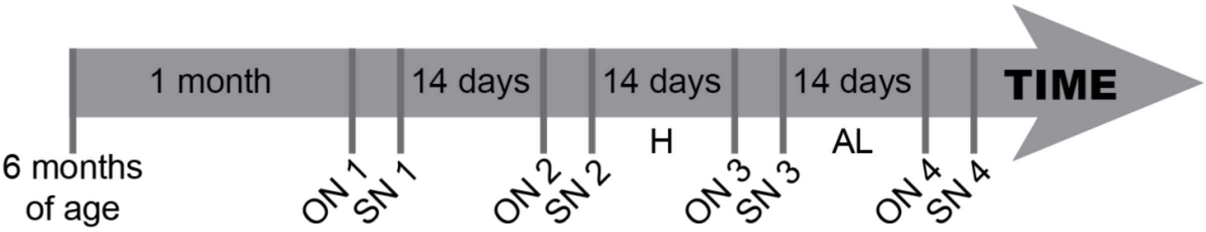

Figure 1. Timeline of the four behavioural experiments. ON – Object Neophobia, SN – Space Neophobia, H – Habituation, AL – Associative learning. Individuals were raised in isolation or in a group for 6 months and then given another month in single housing before the first test.

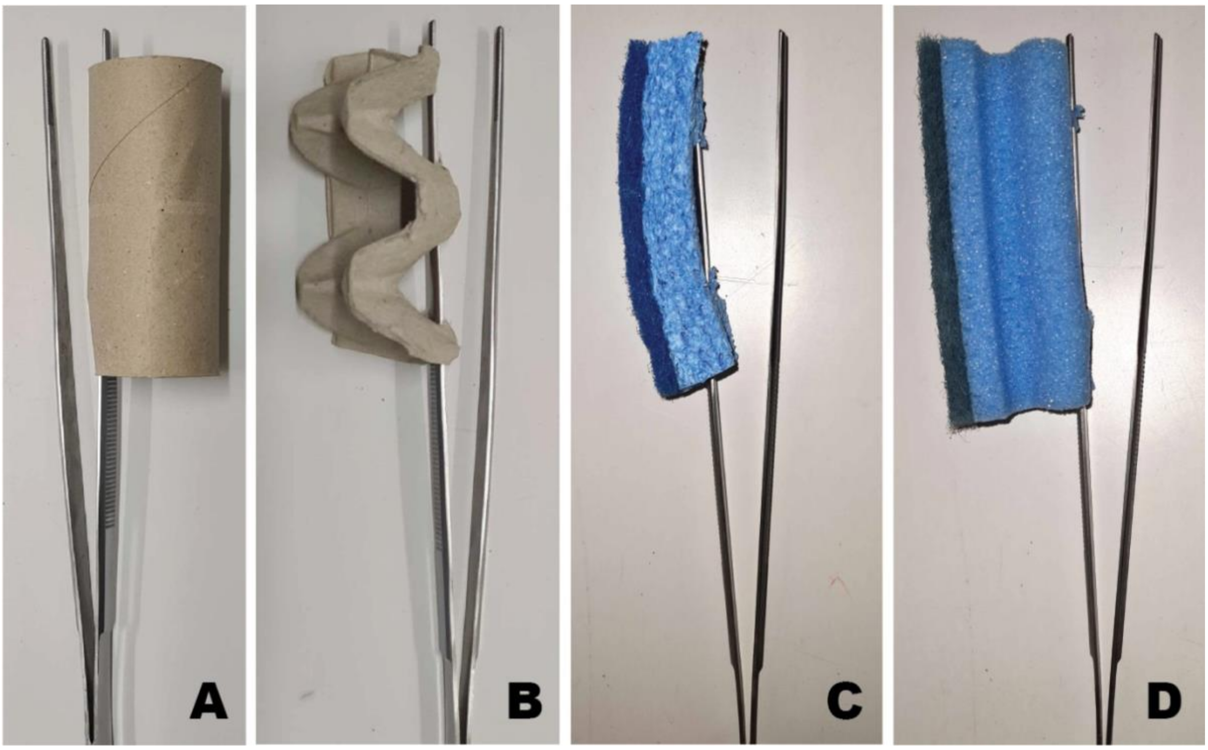

Figure 2. Novel objects used during the object neophobia tests. All objects were attached to 25cm long forceps and were presented in a random but counterbalanced order across individuals. (A) Toilet paper roll (9.5 cm L, 4 cm diameter; picture taken and modified from Szabo and Ringler 2022), (B) egg carton (9.5 cm L x 4.5 cm H x 4 cm W; picture taken and

modified from Szabo and Ringler 2022), (C) course, blue, thin sponge (10 cm L x 2 cm H x 3.8 cm W), and (D) fine, blue, high sponge (11.2 cm Lx 4.2 cm H x 3.4 cm W).

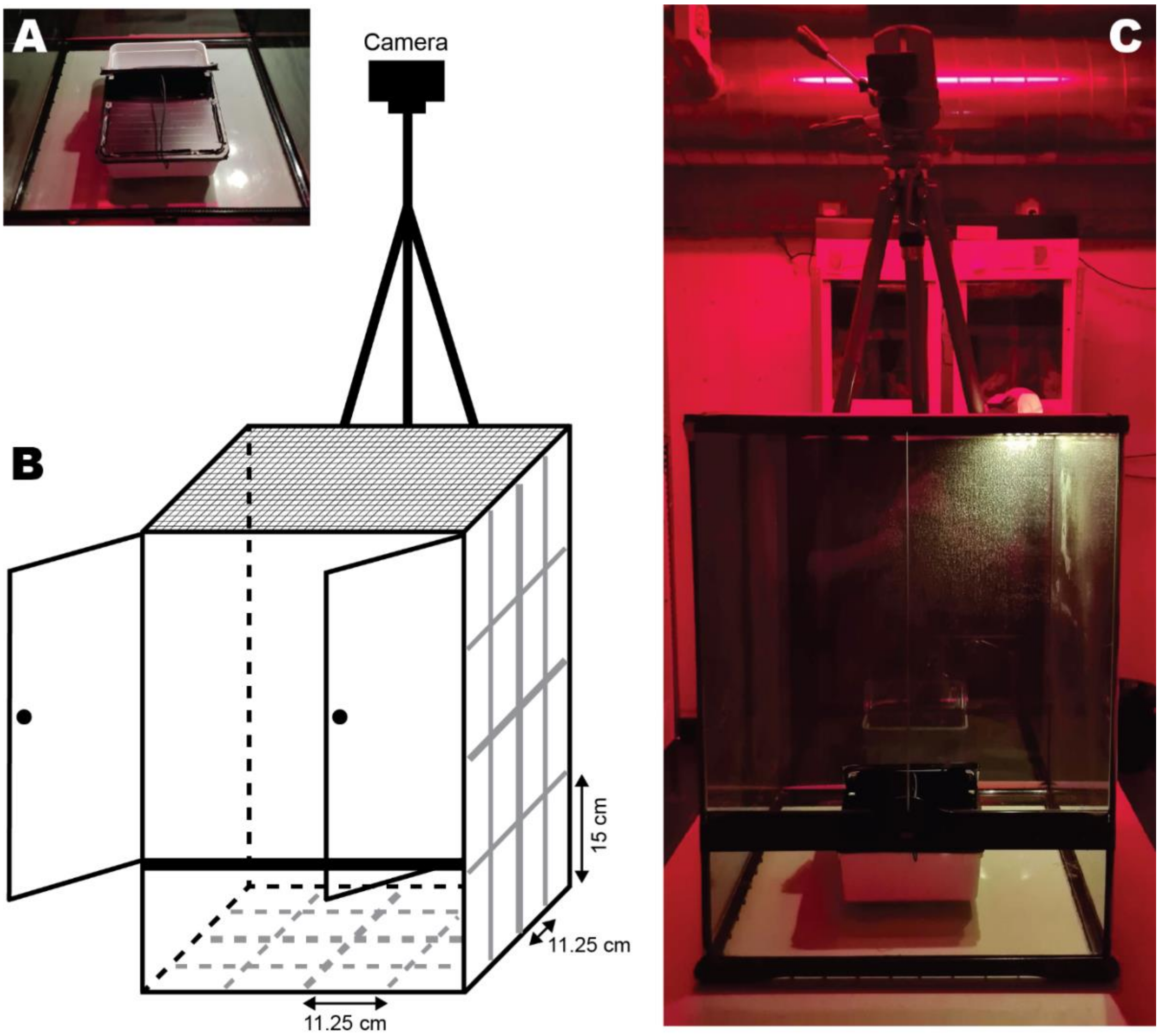

Figure 3. Setup used during the space neophobia test. (A) Picture of the opaque box used to catch lizards (24 cm L x 18 cm W x 7.5 cm H). (B) Schematic representation of the testing tank (45 L x 45 B x 60 H cm) including the camera. The grid painted on all 6 sides of the testing tank to measure exploration is presented in grey. On the long sides, the grid rectangles measured 11.25 cm x 15 cm. On the bottom and the mesh lid, the grid squares measured 11.25 cm x 11.25 cm. (C) Picture of the testing tank including the camera mounted on a tripod and the opaque box inside (grid lines not shown). Sides, except for the front and the lid (made

out of mesh), were covered in black plastic to make them opaque. Pictures and text taken and modified from Szabo and Ringler 2022; 2023.

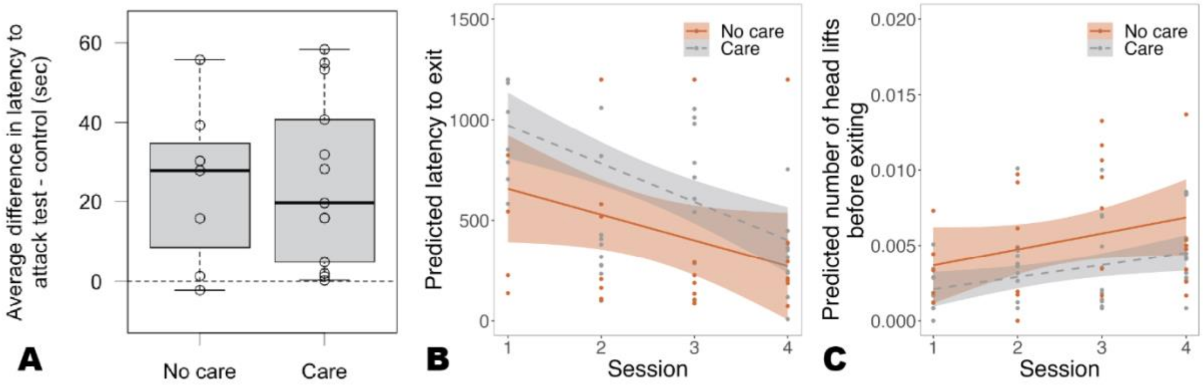

Figure 4. Results from the object and space neophobia test split into rearing treatments (care = family group rearing, no care = rearing in social isolation). (A) Average object neophobia in individuals that received care (N = 13) and those that were raised in isolation (N = 7). Points represent individual performance. The dotted line indicates the same reaction in the control and test trial. The bold line within boxes is the median, the upper box edges are the upper quartile, the lower box edges the lower quartile, the top whisker ends are the maximum and the bottom whisker ends the minimum. (B) Predicted latency to exit across sessions split into individuals that received care (grey, dotted line; N = 13) and those that were raised in isolation (orange, solid line; N = 7). Points represent individual responses. The shaded area indicates the 95% confidence interval. (C) Predicted relative number of head lifts across sessions split into individuals that received care (grey, dotted line; N = 13) and those that were raised in isolation (orange, solid line; N = 7). Points represent individual responses. The shaded area indicates the 95% confidence interval.

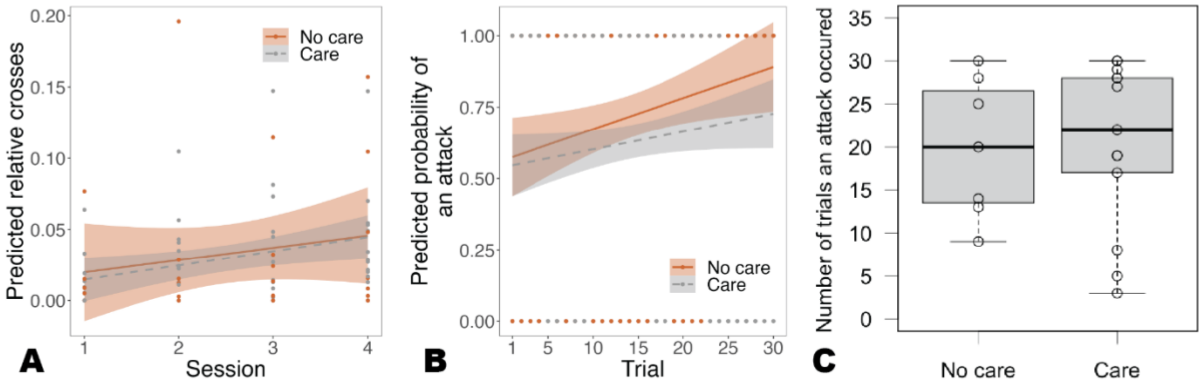

Figure 5. Results for exploration in a novel environment as well as from the habituation test split into rearing treatments (care = family group rearing, no care = rearing in social isolation). (A) Predicted relative number of crosses across sessions split into individuals that received care (grey, dotted line; N = 13) and those that were raised in isolation (orange, solid line; N = 7). Points represent individual responses. The shaded area indicates the 95% confidence interval. (B) Predicted probability to attack a cricket next to a novel cue card across trials split into individuals that received care (grey, dotted line; N = 13) and those that were raised in isolation (orange, solid line; N = 7). Points represent individual responses. The shaded area indicates the 95% confidence interval. (C) Number of crickets consumed in the habituation test in individuals that received care (N = 13) and those that were raised in isolation (N = 7). Points represent individual responses.

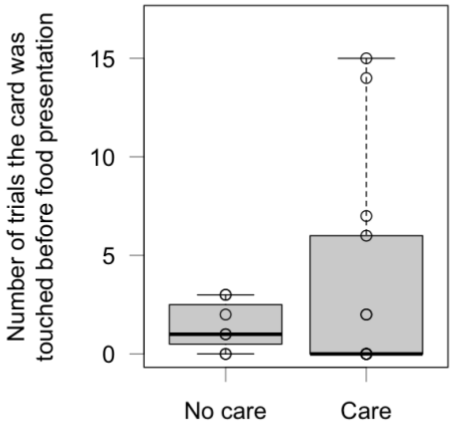

Figure 6. Number of trials in which an individual touched the cue card to receive a reward in individuals that received care (N = 13) and those that were raised alone (N = 7). Points

represent individual performance. The bold line within boxes is the median, the upper box edges are the upper quartile, the lower box edges the lower quartile, the top whisker ends are the maximum and the bottom whisker ends the minimum.

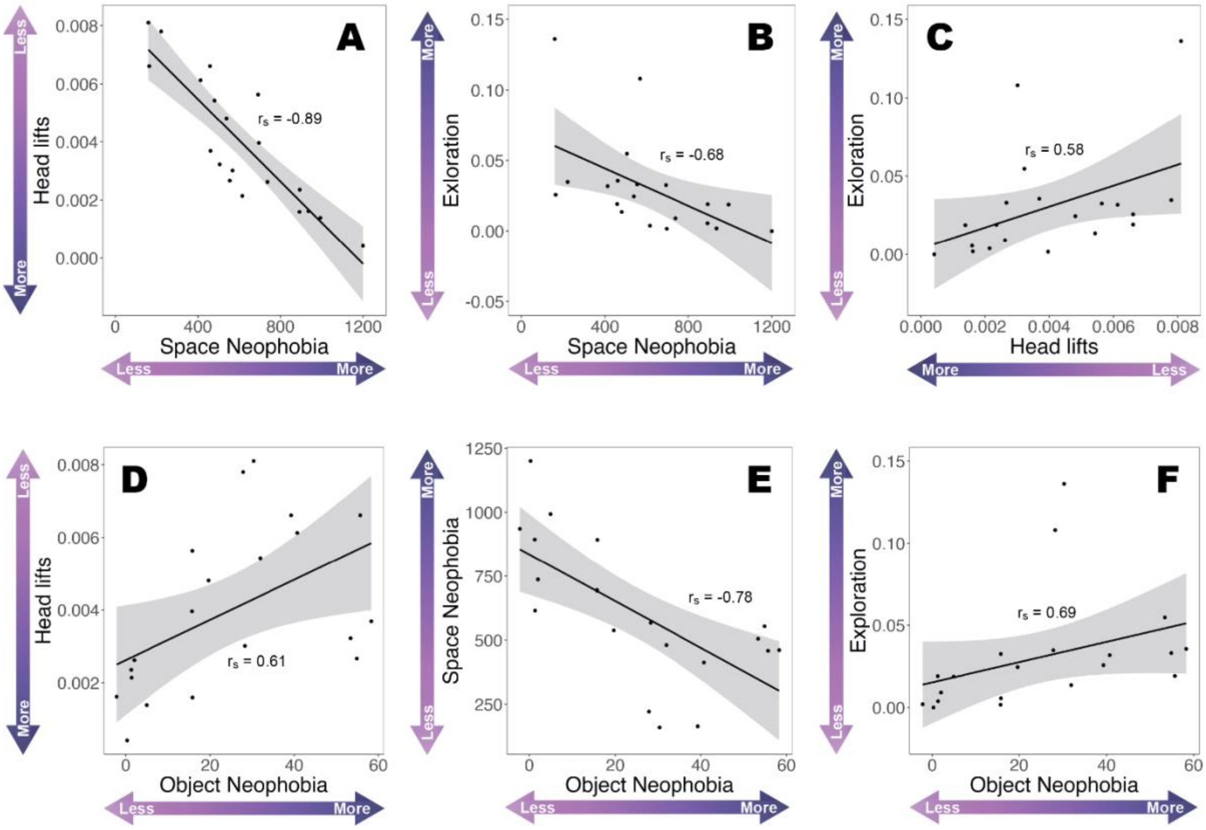

Figure 7. Paired correlations across test performances (only those are shown with a correlation coefficient below -0.5 or above 0.5). Points represent individual performance and the shaded area indicates the 95% confidence interval. (A) Negative correlation between the latency to exit and the relative number of head lifts in the space neophobia test. (B) Negative correlation between the latency to exit and the relative number of line crosses in the space neophobia test. (C) Positive correlation between the relative number of head lifts and the relative number of line crosses in the space neophobia test. (D) Positive correlation between object neophobia and the relative number of head lifts. (E) Negative correlation between object neophobia and the latency to exit in the space neophobia test. (F) Positive correlation between object neophobia and the relative number of line crosses in the space neophobia test. Arrows indicate more or less neophobia and exploration.

Data Accessibility Statement

The datasets generated and analysed during the current study as well as the code used for analysis are available in the Open Science framework repository, https://osf.io/6sp8b/?view_only=08bdb8d4916842a1a242144dd223bd7b

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

BS - Conceptualization; BS - Data curation; BS - Formal analysis; ER - Funding acquisition; BS - Investigation; BS - Methodology; BS - Project administration; BS, ER - Resources; BS - Validation; BS - Visualization; BS - Roles/Writing - original draft; BS, ER - Writing - review & editing.

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Appendix

Table A1. Estimates and test statistics from the model and post hoc test analysing the behaviour shown during the object neophobia test. CI – Credible interval, ROPE – Region of practical equivalence

Parameter	Estimate	95% CI$_{low}$	95% CI$_{up}$	% inside ROPE
Intercept	47.398	-31.169	126.186	3.13
Care yes	0.048	-1.929	2.019	100
High sponge	0.020	-1.949	1.996	100
Low sponge	0.040	-1.961	2.015	100
Toilet paper roll	-0.052	-1.981	1.925	100
Session	0.075	-1.814	1.995	100
Male	-0.191	-2.162	1.766	100
Body condition	-0.520	-1.375	0.345	100
Temperature	-0.357	-2.308	1.590	100
Post hoc test results				
Difference	Estimate	95% CI$_{low}$	95% CI$_{up}$	% inside ROPE
Egg carton – high sponge	-0.026	-2.07	1.91	9.18
Egg carton – low sponge	-0.035	-1.97	1.85	8.82
Egg carton – toilet paper roll	0.055	-1.87	2.00	8.65
High sponge – low sponge	0.005	-2.66	2.76	6.39
High sponge – toilet paper roll	0.075	-2.68	2.87	6.01
Low sponge – toilet paper roll	0.081	-2.70	2.74	6.06

Table A2. Estimates and test statistics from the model analysing the behaviour shown during the space neophobia test. CI – Credible interval, ROPE – Region of practical equivalence. Significant results are highlighted in bold, trends are highlighted in italic.

Latency to exit				
Parameter	Estimate	95% CI$_{low}$	95% CI$_{up}$	% inside ROPE
Intercept	*7.548*	*-1.659*	*16.931*	*0.02*
Care yes	*0.677*	*-0.354*	*1.694*	*0.57*
Session	**-0.475**	**-0.673**	**-0.286**	**0.00**
Male	0.397	-0.693	1.484	1.11
Body condition	0.037	-0.059	0.100	15.19
Temperature	-0.127	-0.454	0.193	3.69
Relative number of heat lifts				
Parameter	Estimate	95% CI$_{low}$	95% CI$_{up}$	% inside ROPE
Intercept	*-0.077*	*-0.186*	*0.026*	*0.94*
Care yes	*0.003*	*-0.007*	*0.013*	*18.22*
Session	0.003	0.001	0.005	13.00
Male	-0.011	-0.023	0.001	2.98
Body condition	-0.001	-0.002	-0.001	100.00
Temperature	0.005	0.001	0.009	2.54

Table A3. Estimates and test statistics from the model analysing exploratory behaviour during the space neophobia test. CI – Credible interval, ROPE – Region of practical equivalence. Significant results are highlighted in bold.

Latency to exit				
Parameter	Estimate	95% CI_{low}	95% CI_{up}	% inside ROPE
Intercept	0.037	-0.256	0.333	2.25
Care yes	-0.003	-0.050	0.045	14.86
Session	**0.010**	**0.005**	**0.014**	**0.00**
Male	-0.003	-0.057	0.050	14.03
Body condition	-0.001	-0.003	0.003	100.00
Temperature	-0.001	-0.010	0.009	64.29

Table A4. Estimates and test statistics from the model analysing habituation. CI – Credible interval, ROPE – Region of practical equivalence.

Latency to exit				
Parameter	Estimate	95% CI_{low}	95% CI_{up}	% inside ROPE
Intercept	-21.380	-50.222	7.489	0.33
Care yes	-0.084	-1.499	1.332	20.58
Trial	0.021	-0.012	0.052	100.00
Male	0.648	-0.901	2.132	13.92
Body condition	0.070	-0.061	0.213	96.19
Temperature	0.627	-0.426	1.654	14.62

Table A5. Estimates and test statistics from the model analysing food motivation during the habituation test. CI – Credible interval, ROPE – Region of practical equivalence.

Latency to exit				
Parameter	Estimate	95% CI_{low}	95% CI_{up}	% inside ROPE
Intercept	2.219	-1.172	5.421	1.73
Care yes	0.152	-0.490	0.764	23.40
Male	0.242	-0.487	0.964	18.49
Body condition	0.005	-0.040	0.052	100.00

Table A6. Estimates and test statistics from the model analysing the number of correct trials performed during the associative learning test. CI – Credible interval, ROPE – Region of practical equivalence.

Latency to exit				
Parameter	Estimate	95% CI_{low}	95% CI_{up}	% inside ROPE
Intercept	11.507	-24.888	47.859	0.34
Care yes	0.029	-1.449	1.478	11.02
Male	0.386	-1.192	1.922	8.98
Body condition	0.014	-0.116	0.140	8.98
Temperature	-0.489	-1.898	0.938	92.96

Table A7. Correlation matrix including both correlation coefficients and p-values across all measures taken during the whole experiment. r_s – Spearman rank correlation coefficient. All p-values are corrected for multiple testing (Holm correction). Significant correlations are highlighted in bold.

	Object neophobia	Latency to exit	Head lifts	Habituation to novel space	Exploration	Habituation to a stimulus card	Food motivation	Correct trials
Object neophobia	$r_s = 1$	**$r_s = -0.78$**	**$r_s = 0.61$**	$r_s = -0.04$	**$r_s = 0.69$**	$r_s = -0.41$	$r_s = -0.13$	$r_s = -0.23$
Latency to exit		$r_s = 1$	**$r_s = -0.89$**	$r_s = 0.01$	**$r_s = -0.68$**	$r_s = 0.11$	$r_s = 0.03$	$r_s = 0.20$
Head lifts			$r_s = 1$	$r_s = -0.02$	**$r_s = 0.58$**	$r_s = 0.06$	$r_s = -0.06$	$r_s = -0.24$
Habituation to novel space				$r_s = 1$	$r_s = 0.16$	$r_s = 0.10$	$r_s = -0.04$	$r_s = -0.19$
Exploration					$r_s = 1$	$r_s = -0.16$	$r_s = -0.04$	$r_s = -0.39$
Habituation to a stimulus card						$r_s = 1$	$r_s = 0.16$	$r_s = 0.06$
Food motivation							$r_s = 1$	$r_s = 0.46$
Correct trials								$r_s = 1$