Title: Developmental trajectories of cognitive traits in meerkats match socio-ecological demands

Tommaso Saccà[1,2], Elisa Protopapa[1,2], Adrian V. Jaeggi[3] & Sofia I. F. Forss[1,2]

[1]*Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland*

[2]*Kalahari Research Centre, Kuruman River Reserve, Northern Cape, South Africa*

[3]*Institute of Evolutionary Medicine, University of Zurich, Zurich, Switzerland*

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Abstract

Understanding cognitive development is fundamental to contextualize adult cognitive phenotypes, and thus the operational pathways for cognitive evolution. The ontogeny of specific cognitive traits is likely influenced by both population-wide pressures, such as ecological demands, and individual-specific factors, including early life experiences. To properly investigate cognitive variation, we must therefore identify species-level developmental trajectories and individual variation from normative ontogeny in natural populations. Towards this goal, we used a longitudinal approach to study the ontogeny of three distinct cognitive traits (physical problem-solving skills, inhibition control, and spatial cognition) in 28 wild meerkats (*Suricata suricatta*), assessed at five key developmental stages from early life to sub-adulthood. Using mixed-effect models, we found that rates of development (learning curves) differed among traits, reflecting variation in the timing of socio-ecological pressures, like the onset of independent foraging and adult cooperative behaviours. Within individuals learning curves, baseline abilities (without the effect of development) or performance at specific time points among the different traits did not correlate, suggesting independent processes underlying performance in the presented tasks. Inhibitory control did not display substantive individual variability in baseline performance and learning curves, possibly reflecting reduced genetic variation or developmental canalization. In contrast, spatial cognition and physical problem-solving both exhibited substantial individual differences in baseline performance and learning curves, suggesting that these traits may be under distinct selective timescales and pressures. Among the measured traits, only physical problem-solving showed consistency in individual performances over time, a pattern that emerged close to the onset of nutritional independence, reflecting critical early timing of foraging competence in this species. Further research should investigate the factors underlying individual differences and their adaptive value.

Introduction

Research on individual differences in cognitive phenotypes is increasingly recognized for its relevance in explaining cognitive evolution (Morand-Ferron et al. 2016). An important and underappreciated source of individual differences in cognitive performance is developmental effects (Thornton and Lukas 2012). The importance of ontogenetically shaped variation in adult cognitive phenotypes for cognitive evolution is twofold. First, individual differences provide the variation upon which selection acts (Darwin 1859). Second, ontogenetically acquired changes in adult cognitive phenotypes can be transmitted to offspring (Zhang et al. 2017; Arai et al. 2009; McGreevy et al. 2019), potentially contributing to differentiation and even speciation (Pfennig et al. 2010; West-Eberhard 2005). Accordingly, species differences in traits measured in adults can be traced back to changes in their developmental trajectories (Rosati et al. 2014). Therefore, studying individual differences in the ontogeny of cognitive traits is essential for understanding cognitive evolution and of particular relevance are studies conducted in the wild, to ensure that results match ecologically relevant pressures (Thornton and Lukas 2012). Recent work has started to evaluate cognitive performance in wild animals at different stages of development. For example, Ashton and colleagues (2018) measured cognitive development experimentally in Australian magpies (*Cracticus tibicen dorsalis*), and Howard-Spink and colleagues (2025) described the ontogeny of foraging competence in orangutans (*Pongo spp.*). However, this line of research is still in its infancy. Empirical work investigating the ontogeny of cognitive traits remains especially sparse beyond the primate taxa and in wild conditions. Overall, we lack detailed information from a multitude of species about normative, population-level trajectories covering distinct cognitive traits, as well as identifying patterns of individuals variability from these norms.

The scarcity of developmental approaches may partly reflect the logistical challenges and resource-intensive nature of longitudinal study designs, which are nevertheless essential for disentangling individual variability from normative developmental trajectories. These challenges are particularly pronounced in species with slow life-histories, such as primates (e.g., Howard-Spink et al. 2025; Rothwell et al. 2022). Ideally, animals should be assessed repeatedly at key points during their ontogeny in their natural environment, with a sampling density sufficient to effectively capture developmental trajectories (e.g. learning curves), and with measures capturing different cognitive traits to ensure wider relevance of findings. Quantifying population-level developmental trajectories and identifying patterns of individual deviations through a longitudinal design is crucial to answer evolutionary questions. First, it characterises individuality within species or populations, providing a foundation for investigating intraspecific evolutionary dynamics. Second, it establishes the baseline needed for phylogenetic comparisons of developmental trajectories and selective pressures.

Within a population, individual variation in ontogenetic cognitive trajectories could facilitate adaptive responses when new selective pressures on existing phenotypes arise due to environmental changes or unpredictability (Dingemanse et al. 2004; Liedtke and Fromhage 2019; Cockrem 2022). For example, given that advanced cognitive abilities may require larger brains, which are energetically costly (Isler and Van Schaik 2009) and thus incur trade-offs with other biological functions such as reproductive success

(Soravia et al. 2022; Kotrschal et al. 2013), periods of food abundance may promote faster cognitive development or higher plateaus, while periods of food scarcity could select for slower developments or lower plateaus (Bell et al. 2018; Fisher et al. 2006). When experienced during early life, ecological pressures such as diet (Nyaradi et al. 2013; Van Heijningen et al. 2022), stress (Pechtel and Pizzagalli 2011; Kosten et al. 2012), physical or social environment (Skoblow et al. 2024; Zeeb et al. 2013; Grimberg-Henrici et al. 2016; Salvanes et al. 2013; Álvarez-Quintero and Kim 2024), have long lasting impacts on the adult cognitive phenotype. Thus, to explain how early-life pressures shape adult phenotypes, we must first determine whether, and how, individuals differ in the early development of cognitive traits. This in turn requires a clear account of normative, species-level developmental trajectories. Crucially, characterising species-typical trajectories is not merely a by-product of studying individual variation, but it provides essential baselines for comparative developmental research.

Heterochrony, or the study of phylogenetic differences in developmental patterns and trajectories, has delivered important scientific advancements in our understanding of the evolution of cognition (Rosati et al. 2014; Wobber et al. 2010a; Langer 2006; Gomez 2005). For example, in the domain of social cognition, comparative studies of early development in areas such as face recognition, gaze following, and goal directed actions suggest that humans rely more heavily on social information than do our closest primate relatives, with such differences emerging early in ontogeny (Herrmann et al. 2007; Rosati et al. 2014). Furthermore, comparisons between closely related chimpanzees and bonobos show that chimpanzees develop both spatial cognition and inhibitory control more rapidly, which has been argued to reflect their more challenging feeding ecology and more despotic social system (Rosati 2019; Wobber et al. 2010b). Although comparative developmental research has provided valuable insights, the field remains disproportionately focused on primates and studies are often conducted in captive or non-ecologically relevant settings. For example, Jacobs et al. (2019) investigated the development of sensorimotor cognition in common ravens (*Corvus corax*) and compared their performance to 13 other species, nine of which were primates and two domesticated species. Their results revealed that ravens reached a sensorimotor stage comparable to that of great apes at only 8-11 weeks of age. This finding challenges the prevailing assumption that extended developmental trajectories are a prerequisite for the emergence of complex cognitive abilities (Rosati 2019). Expanding knowledge of the ontogeny of diverse cognitive traits in multiple taxa, will open new avenues for research and may challenge commonly held assumptions.

Here we present a detailed, longitudinal investigation of early cognitive development in a wild carnivorous mammal, the meerkat (*Suricata suricatta*). We studied meerkat throughout their early ontogeny, from nutritional dependence to sub-adulthood, by experimentally measuring the developmental trajectories of three distinct physical cognitive skills: inhibitory control, spatial cognition, and extractive foraging represented through a physical problem-solving task (Figure 1). These cognitive traits reflect pressures experienced by meerkats in their ecological and social environment of meerkats.

Meerkats are highly social, cooperatively-breeding mammals. Adults and sub-adults contribute to raising offspring, defending against predators and outgroup conspecifics, and maintaining the groups' shared sleeping burrows (Clutton-Brock et al. 2002). Sub-adult, and adult meerkats often must forgo feeding opportunities to engage in cooperative behaviours such as provisioning pups with food (pup feeding), guarding pups at the natal burrow while the rest of the group is foraging (babysitting), or scanning

for predators from elevated positions (raised guarding) (Clutton-Brock and Manser 2016). These cooperative activities, in which individuals supress self-serving behaviours such as foraging to benefit the group, are argued to involve executive functions such as inhibitory control, which enables individuals to suppress short-term goals for longer-term or group-level benefits (Burkart and Van Schaik 2010; Burkart et al. 2014; but see Thornton and McAuliffe 2015).

Moreover, meerkats live in environments with high predation pressure that features limited physical refuges from aerial predators making them rely on underground boltholes that are rapidly accessed in response to alarm calls (Clutton-Brock and Manser 2016). Meerkats seem to possess detailed knowledge of bolthole locations and run directly to the nearest bolthole upon alarm, without relying on random search or immediate environmental cues (Manser and Bell 2004). Consequently, immature individuals must learn proper, adult-like responses to alarm calls (Hollén and Manser 2006). Cognitive processes such as spatial memory and orientation are likely to underpin the ability to quickly and accurately recall the location of these refuges in relation to one's spatial position during foraging and are thus highly fitness-relevant cognitive traits in meerkats.

Finally, meerkats have a complex foraging niche characterised by seasonality and habitat heterogeneity, and immature individuals rely on adults to learn foraging skills, define their food repertoire and acquire complex prey-handling skills (Thornton 2008; Thornton and Hodge 2009; Doolan and Macdonald 1996; Jubber et al. 2025; Thornton and McAuliffe 2006, reviewed in Thornton and Clutton-Brock 2011). Therefore, physical problem-solving is likely an ecologically relevant cognitive trait, particularly in the context of prey handling and foraging success.

Altogether, meerkat pups depend on adults to develop essential survival skills, such as foraging and anti-predator behaviours (Thornton and Clutton-Brock 2011). In the literature, this ontogenetic reliance on social inputs has been linked to predictions about domain-general cognition (i.e. correlated performance across cognitive traits). Burkart and colleagues (2017) propose that reliance on social learning favours the emergence of human-like domain-general intelligence, by enhancing learning efficiency during development and thus increasing any learning capacity (the Cultural Intelligence Hypothesis) which provides fitness benefits that offset the energetic costs of larger brains. On the other hand, strong reliance on social learning may reduce selection pressure on independent, generalized learning abilities (Whiten 2017). The social ecology and cooperative system of meerkats provide an opportunity to evaluate the emergence of domain-general cognition in a non-primate mammalian species.

In this study we repeatedly assessed individual meerkat pups over multiple key developmental life stages (Figure 1). Our longitudinal approach enabled us to ask I) whether distinct cognitive traits develop in parallel within individuals, II) whether relationships among traits were present and whether these change over time, and III) whether performance was consistent across developmental stages. Lastly, we discuss e population-level developmental trajectories for each trait in the context of species-specific socio-ecological demands.

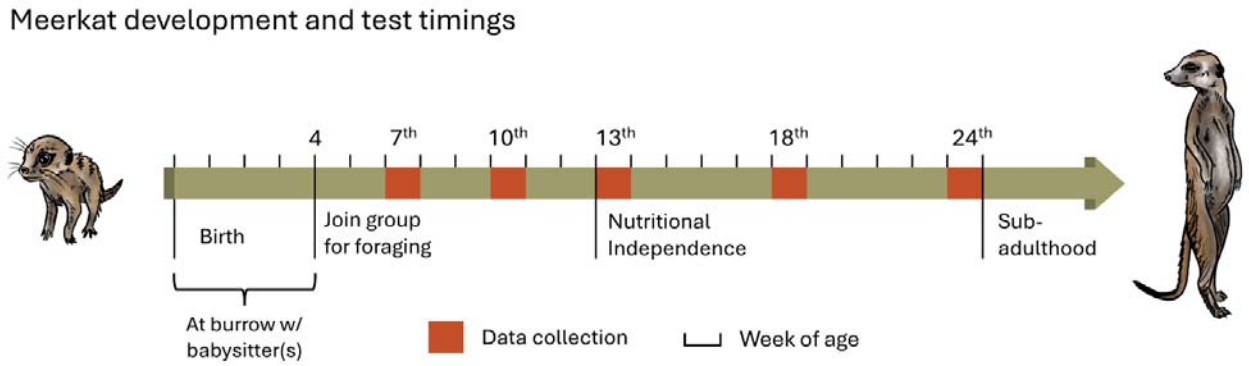

Figure 1: Visual overview of meerkat early life development in relation to data collection. Weeks of age are noted as black ticks, testing weeks as orange rectangles, and key life history stages are noted with longer ticks. See Methods for details.

Methods

Study population

We conducted our study at the Kalahari Research Centre, located in the Kuruman River Reserve (KRR) (26°59′ S, 21°50′ E)in the Kalahari Desert in South Africa. The KRR is a semi-arid savanna with distinct macro-habitats such as red sand dune and shrub grassland (Jubber et al. 2025). Vegetation is sparse during the dry season and more abundant during the wet season (Cozzi et al. 2018). Rainfall averages 266mm per year, and temperatures are on average 30.3 °C during the wet season (maximum 44.2 °C) and 10.1 °C during the dry season (minimum -11.9 °C) (Jubber et al. 2025). Here, we investigated 28 wild meerkats (12 females and 16 males), from 7 groups and 9 litters over two wet Seasons (December 2022 – May 2023, and November 2023 – May 2024). In this species, reproduction is largely monopolised by dominants and the whole group contribute to raise litters and defend against predators or outgroup conspecific (Clutton-Brock and Manser 2016). Males and females are similar in weight and they both contribute to cooperative activities, although males tend to contribute more to raised guard and territory protection and less to offspring rearing (Clutton-Brock et al. 2002; Mares et al. 2012). Females are philopatric and typically remain in their natal group unless forcefully evicted and can maximise fitness by attaining dominance within their group (Clutton-Brock, Brotherton, et al. 1998). Males in contrast must disperse to secure a dominance position, and as subordinates most of their reproductive success comes from prospecting and gaining extra-group copulations (Griffin et al. 2003; Clutton-Brock and Manser 2016; Young et al. 2007). Dispersal is risky due to predators and aggression from neighbours (Clutton-Brock and Manser 2016), and success requires effective decision making under limited cues (Ashton et al. 2020), likely involving cognitive traits such as, but not limited to, spatial cognition for navigating unfamiliar environments, physical problem solving to efficiently locate food, and inhibition control to prioritize effective decision making in this dangerous, highly arousing context.

All groups and individuals included in our study were habituated to close observation and to our test apparatuses before testing, to control for any potential effect of the presence of researchers or introduction of novel materials (Birchmeier et al. 2023).

Ethical statement

Our field experiments and data collection complied with the ethical standards and approval by the University of Pretoria: Ethics Permit NAS061/2022; and research permit from the Northern Cape Province Department of Environment and Nature Conservation, South Africa, FAUNA 0931/2022).

The longitudinal developmental approach

For the first three weeks of life, meerkat pups stay below ground, after which they emerge and remain close to the natal burrow. During this time, they are always joined by usually at least one older group member to ensure their safety (Clutton-Brock, Gaynor, et al. 1998). At about four weeks of age, they start to leave the natal burrow to join their group when it forages. They rely on adults for food acquisition until 12 weeks of age, after which pups are considered nutritionally independent (Clutton-Brock et al. 1999). They are considered sub-adult at 24 weeks of age, and adults at around one year of age after reaching physiological reproductive maturity (Duncan et al. 2025a). We tested individuals on their cognitive performance at five key points during their development (see Figure 1). The earliest point at which we collected data was at the 7th week of life, because this was the earliest time point at which meerkat pups would show interest in interacting with cognitive tests. Around this time pups had left the safety of their natal burrow and were consistently joining their social group for foraging. We re-tested all pups at 10 weeks and 13 weeks, the former being an intermediate point between the first point and nutritional independence, and the latter just after formal nutritional independence and thus during the early juvenile period. At 18 and 24 weeks, we tested all individuals again, the former as an intermediate point in the juvenile period and the latter matching with formal transition to sub-adulthood. Testing weeks were calculated based on supposed date of birth and we allowed on average a two-day flexibility for testing individuals before and after the end of the formal week for the 7th, 10th and 13th week, and four-day flexibility for the 18th and 24th week, to reduce logistical problems in organization. At times, we could not test individuals due to external limitations or to individuals not being interested in the test apparatus.

Test paradigms of cognitive traits

Inhibition control task

To test for the ability to inhibit incorrect intuitive responses, we used a standardized inhibitory control task (referred to as the "cylinder test" in MacLean et al. 2014). Prior to testing, at each developmental week, individuals were habituated to an opaque rectangular box with open ends containing a food reward, training them to access the reward by entering from either side. We presented the box with the opaque side facing the meerkat, and we considered a successful training bout when the meerkat went around the open side and accessed the food reward without touching the opaque side, smelling it or stopping for more than 2 seconds in front of it. After four successful bouts out of five, we assumed the individual had learned the rule associated with the apparatus and was ready to be tested on its ability to recall the learned response and inhibit prepotent but incorrect responses. To do so, we tested the individual

with a transparent version of the same box (Figure 2), presented with the transparent side perpendicular to the individual. We considered a trial successful if the individual didn't touch the transparent side before going around the open side and accessing the food reward. We presented the transparent box five times per individual and developmental week and calculated in how many of the trials each individual performed errors and in how many they successfully passed the criterion. At one developmental week (week 13) for a single group (four individuals), the apparatus was erroneously presented only four times per individual. In other instances, five single tests were excluded post hoc for not meeting specific criteria, such as when individuals failed the trial but did not subsequently access the food reward, and two single tests were not recorded and thus could not be scored. Differences in the number of presentations across developmental weeks were accounted for in the analysis.

Spatial cognition task

We evaluated spatial cognition, focusing on spatial orientation and memory, using a four-armed maze with a central chamber and a starting box at the end of one arm. The starting box, the central chamber and all arms were fully opaque (Figure 2), while the top of the central chamber and the ends of each arm varied between data collection seasons (transparent in the first season and opaque in the second). This change was done to further minimize meerkat possible reliance on external cues that could not be kept constant between trials. The starting box could accommodate an adult meerkat, and the main chamber was spacious enough to allow full movement in all directions regardless of meerkat size. Individuals were habituated to the apparatus each developmental week before testing by positioning them in the apparatus while all three exit arms were fully open for multiple times to ensure they were comfortable with the task materials and being inside the different parts. During habituation, we let each individual (at each developmental week) exit the fully open apparatus from at least two different arms, to avoid them making associations to a specific exit before actual testing. During testing, three exits were covered then by plexiglass, while the fourth was always open and connected to the starting box. At the beginning of each trial, the individual was placed in the starting box, from which it could access the central chamber and all four arms: one leading back to the starting box (which did not allow exit from the maze), two ending in locked barriers, and one that could be opened, constituting the correct exit. During testing, we assessed stress levels by monitoring characteristic lost calls (Collier et al. 2017) and other vocalizations. If the individual showed even mild signs of distress, judged from a combination of vocalizations and physical cues of arousal, we guided them to the correct exit by inserting our hand there and providing visual and auditory cues. We considered the first successful trial as the first trial where the individual successfully found the correct exit without external help. From then on, we tested each individual three more times. In those instances, if the individual became too stressed, we removed it from the test without guiding it to the correct exit and we considered the trial a mistrial. In other cases, when individuals showed no physical cues of stress but produced lost call vocalizations, we allowed the trial to reach its natural conclusion.

The design of the spatial cognition task slightly differed between the first and second season of data collection. During the first season the plastic ends of the three exits and the top of the central chamber were made of transparent plexiglass, and individuals received a small food or water reward only outside the apparatus at the end of testing. In addition, the correct exit for each individual could either be the same as

the previous week or change. During the seventh week of the first study group, the main chamber of the maze was fully transparent. This data point was considered as the same to the datapoints from the first season, for sample size limitations on this particular design. During the second season the plastic end of the three exits were opaque, and to maintain motivation to participate and a positive association with the test individuals received a small food reward inside the apparatus each time they were tested, and the correct exit for each individual always changed between successive weeks, to avoid a purely associative learning effect. We did not consider performance during the first successful trial for each week in the calculation of individual performance, since we could not assume the individual knew the correct exit before the trial started.

Physical problem-solving task

To test the ability to solve physical problems to access a food reward, we presented an apparatus with four chambers, each containing a food reward inside. Three chambers were covered by a different obstacle ('problem', hereafter) to be removed or opened, with one chamber left unobstructed to maintain motivation to participate. One problem was a sheet of toilet paper that was taped to fully close the chamber. The toilet paper for the 7th week of testing was single plied and for successive weeks was double plied, to adjust for the lowest physical strength of seven weeks young pups. The second problem was a transparent flap hanging from the top of the chamber, that needed to be pushed to access the food inside. The third problem featured a transparent door with a hinge on the lower side of the chamber that needed to be pulled opened (see Figure 2). Each problem could be solved with physical motions routinely used while foraging, specifically digging, poking, and pulling. The sides and top of the apparatus were opaque, but the division between internal chambers was made of transparent plastic. To avoid any potential effects linked to neophobia and approaching of novel human-made artefacts (Birchmeier et al. 2023), each week before testing individuals were presented with an apparatus with the four food-baited chambers without any problem to be solved. We only started testing once an individual had eaten from all chambers once in at least two separate presentations to ensure familiarization with the apparatus. During actual test trials, the apparatus consisted of the same four chambers, with each of the three problems blocking the opening of its corresponding chamber and preventing access to the food reward. We considered a problem solved if the individual had found a way to access and eat the food reward inside, even if we could not infer whether the action used was intended to solve the problem. We did not consider a chamber solved if the problem, mainly the transparent door, was opened by accident by an involuntary bump or any other sort of non-active solution.

Role of memory on the development of physical problem-solving task

To investigate whether the ontogeny of performance in the problem-solving task was primarily influenced by learning and memory from repeated exposure over development, we presented the apparatus to an additional six individuals (four males, two females) at ten weeks of age who had not encountered it before at seven weeks of age and recorded their performance. We hypothesised that, if the increase in performance was mainly due to memory and prior exposure, these six individuals would (a) perform similarly to individuals first presented with the apparatus at seven weeks of age, and (b) perform

worse than those same individuals when the latter were re-presented with the apparatus at ten weeks of age.

Data scoring and statistical analyses

We recorded each presentation using video cameras (Hero 9 Black: GoPro Inc., 2020), and we scored cognitive task performance using the software Boris (Friard and Gamba 2016). We scored each behaviour using a predefined ethogram (Supplementary Material Table S1). For the physical problem-solving test, to account for motivational levels, which is known to influence cognitive performance (Van Horik and Madden 2016), we scored the time the individual was interacting with or investigating the test apparatus. For the spatial cognition test, to account for the effect of potential stress on performance, we noted as a binary variable for each trial if the individual produced any “lost call” vocalization during testing. In addition, to account for differences in study design, we noted down whether the design was linked to the first or second season of testing. All analyses were conducted in the open-source software environment R v4.4.0 (R Foundation for Statistical Computing 2024), using RStudio as an interface (Posit team 2025). For Bayesian hierarchical and multivariate model fitting we used the package BRMS (Bürkner 2017). Throughout our analyses, we used weakly informative priors (intercepts: normal(0,2); fixed effects: normal(0,2); standard deviations of random effects: exponential(2); residual correlations: LKJ(2)) to aid model convergence and regularize parameter estimates, thus reducing type I errors (Lemoine 2019). For all models, we confirmed proper model fitting by visual inspection of chain mixing, Rhat values for convergence (all = 1.00) and effective sample size measures (all > 1000). Code and data are available at [add link before submitting].

Population-level developmental trajectories and individual variation

To investigate individual performance over development for each cognitive trait we fitted three sets of Generalized Linear Mixed Models (GLMM) in a Bayesian framework, one for each cognitive task.

Inhibition control - For the performance in the inhibitory control task we used as the response variable the number of trials passed versus the number of total trials per week of testing, assuming a binomial distribution, and we added as explanatory variable the effect of week and of sex.

Spatial cognition - For the performance in the spatial cognition task, we fitted two models, to investigate competing variables linked to study design. First, we used the total amount of errors over the number of trials per week of testing as a response variable, assuming a Poisson distribution, and we added as covariates (a) the number of trials per week where the individual showed mild signs of distress, (b) the week of testing, (c) the sex of the individual, and (d) a binary variable for whether the correct exit was kept the same as for the previous week of testing. Secondly, we fitted a model where all variables were equivalent, but we excluded the binary variable for whether the correct exit changed from the previous week. Instead, we fitted a variable for study design, distinguishing between first and second season. In both models, for the total amount of errors and number of trials we excluded the performance in the first trial per week, since we could not assume the individuals knew the solution and the performance was more due to chance than actual cognitive processing.

In addition, we investigated whether the physical design of the spatial cognition test (i.e., ceiling and arm openings transparent during the first season and opaque during the second season) influenced the level of mild stress experienced by individuals, measured as the occurrence of at least one “lost call” vocalization during a trial. We fitted a Generalized Linear Model (GLM) with the number of trials per individual and week in which mild signs of stress were recorded as the response variable, and season of testing included as an exploratory categorical predictor, assuming a Poisson distribution for the response.

Physical problem-solving - For the performance in the physical problem-solving task we used the number of problems solved over the number of problems available at each developmental timepoint as the response variable, assuming a binomial distribution, and as explanatory variables we used (a) the average time of exploration of the test apparatus for all trials during each week, (b) the sex of the individual, and (b) the week of life (as a continuous variable, week from henceforth).

We added to each of the three models a random individual intercept and a random individual slope for the effect of week. This allowed the models to represent the developmental trend of each individual, accounting for both individual baseline performance after adjusting for the effect of covariates (individual random intercept), and individual differences in developmental rates (individual random slope for the effect of week on task performance). These random effects were estimated as individual deviations (positive or negative) relative to, respectively, the population-level performance (global intercept) and developmental trend (fixed effect of week).

To investigate the amount of variation explained by random intercepts and random slopes, we calculated the proportion of variance explained by each random effect in isolation and in combination of the variation non explained by fixed effects. To do so, we used the function “variance_decomposition” from the package Performance (Lüdecke et al. 2021), which is the suggested approach when working with non-Guassian distribution and complex random structures in Bayesian models fitted with BRMS package, while being functionally equivalent to the widely used adjusted intraclass correlation coefficient (adjusted ICC).

Role of memory on the development of physical problem-solving task

To compare the performance of individuals first presented with the problem-solving task at ten weeks of age with that of individuals first presented at seven weeks and re-presented at ten weeks, we fitted a GLMM with the proportion of problems solved out of those available as the response, assuming binomial distribution. Explanatory variables included sex, the average time spent investigating the apparatus across all trials at each developmental time point, and developmental time point as a factor with three levels according to the experimental condition: (1) first presentation at seven weeks of age, (2) first presentation at ten weeks of age, and (3) second presentation at ten weeks of age. We included individual identity as a random factor.

Individual consistency in task performance

To investigate whether performances could be attributed to individual characteristics, we investigated the proportion of variance explained by the random intercepts and slopes in the models explained in the previous section. However, to investigate whether individual consistency changed over the

course of early life, we used a multivariate hierarchical modelling approach, using the brms package (Bürkner 2021). For each cognitive test, we fitted 5 Generalized Linear Models, one for each week of testing. We fitted the same set of fixed response, explanatory variables and assumed distribution of the models used to investigate individual performance over development, with the exclusion of week of age. For the random part, we allowed the intercept calculation to vary for individual by fitting individual random intercepts. Then, for each cognitive test, we used the multivariate hierarchical design to correlate individual intercepts calculated at each week with each other. Random individual intercepts were calculated as deviation from the global intercept, which was for each model the specific week investigated. Thus, we obtained within each week a set of individual values that highlighted whether the individual performed above or below average, while factoring out the covariates of interests that could confound cognitive performance and create spurious correlations. Thus, comparing individual intercepts among weeks allowed us to investigate whether individuals that performed above average at one point in time (e.g. week 10) were more likely to perform above average at a future developmental stage (e.g. week 13).

Correlation among task performance of the three cognitive traits over the developmental period

To investigate whether performance in one cognitive task was related to performance in another, we extended our hierarchical models into a multivariate framework. We refitted the models described in the section "*Population-level developmental trajectories and individual variation*", retaining for the spatial cognition task the version including study design as a predictor, as it outperformed the alternative model with the binary 'correct exit changed' variable. This multivariate approach allowed us to address two questions: (1) whether individuals who performed better than average in one task also performed better in another, assessed by comparing individual intercepts across tasks/models; and (2) whether individuals who improved more rapidly than average in one task showed similar improvement in another, assessed by comparing individual slopes for the effect of week on performance across tasks/models.

Correlation among task performance of the three cognitive traits at points in time

To investigate whether relationships between performance in any pair of cognitive tasks changed over the course of development, we again used a multivariate hierarchical modelling approach. For each week of testing, we fitted three models (one for each cognitive task) using the same specification (response, predictors, random effects, and assumed distributions) as described in the section "*Individual consistency in task performance*". This framework allowed us to assess, for each week, whether individuals performed above or below average after accounting for confounding variables (individual intercepts). By comparing performance across tasks, we then determined whether relationships between cognitive traits varied across early life.

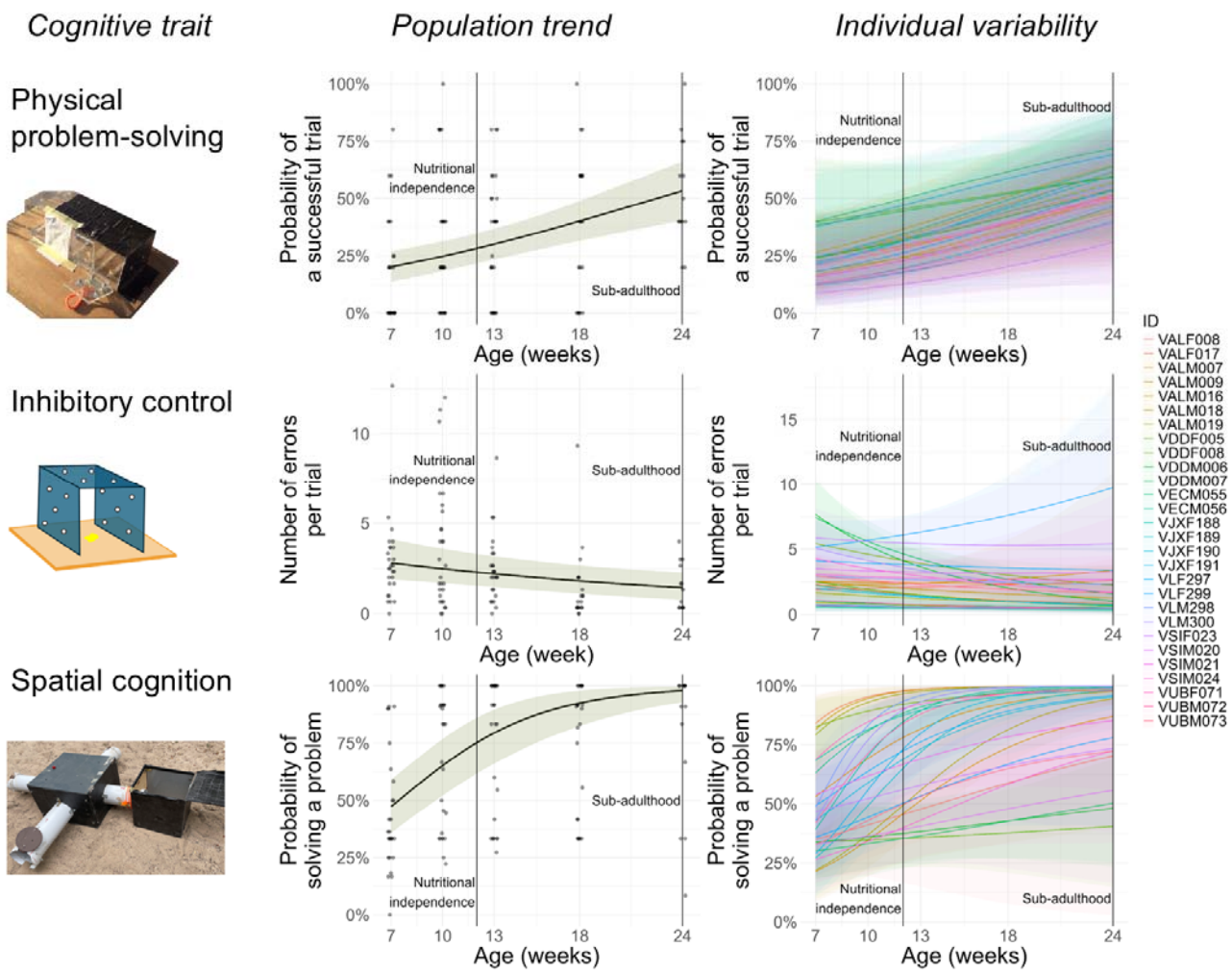

Figure 2: Population-level developmental trajectories (second column) and individual ontogenetic variability (third column) for three cognitive tasks (first column). Vertical lines indicate nutritional independence and sub-adulthood. In all plots, age (weeks of life) is on the x-axis and task performance on the y-axis. Population-level trajectories: black line shows the modelled population mean, green shading indicates the 95% confidence interval, and observed data are plotted in the background. Data points are semi-transparent, with darker shades indicating overlapping points, and jittered along the x-axis for clarity. Individual variability: lines show modelled trajectories for each individual, with shaded 95% confidence intervals; darker shading indicates overlapping intervals. For population-level spatial cognition, predictions average across seasons, and all population-level trends are averaged across sexes.

Results

We report model estimates as the mean with the 95% credible interval in square brackets. Posterior probability ($PP_{support}$) was calculated as the proportion of posterior samples supporting the estimated effect. We encourage readers to treat $PP_{support}$ as a continuous measure of evidence without clear boundaries, and to make their own decision on sufficient levels of credibility. However, to ease interpretation and discussion, we considered effects with $PP_{support} \geq 95\%$ as supported, and effects with $PP_{support}$ of between 70% and 90% as suggestive but inconclusive trends(Farrar et al. 2023). We report the proportion of remaining variation (i.e., not explained by fixed effects) explained by random effects as the median with the 95% credible interval in square brackets. Although negative values for this proportion are numerically impossible, they can appear as artefacts of high variability in the posterior distribution (Lüdecke et al. 2021). When the lower

bound of the 95% credible interval extended below zero, we truncated it at zero and interpreted the effect as not being convincingly different from zero.

Population-level developmental trajectories and individual variation

Inhibition control - Performance in the inhibitory control task increased over ontogeny, with the effect of developmental week having a positive and supported effect (mean effect of week = 0.09, 95% CI [0.05, 0.13], $PP_{support}$ = 100%, Figure 2). There was no evidence that males and females differed in their probability of passing the inhibitory control test (effect of males, relative to females = 0.08, [-0.55, 0.74], $PP_{support}$ = 60.6%). Individual differences in learning curves (random slopes) accounted for 11% [0%, 45%] of the remaining variability that was not explained by fixed effects (from here on referred as "remaining variability"), while individual differences in baseline performance (random intercepts) accounted for 28% [0%, 56%], and the combination of the two explained 18% [0%, 44%]. Thus, we find little evidence for individual deviation from population-level developmental trends in this cognitive task. Individual baseline performance without the effect of covariates (random intercepts) and learning curves (random slopes) showed a non-supported trend towards a negative correlation (correlation = -0.46, [-0.95, 0.62], PP_{suppor}= 83.0%).

Spatial cognition - The performance in the spatial cognition task also showed a supported effect of developmental week (week = -0.04, [-0.07, -0.01], $PP_{support}$ = 99.9%, Figure 2). Stress influenced performance, with individuals being more likely to make mistakes in weeks when they displayed mild signs of stress in a larger number of trials (effect of stress = 0.36, [0.21, 0.50], $PP_{support}$ = 100%). We found no support for a difference between males and females in the average number of mistakes per trial (effect of male, relative to females = -0.03, [-0.61, 0.55], $PP_{support}$ = 54.5%). When the correct exit was kept the same from the previous testing week, we found a non-supported trend in favour of individuals being less likely to make mistakes (consistent exits = -0.12, [-0.42, 0.17], $PP_{support}$= 79%). When we investigated whether test design could influence performance, we found that individuals were less likely to make mistakes during the second season (second season, relative to first season = -0.93, [-1.62, -0.17], $PP_{support}$= 99%). At the same time, they were also more likely to show mild signs of stress during the second rather than the first season of testing (second season, relative to first season = 1.24, [0.04, 2.70], $PP_{support}$= 98%), when ceiling and arm openings were opaque rather than transparent. We used the model including the study design to calculate the proportion of remaining variance explained by random factors, to factor our possible spurious individual effects due to the two seasons.

Including individual learning curves (random slopes) in our model for the development of spatial cognition accounted for 72% [30%, 91%] of remaining variation, while including individual baseline performances (random intercepts) accounted for 82% [34%, 95%] of it. Including the combination of individual learning curves and baseline performance in the model accounted for 56% [0%, 82%] of remaining variability. Thus, we find strong support for individual differences in the development of performance in the spatial cognition task in both baseline abilities and learning curves. The proportion of remaining variability was lower when random slopes and random intercepts were included together, possibly due to the covariance between the two factors (correlation = -0.66, [-0.91, -0.21], $PP_{support}$= 99.9%). This suggests that when analysed separately, each factor also captures part of the variability explained by the other. The negative covariance

between random slopes and intercepts indicates that individuals with above-average baseline performance (i.e., making more errors after accounting for covariates) tended to show below-average rates of developmental change (i.e., a faster decrease in errors over time). Thus, individuals that performed worse at a baseline showed faster learning curves during development.

Physical problem-solving - The performance in the physical problem-solving task increased over ontogeny, with the effect of developmental week having a positive effect (week = 0.27, [0.16 - 0.39], $PP_{support}$= 100%, Figure 2). Individuals that spent more time exploring and interacting with the apparatus were more likely to solve the problems it posed (exploration time = 0.03, [0.01, 0.05], $PP_{support}$ = 100%). We found a trend for males being less likely to solve a task than females, though this finding did not reach significance (males, relative to females = -0.41, [-1.34, 0.52], $PP_{support}$ = 81.6%).

Individual learning curves (random slopes) accounted for 58% [42%, 70%] of the remaining variability, while individual baseline performances (random intercepts) accounted for 42% [9%, 63%] of it. The combination of random slopes and intercepts accounted for 43% [22%, 61%] of remaining variability. Thus, we find moderate to medium to high levels of support for differences in both individual baseline performances and individual rates of development (learning curves). The decrease in variability explained when both random slopes and intercepts are allowed to vary is possibly due to the two random factors covarying with each other (correlation = -0.64, [-0.88, -0.22], $PP_{support}$= 99.5%) and explaining in isolation part of the other factors explained variability. Thus, individuals with poorer baseline performance showed faster learning curves during development.

Role of memory on the development of physical problem-solving task

Performance in the physical problem-solving task in individuals who were presented with it for the first time at seven weeks of age was worse than that of individuals who were presented with it for the first time at ten weeks of age (first presentation at seven weeks, relative to first presentation at ten weeks = -1.11, [-2.19, 0.01], $PP_{support}$ = 98%). We did not find support for a difference in performance between individuals who interacted with the apparatus for the first time at ten weeks, or those that interacted with it for the second time at ten weeks, although there was a non-supported trend for the latter outperforming the former (second presentation at ten week, relative to first presentation at ten week = 0.32, [-0.78, 1.45], $PP_{support}$ = 72%).

Individual consistency across development in task performance

Inhibitory control – We did not find support for individual performance at one developmental time point in predicting performance at the subsequent time point (Figure 3). A non-supported positive trend was observed between week 7 and week 10 (correlation = 0.22, [–0.43, 0.80], PPsupport = 75%), but this disappeared in later comparisons: week 10 vs. week 13 (correlation = –0.07, [–0.72, 0.55], PPsupport = 58%), week 13 vs. week 18 (correlation = –0.09, [–0.74, 0.58], PPsupport = 60%). Likewise, performance at the onset of subadulthood (week 24) was not predicted by any earlier time point (Figure 3): 18 weeks (correlation = 0.02, [–0.65, 0.67], PPsupport = 53%), 13 weeks (correlation = –0.02, [–0.67, 0.64],

PPsupport = 53%), 10 weeks (correlation = 0.05, [–0.63, 0.67], PPsupport = 57%), or 7 weeks (correlation = –0.00, [–0.67, 0.65], PPsupport = 50%).

Spatial cognition – We did not find support for consistency in individual performance across developmental time points (Figure 3), although correlation estimates were consistently positive. A non-supported positive trend was observed between week 7 and week 10 (correlation = 0.24, [–0.30, 0.79], PPsupport = 79%) and between week 13 and week 18 (correlation = 0.21, [–0.41, 0.79], PPsupport = 74%), while support for the week 10–13 comparison was even weaker (correlation = 0.12, [–0.47, 0.74], PPsupport = 65%). Likewise, performance at the onset of sub-adulthood (week 24) was unsupported in predicting by earlier time points: 18 weeks (correlation = 0.14, [–0.53, 0.77], PPsupport = 66%), 13 weeks (correlation = 0.09, [–0.56, 0.72], PPsupport = 61%), 10 weeks (correlation = 0.12, [–0.54, 0.76], PPsupport = 64%), or 7 weeks (correlation = 0.15, [–0.49, 0.78], PPsupport = 67%).

Physical problem-solving – We found strong support for consistency in individual performance across consecutive developmental weeks, emerging early in ontogeny (Figure 3). A non-support positive trend was present between week 7 and week 10 (correlation = 0.24, [–0.30, 0.73], PPsupport = 80%), which became supported at later stages: week 10 versus week 13 (correlation = 0.60, [0.22, 0.93], PPsupport = 99%) and week 13 versus week 18 (correlation = 0.60, [0.22, 0.94], PPsupport = 99%). Reflecting this pattern, performance at the onset of sub-adulthood (week 24) was predicted by performance at week 18 (correlation = 0.51, [0.07, 0.90], PPsupport = 97%), week 13 (correlation = 0.41, [–0.04, 0.79], PPsupport = 96%), and week 10 (correlation = 0.44, [–0.00, 0.85], PPsupport = 96%), while at the earliest stage (week 7) the relationship remained a non-supported trend (correlation = 0.23, [–0.25, 0.73], PPsupport = 80%).

Correlation among task performance of the three cognitive traits over the developmental period

Because performance metrics were scaled in opposite directions (higher values indicated better performance in inhibitory control and physical problem-solving, while lower values indicated better performance in spatial cognition) we mirrored the correlation estimates involving spatial cognition. Accordingly, positive correlations between task performances consistently indicate that higher performance in one task was associated with higher performance in the other, while negative correlations indicate the opposite.

Inhibitory control & spatial cognition – We found a non-supported trend between the rates of development of the two traits, calculated as the random slope of the effect of week on performance for each individual, with faster learning curves in inhibitory control performance associated with slower learning curves in spatial cognition performance (correlation = -0.21, [0.82, -0.44], $PP_{support}$ = 74%). When comparing individuals' baseline performance after removing the effects of covariates (random intercepts), we found another non- supported trend, with a better performance in inhibitory control associated with a worse performance in spatial cognition (correlation = -0.35, [–0.80, 0.14], $PP_{support}$ = 91%).

Spatial cognition & physical problem solving – No supported correlation was detected between developmental rates (correlation = -0.01, [–0.45, 0.43], $PP_{support}$ = 52%). At the baseline performance level,

we observed a non- supported trend, with a better performance in the physical cognition task associated with a worse performance in the spatial cognition task (correlation = -0.27, [–0.68, 0.18], $PP_{support}$ = 88%).

Inhibitory control & physical problem solving – We found non- supported positive trends for both developmental rates (correlation = 0.21, [–0.43, 0.79], $PP_{support}$ = 75%) and baseline individual performance (correlation = 0.22, [–0.31, 0.71], $PP_{support}$ = 79%), with better inhibitory control performance associated with better physical problem-solving performance.

Correlation among task performance of the three cognitive traits at points in time

Similarly to the previous paragraph, we mirrored the correlation estimates involving spatial cognition so that positive correlations between task performances consistently indicate higher performance in one task being associated with higher performance in another, while negative correlations indicate the opposite.

Inhibitory control & spatial cognition – We found no supported associations between inhibitory control and spatial cognition at any time point (Figure 3). Non- supported negative trends were present at 7 weeks (correlation = –0.17, [–0.77, 0.41], $PP_{support}$ = 71%) and 10 weeks of age (correlation = –0.38, [–0.79, 0.08], $PP_{support}$ = 94%). These trends disappeared at later time points: 13 weeks (correlation = 0.00, [–0.76, 0.69], $PP_{support}$ = 50%), 18 weeks (correlation = –0.12, [–0.80, 0.57], $PP_{support}$ = 63%), and 24 weeks (correlation = 0.05, [–0.71, 0.78], $PP_{support}$ = 56%).

Spatial cognition & physical problem solving – Associations between spatial cognition and physical problem solving were also non- supported at all time points (Figure 3). Estimates were consistently positive across development, with posterior support increasing from 7 weeks (correlation = 0.09, [–0.41, 0.58], $PP_{support}$ = 64%) to 10 weeks (correlation = 0.22, [–0.19, 0.63], $PP_{support}$ = 83%) and 13 weeks of age (correlation = 0.39, [–0.16, 0.91], $PP_{support}$ = 90%), although none reached significance. Support for a positive correlation then declined at 18 weeks (correlation = 0.04, [–0.49, 0.54], $PP_{support}$ = 55%) and 24 weeks (correlation = 0.15, [–0.55, 0.84], $PP_{support}$ = 66%).

Inhibitory control & physical problem solving – No supported associations were detected between inhibitory control and physical problem solving at any time point (Figure 3). Trends fluctuated across development: at 7 weeks (correlation = –0.03, [–0.67, 0.61], $PP_{support}$ = 54%), 10 weeks (correlation = 0.01, [–0.44, 0.48], $PP_{support}$ = 51%), and 13 weeks (correlation = –0.08, [–0.72, 0.60], $PP_{support}$ = 60%), and remained similarly inconsistent at 18 weeks (correlation = –0.08, [–0.74, 0.62], $PP_{support}$ = 60%) and 24 weeks (correlation = 0.22, [–0.52, 0.88], $PP_{support}$ = 72%).

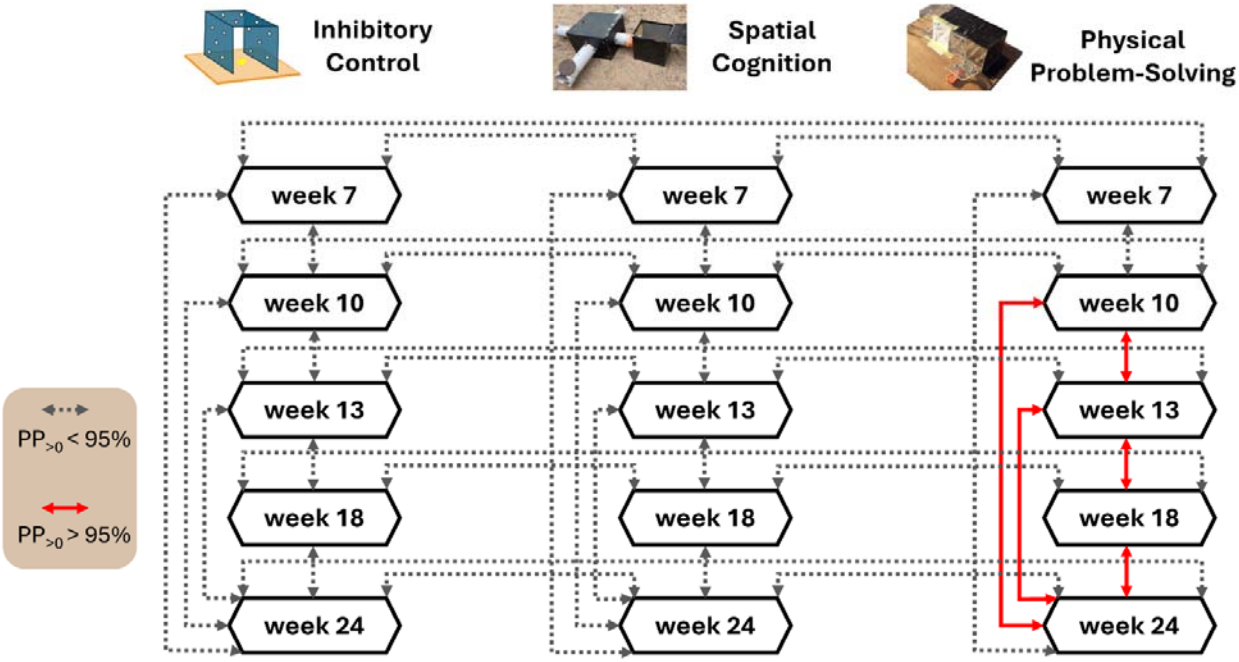

Figure 3: Summary of correlations between individual random intercepts among tasks, and between tasks, over the developmental period. Full, red lines are positive, supported correlations, while dotted lines are non-supported correlations.

Discussion

In this study, we investigated the developmental trajectories of three ecologically relevant cognitive traits in wild meerkats. We found evidence that meerkat pups increase their cognitive performance over their ontogeny, spanning from early life to early sub-adulthood, and that this cognitive development was present for all measured traits: inhibition control, spatial cognition and physical problem-solving skills. At the population level, physical problem-solving skills showed the fastest increase in performance (steepest learning curves, Figure 2) and reaches a plateau before pups grew into sub-adulthood. Inhibitory control and spatial cognition (spatial orientation and memory) showed instead a more linear increase in performance and did not reach a plateau in the developmental timeframe investigated (Figure 2). The timing of cognitive development in each trait can be linked to specific socio-ecological demands in meerkats. Young meerkats must reach sufficient independent foraging competence around week 12, as social provisioning by adults stops around this age. Thus, meerkat pups face early in their development a necessity to solve physical problems to access and process food resources. This timing aligns with our findings on the cognitive ability to solve extractive physical problems, where meerkats had a 76% (CI 95% [57%, 89%]) probability of solving a physical barrier assuming 30 seconds of exploration at 12 weeks of age. Despite an early onset of independent foraging ability (Duncan et al. 2025a), meerkat pups remain within their family groups way beyond their foraging competence is reached, up until three years of age before potentially founding or immigrating to a new group (Clutton-Brock et al. 2002). Contrary to physical problem-solving skills necessary for successful foraging, meerkats can rely on social information and cues from their group members for collective coordination and spatial navigation throughout life. Accordingly, our findings suggest that the developmental trajectory of spatial cognition and inhibitory control show slower

learning curves and lack of clear plateaus within the developmental timeframe we investigated (Figure 2), reflecting less urgent need for such cognitive capacities early on in meerkat life. Even when reacting to aerial alarm calls, critical for survival, pups can follow the heading of nearby older individuals to reach safety (Thornton and Clutton-Brock 2011; Hollén and Manser 2006). Since investing in neuro tissue is known to be an expensive evolutionary pathway (Isler and Van Schaik 2009; Navarrete et al. 2011; Kotrschal et al. 2013; Van Schaik et al. 2023), relying on collective information can represent an energetically conservative strategy compared to costly investment in individual intelligence (Simons 2004; Berdahl et al. 2013), particularly during early life. Accurate spatial memory, to find protective locations relevant for survival such as boltholes, may require repeated visits to each part of the groups' territory providing direct experience with such locations. Therefore, spatial memory is likely to take longer to develop effectively. Accordingly, an early peak in spatial cognition could incur increased energetic costs rather than fitness benefits. A similar argument can be made for our findings from the inhibitory control task, yet in the context of social interactions and group coordination. We hypothesized that meerkats need a certain level of inhibitory control due to their cooperative social caretaking behaviour, where sub-adults and adult helpers significantly contribute to feeding the offspring of the dominant pair, and thereby frequently must restrain own food consumption in favour of offspring needs (Clutton-Brock et al. 2001). However, juveniles are seen to contribute less to these cooperative activities than older individuals (Clutton-Brock et al. 2002) and as such, inhibitory control may also be energetically constrained during early development. The timing of the developmental trajectories of inhibitory control, spatial cognition, and physical problem solving, in relation to meerkat socio-ecological demands, suggests that these traits reflect information-processing abilities central to the meerkat cognitive niche.

Meerkats show consistent and repeatable differences in their contributions to cooperative behaviours, with some individuals helping more than others (English et al. 2010; Carter et al. 2014) and males' relative contributions differing from females' (Clutton-Brock et al. 2002). We hypothesized that the ability to self-inhibit behaviour would be a cognitive underpinning of cooperative behaviours (Burkart and Van Schaik 2010; Burkart et al. 2009). However, we found little individual variation in inhibition control for either baseline performance or developmental trajectories in early ontogeny. In addition, we did not find a difference in performance between male and female meerkats. Although differences in contributions to cooperative activities could be linked to inhibitory control, meerkats contributions are also based on body condition (Clutton-Brock et al. 2000), foraging success (Clutton-Brock et al. 2001), individual necessities (e.g., gathering information for future dispersal: Clutton-Brock et al. 2002), but not on kinship (Clutton-Brock et al. 2001; 2000), and are under hormonal control (Dantzer et al. 2019). Thus, individual differences in cooperative contributions could be linked to differences in individual characteristics, such as feeding skills or personality traits, rather than differences in ability to inhibit behavioural responses. The conserved early life development of inhibitory control in meerkats could be due to reduced genetic variability underlying this trait. This could be due to two possible mechanisms: (1) selection removing sub-optimal variance due to the highest values being energetically expensive and the lowest values being behaviourally dysfunctional, or (2) generally low genetic variability in this population, where a large proportion of individuals showed signs of inbreeding (Nielsen et al. 2012). Alternatively, genetic variability could still be present but the observed trait could be developmentally canalized, where the influence of environmental or genetic factors on

resulting phenotypes is limited (Siegal and Bergman 2002). The latter idea could be supported by the argument that pressures experienced by meerkats on inhibitory control are specific to different stages of early development. Thus, individuals could gain more benefits from matching optimal levels of inhibition control rather than exploit cognitive niches of specialization through individual differentiation. Specifically, meerkat pups may be selected for little inhibitory control early in their development, as adults react to signals of hunger and feed more often pups that beg more intensively and persistently (Brotherton et al. 2001; Manser et al. 2008). However, this strategy poses diminishing returns as pups grow older and adults stop responding to their begging calls after three to four months of age (Madden et al. 2009). Older meerkats could need a minimum level of inhibitory control to engage in cooperative activities by supressing prepotent, self-serving behaviours such as ingesting foraged prey, after which internal and physiological states could drive individual variation. However, although we did not detect individual variation in this cognitive trait in early development, such individual signatures could emerge later in life under different ecological or social pressures. Future studies should investigate the repeatability of performance in adulthood and if performance is linked to enduring differences in cooperative contributions.

In the spatial cognition task, we found strong evidence for differences in individual baseline performances (without the effect of development, apparatus design or stress), as well as different rates of development (learning curves) of this trait. Differences in baseline performances could be due to intrinsic individual characteristics underlying spatial cognitive traits involved in this task (spatial navigation and memory), intergenerational hormonal effects (Walkenhorst et al. 2025) or variation in individual tendencies to use external or internal cues for orientation. Spatial orientation can be either based on position in space in relation to an individual's own position and direction (egocentric orientation), or on external cues like landmarks (allocentric orientation) (Bottini and Doeller 2020). Our study design focused on egocentric orientation, as the apparatus was opaque and the orientation of the correct exit in relation to any other perceivable external cue like magnetic field and group position (through sound) was inconsistent among trials. We found that when the apparatus was even partially transparent during the first season, meerkats were more likely to make mistakes. Taking this experimental change into consideration in our statistical analyses, we evaluated whether differences in performance among the two field seasons of data collection could be explained by different levels of stress, or other methodological issues such as maintaining the same correct exit as the previous testing period. However, individuals were more likely to be stressed during the season in which they performed better. In addition, we did not find strong support for maintaining the correct exit as the previous testing period in explaining individual performance. Therefore, a decrease in performance during the first season could be linked directly to the partial transparency of the apparatus. Partial transparency could have influenced performance in two ways. First, it could have involved the ability to inhibit intuitive responses, as individuals had to inhibit their attempts to go through a transparent obstacle. However, we did not find that performance in the inhibition control predict performance in the spatial maze in our dataset. Secondly, individuals may have had increased access to inconsistent external cues. Increased use of allocentric orientation in navigating the maze would have decreased performance as external cues were not kept constant during testing. Interestingly, individuals that were below average in baseline abilities (higher number of errors throughout development without the effect of covariates such as sex and stress) had faster learning curves (they decreased their number of errors more strongly during

development), suggesting that there are minimum levels of cognitive functions that individuals are selected to reach at the onset of sub-adulthood. Future research should investigate whether individual differences in learning curves can be linked to the socio-ecological environment experienced during early life. Individuals living in ranges more frequented by aerial predators could encounter more occasions to learn spatial cognition skills by repeatedly reacting to alarm calls, while living in a larger group could provide more chances to learn correct response socially.

In the physical problem-solving task, we found moderate to high levels of support for differences in performance both at an individual baseline, as well as for individually different rates of increase in cognitive performance over development (learning curves). In the calculation of these parameters, we accounted for the effects of normative development, sex and explorative effort. Individual performance was consistent from the 10th week until sub-adulthood, suggesting that differences in physical problem-solving performance in meerkats arise early in development and are enduring. Individuals who were presented the task for the first time at ten weeks of age outperformed their peers who were presented it for the first time at seven weeks and were not substantially different from those same peers when the latter were re-presented with it at ten weeks of age. This suggest that the increase in performance we observe during early development is not exclusively due to memory and previous test experience, but in fact likely linked to the development of brain functions and motor skills. Although motor skills are usually seen as a confounding factors when investigating underlying cognitive ability, recent work has questioned whether motor skills and cognitive abilities could be meaningfully disentangled from each other (Barton and Barrett 2025). As such, a physical problem-solving test where motor skills are involved is a meaningful assessment of cognitive ability. Our results can be linked to different strategies that meerkats use when they forage. During natural foraging individuals scan the ground and can find preys on the surface or identify specific places in the environment where they commit to a foraging bout with the chance of finding prey below ground. Foraging strategy changes with age, with meerkats at different life stages preferring different prey types and sizes (Jubber et al. 2025; Duncan et al. 2025b). Young individuals may also vary in their approach, either engaging more frequently in energetically costly foraging bouts with uncertain returns but valuable learning opportunities, or spending more time scanning the surface, expending less energy and committing to foraging only when more certain cues are detected. These different strategies could reflect variation in individual baselines and learning curves in their physical problem-solving abilities and be linked to the conditions experienced during development. For example, social differences in early life (Turner et al. 2025) or physical environment could provide individuals with different foraging learning opportunities from social or non-social cues, as helpers differ in their teaching contributions (Thornton 2008b) and food availability is heavily seasonal and affected by rainfall in the study region (Doolan and Macdonald 1996). In addition, similarly to performance in the spatial cognition task, when individuals had a lower overall performance, they showed faster learning curves. Thus, meerkats could be selected to reach a minimal necessary level of physical cognition at the onset of sub-adulthood to handle ecological challenges arising from independent foraging.

Individual performances across the three tasks were uncorrelated, both in their learning curves, individuals' baseline abilities, or performance at any point in time, suggesting that in meerkats inhibitory control, spatial cognition (navigation and memory) and problem-solving ability are more likely to represent

modular rather than domain-general adaptations (Burkart et al. 2017). Their cognitive underpinnings may therefore be independent of one another, and potentially subject to separate selective pressures. In addition, we found that meerkats' chances of successfully passing a standardized inhibitory control test at the onset of sub-adulthood (model predicted performance = 53.3%, 95% CI [37.7%, 68.1%]) were worse than 20 of 32 species investigated by MacLean and colleagues (2014) for which data on cylinder task performance was present. However, meerkat performance in inhibitory control could be not fully developed by this point in their ontogeny. Since meerkats are a cooperative species that show extensive reliance on social learning to acquire foraging skills and antipredator behaviours (Thornton and McAuliffe 2006; Thornton and Clutton-Brock 2011; Thornton and Hodge 2009; Thornton 2008a), our results from a cooperative mammal do not align with the hypotheses that explain primate general intelligence, where a strong reliance on social learning (Burkart et al. 2017) and cooperative care (Van Schaik et al. 2023; Burkart and Van Schaik 2010; Burkart et al. 2009) select for general intelligence (e.g., Forss et al. 2016) or enhanced cognitive abilities. Our results highlight that selective pressures on cognition may not be operating uniformly and require fine scale investigations including different animal taxa.

Conclusion

In this study, we investigated the development of three cognitive traits in wild meerkats during a critical developmental period, spanning from early life through nutritional independence to the onset of sub-adulthood. We found evidence that physical problem-solving, inhibition control and spatial cognition (spatial orientation and memory) emerge at different times of development, likely because of distinct socio-ecological demands. Support for individual deviations from population-level trends was present for problem-solving ability and spatial cognition, but not for inhibitory control. This suggests that while the development of inhibitory control is to some extent conserved in wild meerkats, the development of problem-solving ability and spatial cognition appears less constraint and may be more influenced by genetic or environmental factors. Future studies should uncover the effect of intrinsic individual characteristics (e.g. genetics) as well as external early life influences (social and ecological environment) in determining individual differences in cognitive development and their adaptive benefits.

Author contributions

Tommaso Saccà: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Software, Visualization, Writing – Original Draft. Elisa Protopapa: Investigation, Data Curation, Writing – Review & Editing. Adrian V. Jaeggi: Methodology, Supervision, Writing – Review & Editing. Sofia I. F. Forss: Conceptualization, Methodology, Supervision, Funding Acquisition, Writing – Review & Editing

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Declaration of interests

The authors declare no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT (OpenAI, 2025) to improve grammar, clarity and quality of language. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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