Individual variation in cognitive performance: developmental and evolutionary perspectives

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Animal cognition experiments frequently reveal striking individual variation but rarely consider its causes and largely ignore its potential consequences. Studies often focus on a subset of high-performing subjects, sometimes viewing evidence from a single individual as sufficient to demonstrate the cognitive capacity of a species. We argue that the emphasis on demonstrating species-level cognitive capacities detracts from the value of individual variation in understanding cognitive development and evolution. We consider developmental and evolutionary interpretations of individual variation and use meta-analyses of data from published studies to examine predictors of individual performance. We show that reliance on small sample sizes precludes robust conclusions about individual abilities as well as inter- and intraspecific differences. We advocate standardisation of experimental protocols and pooling of data between laboratories to improve statistical rigour. Our analyses show that cognitive performance is influenced by age, sex, rearing conditions and previous experience. These effects limit the validity of comparative analyses unless developmental histories are taken into account, and complicate attempts to understand how cognitive traits are expressed and selected under natural conditions. Further understanding of cognitive evolution requires efforts to elucidate the heritability of cognitive traits and establish whether elevated cognitive performance confers fitness advantages in nature.

Keywords: cognition; development; evolution; individual differences; meta-analysis; reproductive fitness

Running headline: Individual cognitive variation

1. INTRODUCTION

Imagine a team of alien scientists visiting London during the summer of 2012, selecting a random sample of 20 humans and conducting experiments to test theories of human evolution. Some trials involve swimming, and most subjects perform rather poorly. However, one subject happens to be Michael Phelps, the Olympic record holder. Based on Phelps' performance, the aliens conclude that humans have an astounding capacity for high-speed movement through water, underpinned by physiological and behavioural adaptations including efficient conversion of stored carbohydrates to sugars and fine-scale motor control for efficient propulsion. From this, they argue in favour of the aquatic ape hypothesis, which postulates that ancestral humans were under strong selection for an aquatic existence.

Though this story is a fanciful caricature, it has important parallels in the modern science of comparative cognition, where great emphasis is often placed on the performance of a small number of subjects. Striking individual variation in performance is typical of many cognitive tests, and many influential papers in the field focus on the successful performance of a small subset of individuals, with relatively little emphasis on those that do not succeed. Indeed, the remarkable abilities of celebrated animals such as Kanzi the bonobo, Alex the African grey parrot and Betty the New Caledonian crow are often taken to be indicative of the abilities of their species as a whole. Here, we consider how individual differences in performance on cognitive tests might be interpreted from developmental and evolutionary perspectives and examine predictors of individual performance from data in published papers.

As Darwin pointed out, individual differences are of critical importance in biology, as they "afford materials for natural selection to act on" ([1] pp. 59-60). Following this insight, Darwin's cousin, Francis Galton, along with other founding figures of psychology such as Spearman and Thorndike, placed great emphasis on the differences between individuals, a tradition that continues today in psychometric research. In contrast, most comparative researchers tended to pay scant attention to variation within species. Indeed, the behaviourist tradition in comparative psychology, with its emphasis on universal learning processes [2], and ethology, with its focus on species-typical adaptations or "instinct" [3], traditionally ignored individual variation, treating it simply as noise around the population mean.

More recently, two developments have re-focused attention on individual differences. First, the influence of Piagetian developmental psychology [4] and the cognitive revolution of the 1950s [5] inspired comparative researchers to develop paradigms to test their subjects' capacities to form mental representations, make inferences, reason and even learn language [6]. Many of these studies involved intensive contact with only one or a few animals, leading researchers to report individual-level data and notice their subjects' idiosyncrasies and individuality. However, the causes of individual differences in test performance were seldom investigated and their ecological and evolutionary consequences remained unexplored.

The second advance occurred within behavioural ecology. Long term field studies of individually recognisable animals allowed researchers to examine individual behaviour in response to challenges in the physical and social environment and relate behaviour to reproductive fitness [7]. Over time, it became apparent that animals commonly show consistent individual differences in behaviour across contexts, leading to the development of the field of animal personality [8,9]. Towards the end of the twentieth century, an upsurge of interest in socially-learned animal traditions and culture led to an increased focus on the generation and transmission of novel behaviours through populations [10,11]. Consequently, some researchers began to examine the characteristics of the individual innovators that generate solutions to novel problems [10]. However, while this research has improved our understanding of the potential fitness consequences of individual behavioural differences and the effects of individual characteristics on innovative propensities, it has tended to ignore underlying psychological mechanisms. Consequently, the variation revealed in cognitive studies remains difficult to interpret. Systematic analyses are thus necessary to understand how this variation arises.

(a) Meta-analyses of individual variation

Rigorous investigations of factors contributing to individual differences are often limited by low sample sizes. To overcome this limitation, we performed systematic searches of the animal cognition literature and conducted meta-analyses on data pooled from multiple studies. We focused on four experimental paradigms, chosen because individual performances (rather than just mean performances) were reported relatively frequently:

Object permanence (OP) studies test whether subjects understand that objects continue to exist when out of sight. Subjects must typically search for an object that has been moved directly behind one or more barriers (visible displacement) or placed into a container that is then moved behind one or more barriers (invisible displacement). Performance, generally measured in relation to Piaget’s six developmental stages of object permanence in children [4], is assessed by recording where the subject searches for the hidden object.

Functional properties of objects (FPO) studies test whether subjects recognise the physical properties that (e.g. length, rigidity) render objects (e.g. tools) suitable for use to access a reward. Subjects must choose between objects that are suitable or unsuitable for the task across a number of trials.

Causal reasoning (CR) ‘folk physics’ studies test whether subjects’ ability to gain rewards from a physical task (often with the use of a tool) is based on an understanding of the causal structure of the task. Subjects are generally given a series of training trials to learn the basic requirements of the task. Those that reach a specified criterion are then given one of more transfer tests of their ability to respond appropriately to the causally relevant features of the task (e.g. traps where food rewards may fall and be lost).

Mark tests of mirror self-recognition (MSR) examine whether subjects will use a mirror to inspect a mark placed on some visually inaccessible part of their body. A colourless, odourless “sham” mark is generally used a control. Elevated levels of mark-directed behaviour when in front of a mirror are taken as evidence that the subject recognises the reflection as itself.

We obtained information on 46 studies of OP, 30 studies of FPO, 28 studies of CR and 14 studies of MSR. Of the 118 studies, only 68 (= 58%) provided information on individual performance and, of these, 54 reported full information on the sex, age and history of subjects. We obtained information on subjects’ characteristics in a further seven studies by cross-referencing other papers or from replies to requests to authors (further details in electronic supplementary material, ESM). The dataset for subjects with full information incorporated 42 different species from 1691 individual experiments. To facilitate future research, we strongly urge researchers in all areas of animal cognition to report the performances and individual characteristics of their subjects.

We identified the effects of individual characteristics on performance in experiments using generalized linear binomial models in R (R Development Core Team, http://www.R-project.org). For all paradigms except MSR, the dependent variable was a binomial term with the number of successful trials as the numerator and the total number of trials attempted as the denominator. For MSR, measures of performance differed between studies (e.g. time spent touching marks; number of touches), so the response was a binary term (1 or 0) indicating success or failure as coded by experimenters. Separate analyses were run for each paradigm, including individual identity, species and study as random factors to control for repeated measures. For CR studies, we ran separate analyses of training trials and transfer tests. Dependent factors were 'Place of birth': wild/captivity; 'Rearing history': mother-reared/hand-reared/enculturated; 'Prior experimental experience': none/participated in experiments on other topics/same topic, 'Age': juvenile/adult and ‘Sex’: female/male. Additional factors were, for CR studies, whether or not the task involved ‘Tool use’ and, for OP studies, the respective 'Piagetian stage': 1-6 and whether the task involved ‘Visible’ or invisible displacements. We started with full models and identified the significance of each factor by removing it from the model and comparing the AIC of the two models using ANOVAS (see Methods, Table S1, Table S2 in ESM). We incorporate our results into a broader review of the causes of individual cognitive variation and their potential evolutionary implications.

2. LIMITATIONS OF THE “COGNITIVE CAPACITY” PERSPECTIVE

Some authors take the view that convincing evidence from a single individual is sufficient to demonstrate that a given cognitive trait is within the capacity of the species (e.g. [12]). Although true in a trivial sense, this perspective imposes two important limitations on the field. First, it is extremely sensitive to the criteria used to infer success or failure and hence risks generating both false positives and negatives. Second, it may foster a binary perspective, treating cognitive traits as either present or absent within a species, rather than falling along a continuum. This detracts attention from the extent of variation within and between species, and hence limits the power of the field comparative cognition to be truly comparative.

(a) What does success or failure really mean?

In many studies, a subject is considered to have passed a test if it chooses the correct option significantly more often than chance. For instance, in CR studies, subjects that reach criterion on initial training trials may be presented with transfer tests intended to preclude the use of learned rules based on visible cues (see [13]). However, as transfer tests typically involve the same binary choice over multiple trials, subjects could learn a new rule based on the visible properties of the new task. For instance, a subject adopting a “win-stay, lose-shift” strategy of repeating its choice if successful on the first trial or switching if unsuccessful, could attain nine or ten correct choices out of ten trials, and thus reach criterion without understanding anything about the causal structure of the problem. It is therefore difficult to say with certainty that individuals that pass tests really possess the cognitive ability under investigation. Rather than giving subjects multiple trials of one or two transfer tests, a more powerful approach may be to provide them with a single trial of many different tests (see also [14]). Here, spontaneous correct performance despite variations in the visible characteristics of the apparatus would provide stronger evidence for an understanding of cause-and-effect.

What of the unsuccessful individuals? Perhaps their cognitive abilities are simply inferior. Alternatively, echoing MacPhail’s arguments for a lack of species-level intelligence differences [15], poor performance may instead reflect non-cognitive contextual variables including motivation, visual acuity or dexterity. Poor performance could also result not from deficiencies in the cognitive ability under examination, but from failures to focus on relevant information and inhibit unnecessary prepotent behavioural responses. For instance, in our FPO dataset 25% of the subjects that failed showed a 0% success rate, indicating that rather than choosing at random they adopted a strategy of attending to a cue that was incorrect (figure S1). Thus, an unfortunate learned association could potentially mask some subjects' true abilities. Similarly, in trap-tube tests on New Caledonian crows (*Corvus moneduloides*), Taylor et al. [14] argued that failures by some subjects may have resulted from difficulties in inhibiting the tendency to pull food towards themselves. Standardised measures of inhibitory control, coupled with detailed analyses of behaviour during successes and failures, as advocated by Seed et al. [13] and Chappell & Hawes [16] may also prove highly informative in determining the causes of variation in performance.

(b) Sample sizes limit comparisons in comparative cognition

Rather than the binary distribution implied by the "cognitive capacity" perspective, many cognitive traits are likely to show quantitative variation between individuals and species. However, small sample sizes often limit the potential for systematic analyses of quantitative data within individuals, within species and between species. At the individual level, protocols allowing only a few trials or tasks per subject may not provide sensitive measures of performance. For example, all five chimpanzees in our dataset that participated in more than five tests of Piagetian stage 6 object permanence failed in at least one of the tests, whereas seven of the nine subjects given fewer tests showed a 100% success rate across tests. This suggests that small numbers of tasks are insufficient to capture the true variation in individual abilities, rendering comparisons between conspecifics difficult. Similarly, in OP (figure 1*a*), FPO (figure 1*b*) and CR transfer tests (figure 1*c*) larger sample sizes of subjects show greater variation between conspecifics (see figure S2, Relationship between sample size and variance in ESM; note that plots for MSR were not possible as measures of individual success were binary). Thus, the validity of comparative analyses across species is limited because, for most species, too few individuals have been tested to determine robust measures of the range of performance, average performance or maximal performance. Standardised testing may greatly improve the scope for such comparisons. For example, in a large-scale test battery, Herrmann et al. found that children consistently outperformed chimpanzees on social but not physical tasks, suggesting that humans have specialised socio-cognitive skills in addition to relatively conserved skills for dealing with the physical world [17]. Greater collaboration between researchers, including greater standardisation of experimental protocols and the use of online data repositories to facilitate pooled analyses of subjects' performances from different laboratories (see [18,19]) will also improve the scope for robust analyses. In particular, there is ample scope for analyses of the predictors of individual differences, incorporating information on characteristics such as sex, age, body condition, breeding status and rearing conditions.

3. DEVELOPMENTAL INFLUENCES ON COGNITION

Behavioural and cognitive phenotypes, and particularly those associated with cortical brain regions, tend to show greater plasticity than morphological traits [20]. This plasticity is particularly prevalent in large-brained species with extended developmental periods [21], such as the primates and corvids that are the favoured subjects of much current research in comparative cognition. Consequently, even if methodological and analytical advances allow for more robust conclusions as to the cognitive abilities of test subjects, our ability to interpret the evolutionary significance of these abilities may remain limited unless we examine how cognitive traits are manifested under varying conditions, and how they change during development. For many cognitive traits, we may expect to see improvements into adulthood, as neural systems develop and individuals acquire greater experience. This is borne out in our analyses of CR transfers, where, across species, adults tend to outperform juveniles (figure 2*c*; note that figure 2 shows raw data). In contrast, juveniles outperform adults in CR training (figure 2*d*), perhaps due to elevated curiosity or motivation. Interestingly, developmental trajectories appear to be influenced by sex, with juvenile females outperforming males while males outperform females in adulthood in FPO (figure 2*b*). We hope that future meta-analyses will establish the robustness of such sex effects and spur research into their causes.

(a) Development, evolution and the "cognitive capacity" perspective

Successful completion of a cognitive task by a small subset of subjects is typically reported with warnings that "results should be interpreted with caution". Nevertheless, authors often go on to claim that the species has a "capacity" for the trait in question and may suggest that the trait is adaptive or, if the study involves primates, that it represents an "evolutionary precursor" of a human trait. However, the fact that the brain of one individual can generate a particular cognitive solution tells us little about the relative influence of developmental and genetic factors, the prevalence of the cognitive trait in the population as a whole, or whether the trait is of adaptive value. For any given genotype, environmental variation may often generate a range of phenotypes. Consequently, observations from a small number of individuals offer limited insights into the range of possible phenotypes, particularly if tests are conducted in highly artificial environmental conditions. For example, Mr Akira Haraguchi can recite pi to 83,431 decimal places, but given that this took years of training, what does it really tell us about human memory capacities in general? One might make similar arguments about the abilities of certain animals in cognitive tests, particularly given that previous experimental experience often leads to substantial increases in performance (figure 2*a*, *b*, *d*, *e*). If abilities are only manifested by a few individuals under artificial conditions and with extensive training, it is difficult to envisage how they could be selected for. We argue that the field would benefit from moving away from the notion of a species-level cognitive capacity and instead advocate a broader approach, charting how cognitive abilities vary in response to environmental and genetic factors.

(b) Effects of rearing environments

Henrich and colleagues [22] have pointed out that, in human psychology, grand claims are made all too often on the basis of samples of people derived entirely of what they term WEIRD (Western, Educated, Industrialised, Rich and Democratic) societies. They have argued persuasively that such sampling biases fail to account for developmental influences of local conditions and cultures and hence fail to explain the diversity of behavioural and cognitive processes across human populations. In many cases it seems that WEIRD subjects may in fact be particularly non-representative outliers. For instance, in cross-cultural studies of the Müller-Lyer visual illusion and economic games testing cooperation, punishment and fairness, WEIRD subjects differ significantly from people of other backgrounds, typically clustering at extreme ends of the human distribution [22]. Clearly, perceptual and decision-making processes are subject to developmental influences, and great caution is needed before making claims of human universals.

Similar arguments hold true for studies of non-human animals. Comparative cognition relies to a large extent on captive animals whose developmental trajectories may be radically different from their free-living counterparts, thus complicating attempts to understand the function and developmental and evolutionary history of cognitive traits. In some cases, the captive environment may artificially dampen abilities typical of wild animals. For instance, Boesch has argued that the poor performance of captive chimpanzees in experimental studies of prosociality and cooperation is at odds with their seemingly complex cooperation and coordination when hunting or encountering rival groups in the wild [23,24]. While claims of cognitive sophistication derived from observational data on wild animals in the absence of experiments must be taken with a pinch of salt [25], we must also be careful in judging seemingly poor abilities in caged subjects. There may also be instances in which the relative comfort and lack of risk in captivity may result in artificially elevated results. For example, the presence of abundant food and lack of predation pressure may facilitate the persistence of arbitrary, socially learned traditions [26] and promote the manufacture and use of tools in normally non-tool using species [27,28]. Impressive feats by captive animals may be the manifestation of cognitive abilities latent in their wild counterparts, but unless we understand the developmental inputs necessary for such abilities to be expressed we cannot begin to unravel how they evolved.

Differences in rearing environments also have important implications for comparisons between species, or between conspecifics. Social or physical deprivation during early life can alter patterns of gene expression [29] and lead to severe impairments in neural, emotional and cognitive development [30–32]. At the other extreme, enculturation in great apes has been suggested to promote an understanding of intentions which would not otherwise develop [33]. Comparative studies between or within species may therefore only be appropriate if variations in rearing environments are taken into account. For instance, comparisons of captive non-humans with “wild” (but typically WEIRD) humans might simply reveal the outcome of differing developmental environments, rather than realised species differences in ability [23,24]. Indeed, unlike orphaned, sanctuary-raised chimpanzees [17], enculturated chimpanzees' social skills appear comparable to those of children [34]. Similarly, in our dataset, enculturated individuals consistently outperformed others across all paradigms except MSR (figure 2*a*-*d*). In addition, hand-reared individuals outperformed mother-reared subjects in OP (figure 2*a*) and CR transfer tests (figure 2*c*). An understanding of individual variation between and within species must incorporate analyses of the effects of differences in developmental histories.

4. INDIVIDUAL VARAIATION AND GENERAL INTELLIGENCE

When a subject performs well in a cognitive test, does it have a specific aptitude for the ability under investigation, or might it be an all-rounder with elevated abilities across cognitive domains? The dominant, ecological approach in comparative cognition tends to emphasise cognitive adaptations to specific environmental challenges [6]. Perhaps as a result, individual performance in a given test tends to be interpreted in isolation despite the fact that, for many subjects, information is available from a multitude of different experiments. The extent to which individual cognitive abilities are specialised in particular domains has major implications for debates regarding mental modularity that are the focus of Call's contribution to this issue [35], so we review the evidence only briefly here.

In human psychometric tests, individual cognitive performances tend to correlate strongly across different domains. Typically, up to 50% of the variance in cognitive test batteries is accounted for by a single factor, termed "general intelligence" or *g*. *G* factors across different test batteries tend to be strongly positively correlated, and are associated with key health and life outcomes (reviewed in [36,37]). However, despite these important findings, comparative researchers have largely eschewed *g*, so little is known about how general intelligence evolved, the mechanisms underpinning it, or how it is manifested across species.

Recent meta-analyses are suggestive of genus-level differences in general intelligence among primates, with great apes consistently out-performing other genera across cognitive domains [38,39]. However, similar analyses including non-primates remain difficult due to sample size limitations and differences in experimental protocols. In our dataset, information from more than one experimental paradigm is available for only 16 of the 42 species and, for these, performance in one paradigm does not predict performance in others (figure S3; figure S4). Moreover, in studies of FPO and in the training phases of CR experiments, ‘study’ but not ‘species’ as a random term accounted for a substantial proportion of the total variance, suggesting that variation in experimental design between studies precludes detection of species-level differences (table S2, figure S3). In OP, MSR and CR transfer tests our analyses did show significant differences between species (table S2), but these may be of limited validity. First, contrary to expectation, closely related species were not similar in performance (table S3). Second, performances between studies may not always be comparable. For example, pigeons appear to score very highly in mark tests of MSR, but this is due to the use of an intensive training regimen [40]. The fact that species rankings differed between the paradigms may therefore be explained by variation in experimental design rather than a lack of species-level intelligence differences.

At the individual level, the evidence for general intelligence remains equivocal. Two recent field experiments on birds found no clear intercorrelations between tasks [41,42], while in song sparrows *Melospiza melodia*, individual song repertoire size (an indicator of vocal learning ability) correlated positively with performance on a laboratory test of inhibitory control, but not with performance on a motor task, colour association learning or reversal learning [43]. More standardised test batteries showed evidence for a *g* factor accounting for more than 30% of variance in performance in mice (*Mus musculus*; reviewed in [44]), and weaker but statistically significant effects in cotton-top tamarins (*Saguinus oedipus*) [45]. However, like many human psychometric test batteries, these studies employed a narrow range of tasks with the emphasis on physical problem solving and few if any tests of social cognition. Individual-level analyses of Herrmann et al.'s test battery, which comprised equal numbers of social and physical tasks, found little support for a unitary *g* factor. Instead, performance among children was best explained by separate spatial, physical and social factors, while for chimpanzees physical and social cognition loaded onto a single factor, in addition to the spatial factor [46]. Analyses by Vonk & Povinelli of the performance of seven chimpanzees across 136 tasks over more than a decade also failed to provide strong support for a unitary *g* factor. Here, one female, Megan, generally outperformed her peers, showing similar accuracy in physical and social tasks, but other subjects appeared to be more specialised in one or other domain [47]. The great wealth of data from comparative cognition laboratories will be invaluable in understanding the extent of individual cognitive specialisations in non-human animals.

5. INDIVIDUAL VARIATION AND THE EVOLUTION OF COGNITION

A central aim of comparative cognition is to elucidate the evolutionary origins of cognitive mechanisms across species. Two central components of this aim are efforts to delineate and categorise cognitive mechanisms (e.g. [16,48–50], this issue) and implement phylogenetic analyses to reconstruct their evolutionary history [19]. Equally importantly, we must seek to determine the selective pressures driving cognitive evolution by considering individual variation in its ecological and evolutionary context. Natural selection acts on heritable traits that confer a competitive advantage in access to resources or mating opportunities.

Consequently, when a subset of subjects appears to be capable of a certain cognitive feat, we must ask two questions. First, is the trait heritable? Second, does it confer fitness benefits?

(a) Heritability of cognitive traits

The extent to which the cognitive abilities of parents are inherited by their offspring is central to our understanding of cognitive evolution, but has received surprisingly little attention from comparative researchers and most work has been conducted on humans. Twin and adoption studies have consistently revealed that a substantial proportion of the variance in general intelligence can be attributed to genetic influences, with estimates ranging from 30-80%, increasing with age [36]. Strong genetic influences have also been reported for various brain structures and regions, for elements of brain functioning [51], and for specialised abilities such as face perception and recognition [52,53]. Nevertheless, at a molecular level, there are still no genetic loci reliably associated with intelligence in healthy individuals. Indeed, continuous variation in cognitive abilities is likely to be influenced by numerous interacting quantitative trait loci, rather than being closely associated with particular genes [36].

A growing number of studies also points towards a significant genetic contribution to individual cognitive variation in non-humans (reviewed in [54,55]). Perhaps the strongest evidence comes from insects, where experiments have shown rapid divergence in associative learning abilities in artificial selection lines [54]. Moreover, high-learning lines show concomitant declines in larval competitive ability, suggesting that evolutionary trade-offs play a role in maintaining genetic variation in associative learning abilities [56]. The extent of genetic influences on the more specialised cognitive abilities that are the principal focus of contemporary comparative cognition remains unknown. Are the top performers in cognitive tests likely to produce bright offspring? The small number of subjects in most comparative laboratories will limit our ability to answer this question, but two recent developments provide cause for hope. First, research is increasingly revealing a host of often surprisingly sophisticated cognitive abilities in invertebrates, fish, rodents and other animals that can be kept in large numbers [57–59] and are thus amenable to quantitative and molecular genetic studies. Second, there is a growing emphasis on studying cognition in the wild. Field researchers have developed a host of ingenious experimental methods to examine a range of cognitive abilities, including navigation in a range of invertebrates and vertebrates [60], spatial memory in hummingbirds and passerines [61] physical cognition in tool-using birds and primates [62–64] and social cognition in group-living mammals [65,66]. Moreover, novel statistical techniques now allow identification of multiple co-occurring mechanisms of learning and cognition in natural populations [67], while quantitative geneticists are developing increasingly sophisticated tools to map the genetic structure of behavioural and neuroanatomical traits within populations [68,69]. The integration of these approaches, particularly in taxa such as birds where genetic and environmental effects can be manipulated through cross-fostering, is likely to yield important insights in coming years.

(b) Do cognitive abilities confer fitness benefits?

Might the variation we see in cognitive tests have evolutionary consequences? Evolutionary hypotheses typically invoke adaptive advantages of cognitive abilities, from extracting embedded food items [70] to manipulating or learning from conspecifics [71,72], yet the consequences of individual cognitive variation are rarely tested explicitly. Studies investigating whether and how individual variation in cognition is reflected in reproductive success is essential to further our understanding of cognitive evolution.

The most direct approach is to move out of the laboratory and examine how variation in the cognitive abilities of wild animals relates to their ability to compete for resources and mates and, ultimately, to maximise their genetic contribution to the next generation. No study has yet related individual cognitive variation directly to reproductive fitness, but recent work on great tits (*Parus major*) provides evidence for a relationship between cognition and competitive abilities. Cole & Quinn quantified individual tits' propensities to solve a novel lever-pulling foraging task (presumed to reflect underlying cognitive traits) and explore a new environment (a personality trait on the proactive-reactive axis) in standardised conditions in captivity, finding that both traits showed high individual repeatability. Interestingly, while exploratory behaviour correlated positively with the ability to competitively monopolise food resources in the wild, problem-solving was negatively correlated with competitive ability [73]. These findings raise the intriguing possibility that poor competitors may employ elevated cognitive abilities as an alternative strategy to obtain resources. However, it is important to note that the psychological processes underpinning problem-solving in this study and the extent to which they are under cognitive control are unknown. It may be that, rather than understanding anything about the logical structure of the task, successful problem solvers simply persist in manipulating the task at random until they are rewarded [74,75].

In addition to their potential role in obtaining resources, cognitive traits may come under sexual selection if individuals value the abilities of prospective partners. In humans, ample evidence suggests that individuals of both sexes place great value on cognitive abilities when choosing mates (e.g. [76,77]). Moreover, general intelligence, measured through cognitive test batteries, correlates positively with male semen quality, suggesting a possible link between cognition and fitness [78]. In other species, the strongest links between psychological traits and fitness have been found in studies of bird song. The development of song control nuclei in the brain is highly sensitive to stressors in early life. Consequently, males that experience relatively benign developmental conditions, or whose genotypes confer resilience to stressors tend to learn songs that are more attractive to females and have elevated reproductive success [79]. There is also some evidence to suggest that good singers may perform better on foraging tasks, raising the possibility that song-learning may be related to other cognitive traits [43]. Beyond song learning, the most compelling evidence for a relationship between mate choice and cognition comes from a recent study on satin bower birds (*Ptilonorhynchus violaceus*). Keagy et al. [80] presented birds with two problem-solving tasks that exploited males' aversion to red objects on their bowers. Males that were quicker to remove or cover up offending objects obtained more copulations than did poor problem-solvers. However, as with other studies of innovative problem-solving, the cognitive abilities (if any) involved in removing or covering red objects have not been characterised. Moreover, as females did not directly observe males' problem-solving performance, their mate choice preferences must have been mediated by other, unmeasured intervening variables.

While studies of the fitness consequences of conserved learning mechanisms and general problem solving capacities are beginning to generate important insights [54,55,73], they may tell us little about the consequences of variation in "higher" processes such as inferential learning, causal reasoning or theory of mind that are the focus of much attention in comparative cognition. Arguably the strongest, albeit indirect, evidence that variance in such abilities impacts on fitness comes from studies of wild cercopithecine primates. Here, playback experiments have revealed that cognitive abilities including transitive inference, recognition of third-party relationships and representations of hierarchically structured relationships underpin the formation and maintenance of social relationships [65,81]. There is also clear evidence that the quality of individuals' social bonds has major fitness consequences for both males and females [82,83]. Together, these two lines of evidence suggest that, in these species, it pays to be smart. Of course, it is possible that much of the individual variation captured in cognitive tests merely represents non-adaptive phenotypic plasticity with no functional consequences (see [54]). However, if we are to understand how cognition evolves, further research linking carefully characterised individual differences in cognitive abilities with reproductive success in wild animals is a clear priority.

6. CONCLUSIONS

Far from being mere noise, information on individual differences is critical for the future development of the field of comparative cognition. Rather than focusing on the most successful or apparently human-like performances among test subjects, we advocate a move towards explicit consideration of the factors that generate individual differences. We urge researchers to report individual characteristics and performance (including negative results) as a matter of course, to develop standardised protocols to facilitate comparisons between studies wherever possible and to deposit results in online repositories to facilitate meta-analyses. Careful examination of the factors influencing individual performance can help unravel the developmental influences on cognitive traits and assist in determining whether variation represents adaptive plasticity in response to local conditions. In time, collated datasets may also permit us to develop sophisticated phylogenetic analyses charting not only the presence or absence of cognitive traits, but also their relative prevalence in different species. Finally, we must ask whether individual differences in cognitive traits are heritable and whether they have consequences for reproductive fitness. Together, these different approaches can harness the value of individual cognitive variation to unravel the evolution of animal minds.

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FIGURE LEGENDS

Figure 1: Variation in success rates of individuals of different species in experiments of (*a*) object permanence, (*b*) object properties and (*c*) causality transfers. Each dot represents a single individual; dots arranged in a single vertical line represent multiple individuals from one species. Variation among individuals within species increases with sample size, limiting the validity of between-species comparisons where few individuals have been tested.

Species from left to right, with sample sizes of individuals and number of studies in brackets:

(*a*) *Ara maracana* (1 individual/1 study); *Macaca fuscata*(1/1); *Melopsittacus undulatus* (1/1); *Nymphicus hollandicus* (1/1); *Gorilla gorilla* (2/2); *Nomascus gabriellae* (2/1); *Nomascus leucogenys* (2/1); *Pan paniscus* (2/1); *Psittacus erithacus* (2/2); *Symphalangus syndactylus* (2/1); *Cebus capuchinus* (3/1); *Leucopsa rothschildi* (3/1); *Oreonax flavica* (3/1); *Garrulus glandarius* (4/1); *Hylobates lar* (4/1); *Streptopelia risoria* (4/1); *Macaca mulatta* (7/2); *Saimiri sciureus* (7/1); *Saguinus oedipus* (8/1); *Tursiops truncatus* (8/1); *Callitrhix jacchus* (11/1); *Pongo pygmaeus* (12/3); *Pan troglodytes* (18/8); *Canis canis* (32/2); *Felis catus* (33/2).

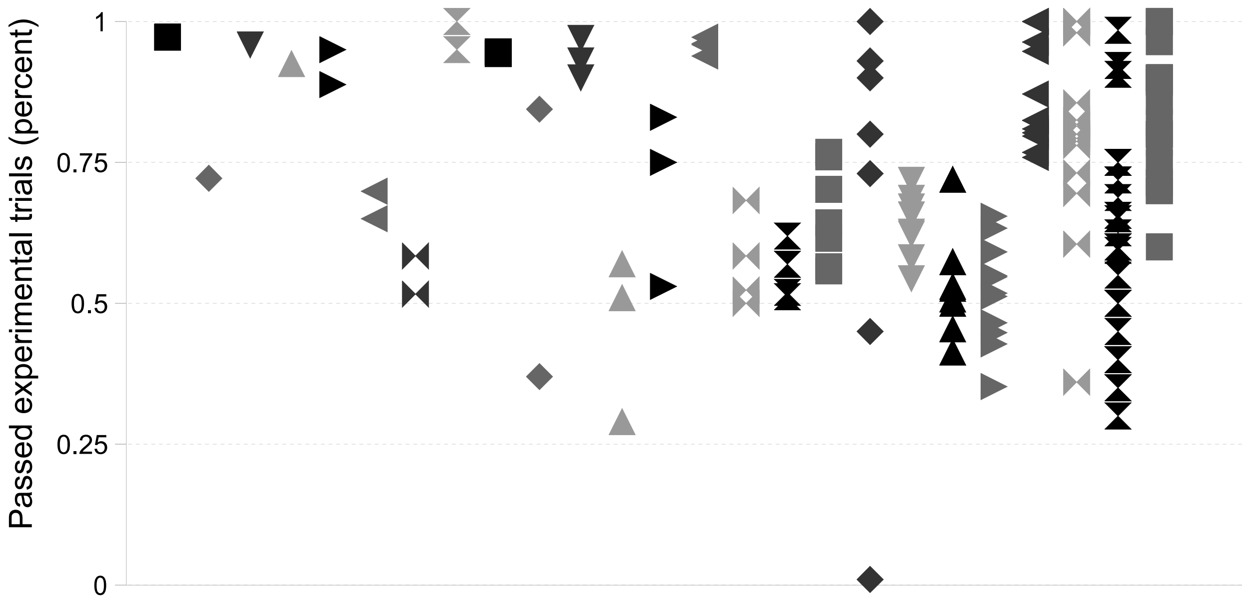
(*b*) *Corvus moneduloides* (2 individuals/2 studies); *Octodon degus* (4/1); *Cactospiza pallida* (5/1); *Gorilla gorilla* (6/1); *Pongo pygmaeus* (8/2); *Cebus libidinosus* (10/3); *Cebus apella* (19/3); *Pan troglodytes* (22/3).

(*c*) *Gorilla gorilla* (3 individuals/2 studies); *Bunopithecus hoolock* (4/1); *Corvus moneduloides* (7/2); *Cactospiza pallida* (9/2); *Pan paniscus* (9/3); *Pongo pygmaeus* (9/3); *Cebus apella* (10/3); *Corvus frugilegus* (10/2); *Pan troglodytes* (18/5).

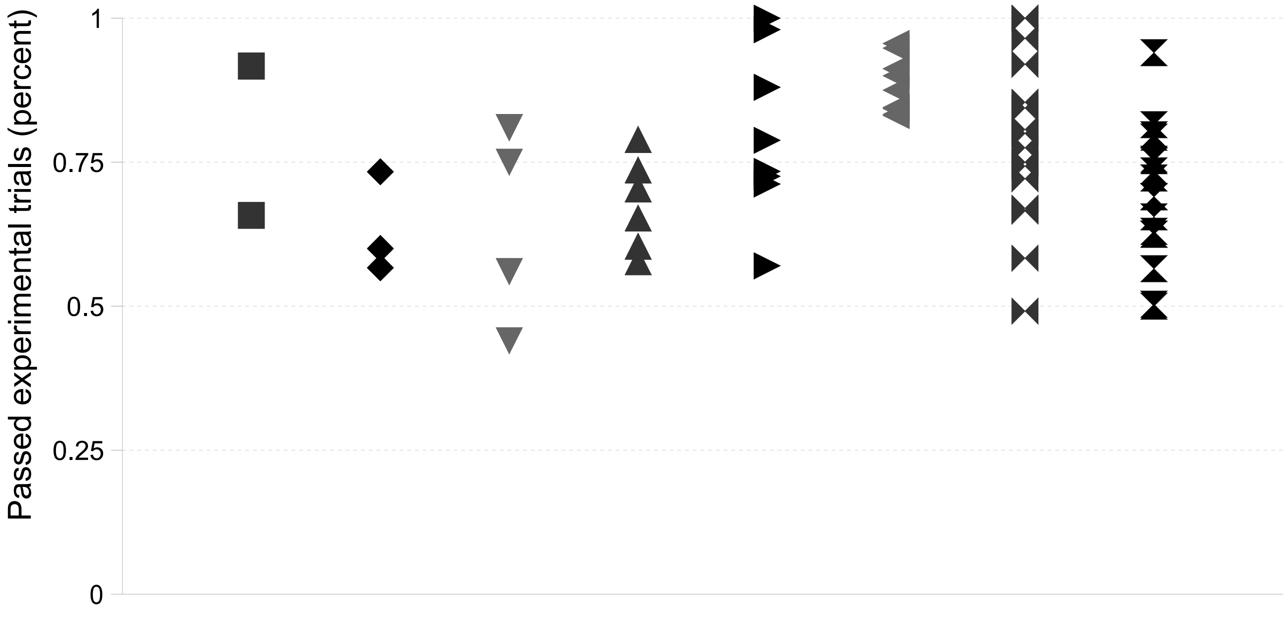
Figure 2: Success rate by individual characteristics in experiments of (*a*) object permanence, (*b*) object properties, (*c*) causality transfer, (*d*) causality training and (*e*) mirror self-recognition. The black lines in the boxplots (*a*)-(*d*) depict the median percentage of trials solved in a given experiment, with boxes and whiskers indicating the quantiles. Values are based on raw data and can contain multiple entries per individual. The bars in (*e*) depict the

percentage of individuals deemed by experimenters to have passed the mark test. Lines above the boxplots and bars connect values that are significantly different in GLMM analyses, correcting for other factors. Stars indicate significant differences: two stars indicate categories with significantly higher success rates than those with one star, which in turn had higher success rates than those with no stars. Note that, as the figure shows raw data, not controlling for other significant factors, some significant differences are not apparent from visual inspection alone.

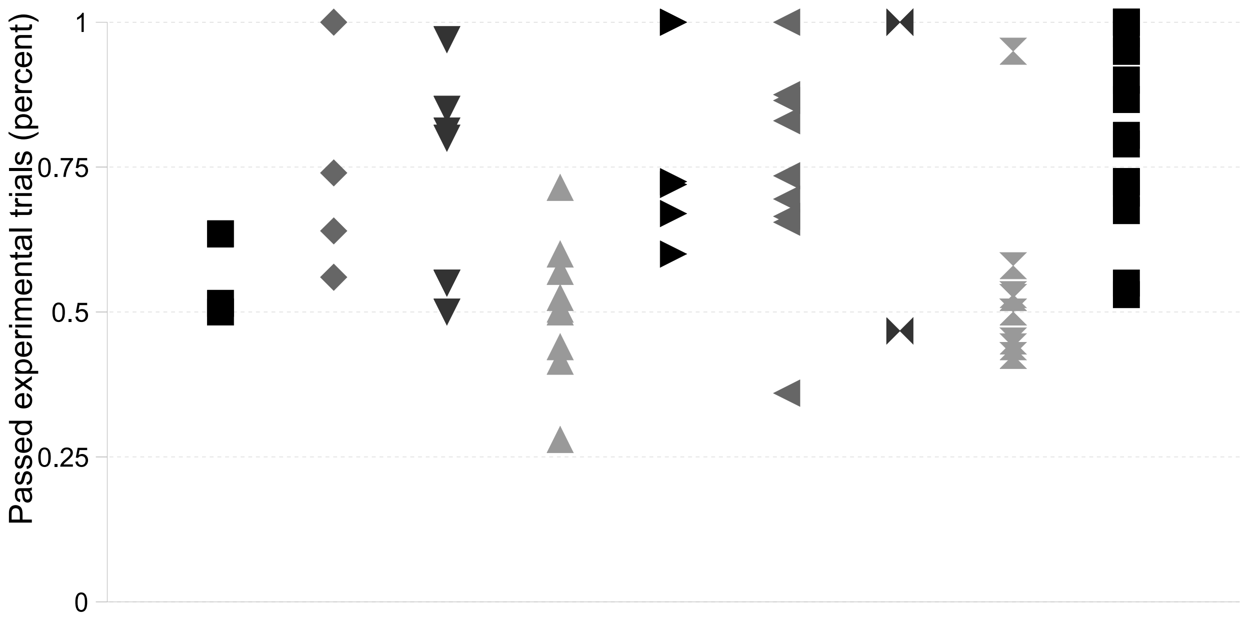
a) Object Permanence

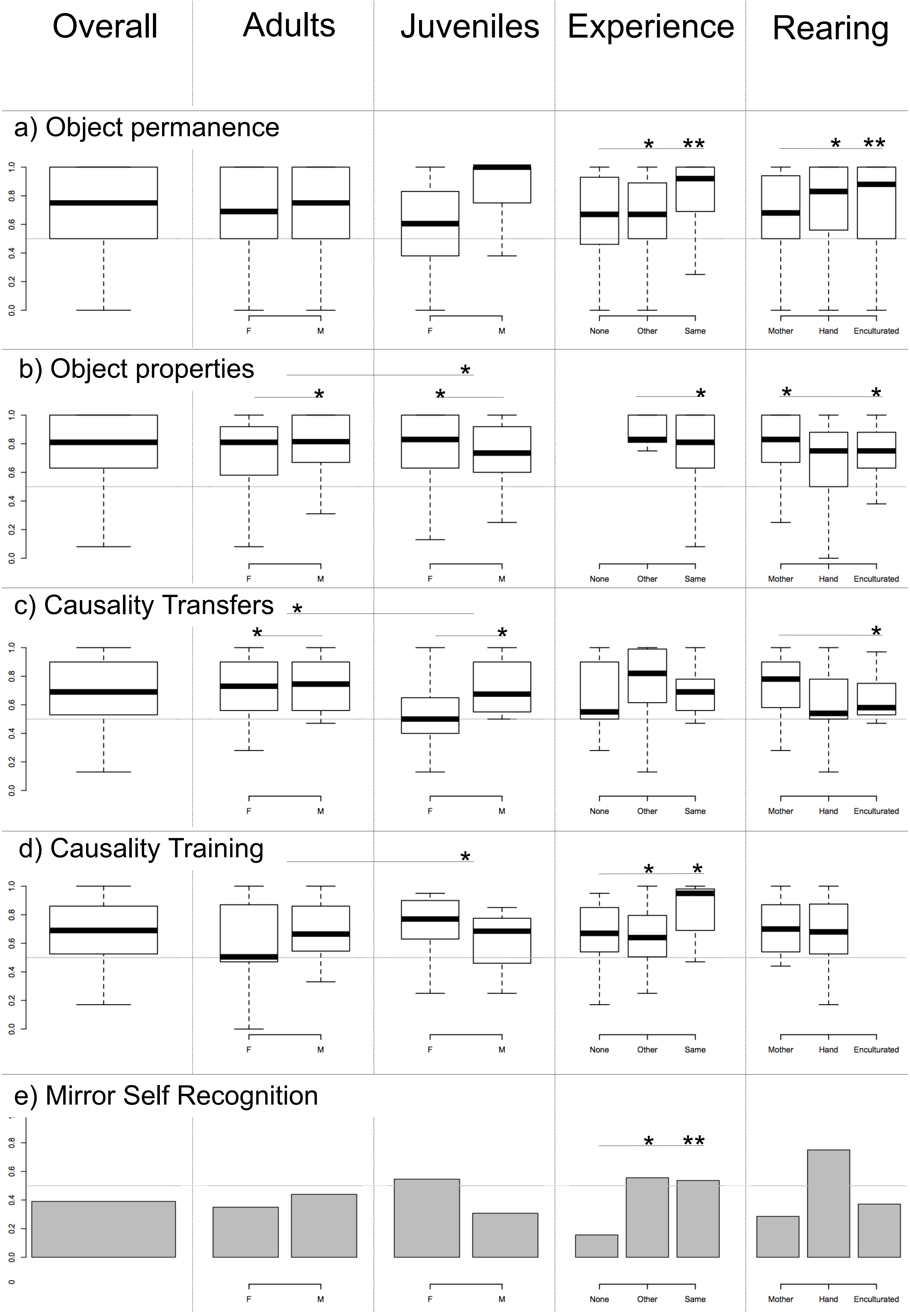


b) Object Properties



c) Causality Transfers




Overall
Adults
Juveniles
Experience
Rearing
a) Object permanence
b) Object properties
c) Causality Transfers
d) Causality Training
e) Mirror Self Recognition
0.0
0.2
0.4
0.6
0.8
1.0
F
M
None
Other
Same
Mother
Hand
Enculturated
*
**