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Differential participation in cognitive tests is driven by personality, sex, body condition and experience

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ABSTRACT

Failure to participate in a cognitive test may result in sampling biases when measuring inter-individual variation in cognitive performances in both captive and wild populations. This would be problematic if particular classes of individuals consistently fail to participate, skewing data and making generalisations or comparisons difficult. We presented 144 pheasant chicks, raised under standardised conditions, with a battery of cognitive tests to investigate whether sex, body condition or personality traits, measured by differences in latencies to explore a novel object, novel environment or unknown conspecific, predicted individual variation in voluntary participation across 37 test sessions. In general, participation increased across testing sessions, yet patterns of participation differed with sex and body condition. Males with a high body condition were more likely to participate in early test sessions compared to males with a low body condition or females. While participation among males in high body condition was consistent across sessions, males with a low body condition and females, regardless of body condition, were more likely to participate in later, rather than earlier sessions. Individuals also showed repeatable behaviours across time and different contexts, revealing not only that the exploration of novelty, but also that the order that subjects entered the testing arena and their latencies to acquire a freely available meal-worm reward may be considered valid proxies for different personality traits. During each test session, those individuals that were among the first to voluntarily enter the testing arena were more likely to participate in subsequent trials. Moreover, when isolated in the testing arena, individuals that rapidly acquired a freely available meal-worm, positioned on the testing apparatus, were also more likely to participate in a cognitive test. Our findings therefore reveal that sex, body condition and personality traits, along with habituation to the testing paradigms, all play important roles in determining whether or not particular individuals participate in cognitive tests. Sampling biases may therefore misrepresent our understanding of variation in cognitive performance in wild and captive populations, making individual differences in cognition difficult to interpret.

Contents

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1. Introduction

Investigating the cognitive performances of animals has historically been conducted in captivity where external variation that may influence a subject's performance can be controlled. This allows an experimenter to standardise their subject's experience of testing regimes and to invest time shaping those individuals that are more reluctant to engage in a task. Yet inevitably, some individuals repeatedly fail to participate and their performances are excluded from analysis. The number of non-participating individuals is seldom reported and explanations that address why some individuals regularly fail to participate in testing regimes have received little attention (Biro and Dingemanse, 2009).

Recent interest in the mechanisms that underlie individual variation in cognitive performance have led to a growing body of literature, with a focus on studying large numbers of individuals, often from free-ranging populations in the wild (Pritchard et al., 2016; Rowe and Healy, 2014; Thornton et al., 2014; Thornton and Lukas, 2012). While it remains unclear what facets of cognition are assessed using problem solving paradigms (Griffin and Guez, 2014; Morand-Ferron et al., 2015; Rowe and Healy, 2014; van Horik and Madden, 2016), cognitive performances can only be assessed among those individuals that participate in test regimes. Many individuals, however, fail to participate (either fully or partially) in cognitive tests, particularly if tested in the wild. Low rates of success have been reported from species that interact with innovative problem- solving tasks in the wild. For example, successful individuals comprised of 15% of 62 hyenas, *Crocuta crocuta*, (Benson-Amram and Holekamp, 2012), 32% of 53 vervet monkeys, *Chlorocebus pygerythrus*, (van de Waal and Bshary, 2010), 7% of 30 vervets from groups that had minimal exposure to humans (van de Waal and Bshary, 2010) and 14% of 236 great tits, *Parus major*, and blue tits, *Cyanistes caeruleus*, (Morand-Ferron et al., 2011). Few studies report the number of individuals that fail to participate at all in such tasks, and when these data are presented, it appears that universal participation is seldom, if ever, achieved. Thornton and Samson (2012) found that 47% of 135 meerkats, *Suricata suricatta,* interacted with innovative foraging tasks, with 8% of these individuals successfully retrieving the food reward. Four of 20 robins, *Petroica longipes*, failed to complete a battery of cognitive tasks (Shaw et al., 2015). Five of 19 spotted bower birds, *Ptilonorhynchus maculat*us, failed to participate in a suite of cognitive tests, while, of the remaining 14 individuals, three failed to participate in at least one of the tasks (Isden et al., 2013). While it may be difficult to identify all individuals within wild populations to ascertain the proportion of those that fail to participate, some attempts have been made. For example, in a population of wild great tits in which 90% of individuals were estimated to be marked (Aplin et al., 2013), only 8% of 1061 known individuals visited an artificial feeder, with 6% of individuals pecking at least once at the test apparatus (Morand-Ferron et al., 2015). Moreover, of 2832 marked individuals of four Parid species, only 3–8% of these individuals visited a test apparatus at least once, with between 0.5–6% making at least one peck at the test apparatus (Morand-Ferron et al., 2015). Our understanding of variation in cognitive performances of a given species may therefore be limited to a subset of individuals that are willing to participate in a given task. The fact that significant numbers of individuals fail to participate in such tests suggest that these individuals may also be characterised by particular personality traits that impede participation and hence present a bias in our sampling procedures (Biro and Dingemanse, 2009; Carere and Locurto, 2011). It is therefore important to address whether motivational or personality traits influence an individual's likelihood of interacting with, and hence participating in, cognitive tests.

Sampling biases may not only be restricted to testing wild animals. Captive subjects brought in from wild populations may also be subject to such sampling biases as a result of individual variation in susceptibility to trapping (Carter et al., 2012). For example, in some species of fish, bold individuals are more susceptible to capture, or capture through certain trapping procedures (Biro et al., 2006; Biro and Post, 2008; Réale et al., 2007; Webster and Lefebvre, 2001). Shy bighorn sheep, *Ovis canadensis*, are less likely to be trapped compared to their bolder counterparts (Réale et al., 2000) and red squirrels, *Tamiasciurus hudsonicus*, that are more active are also more likely to be trapped (Boon et al., 2008). Moreover, particularly shy individuals may never be caught (Réale et al., 2007; Tuyttens et al., 1999; Wilson et al., 1993) or therefore tested.

Sampling biases may be further compounded because personality traits have previously been found to predict performances on cognitive tasks (Carere and Locurto, 2011; Cole and Quinn, 2011; Guillette et al., 2009; Sih and Del Giudice, 2012). Individuals with proactive traits (e.g. bold, explorative, aggressive) have been found to learn associations faster than timid, less explorative, nonaggressive and hence, reactive individuals (Dugatkin and Alfieri, 2003; Guenther et al., 2014). Reactive individuals, however, outperform proactive individuals at reversal learning tasks (Guenther et al., 2014; Guillette et al., 2011). Hence, differences in cognitive performance may be a result of different behavioural strategies. Reactive individuals may be more sensitive to changes in their environment, whereas proactive individuals tend to persist with previously learnt responses, even when they are no longer rewarded (Benus et al., 1987; Ruiz-Gomez et al., 2011). Cognitive performances of individuals therefore appear to depend on an interaction between personality traits and the type of cognitive tests administered. Further complications may also arise if an individual's performance on cognitive tests interacts with other attributes, for example their personality or sex (Titulaer et al., 2012).

We used pheasants, *Phasianus colchicus*, to test whether an individual's likelihood of participating in a cognitive test is uniform, or whether some individuals are more or less likely to participate in a test as a consequence of particular personality traits, sex or body condition, which may lead to sampling biases. Pheasant chicks can be hatched in large numbers simultaneously and reared under controlled conditions from one day old, allowing for age and early life

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