Curiosity boosts orang-utan problem-solving ability

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Investigating the mechanisms underlying individual variation in cognitive performance is a crucial step towards understanding the structure and evolution of cognition. In this study, we investigated phenotypic plasticity of 61 Bornean, Pongo pygmaeus, and Sumatran, Pongo abelii, orang-utans to gain insight into how rearing history shapes problem-solving approaches. We first examined the determinants of an individual’s response-and-exploration style, which we assessed using five independent novelty response and exploration tasks. Our findings revealed that both previous care by humans and social housing with conspecifics elicited a curious response-and-exploration style (characterized by a positive response to novelty and a high motivation to explore). Second, we investigated how the response-and-exploration style and previous experiences affected an individual’s problem-solving performance in a variety of tasks aimed at assessing physical cognition, including reversal learning, inhibitory control, causal reasoning and tool use. We found curiosity to be the sole predictor of problem-solving performance. However, curiosity is strikingly rare in wild orang-utans, being mainly induced by contact with humans and living in a safe and stimulating physical and social environment. We therefore suggest that curiosity in orang-utans is an artefact of captivity, a potential only expressed under special conditions. The origin of curiosity in our own lineage may have been an important contributor to the rapid rise in the complexity of our ancestors’ material culture.

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intonation (Call & Herrmann, 2014; Herrmann & Call, 2012; Neisser et al., 1996; Nisbett et al., 2012; Thornton & Lukas, 2012). Numerous experiments have shown that adult cognitive performance in animals is affected by environmental conditions during early development, be they enriched physical environments (Cooper & Zubek, 1958), enhanced nutrition (Arnold, Ramsay, Donaldson, & Adam, 2007), enculturation (Call & Tomasello, 1996; Tomasello & Call, 2004) or extreme social deprivation (Brent, Bloomsmith, & Fisher, 1995; Mason, 1968; van Schaik & Burkart, 2011; Schrijver, Pallier, Brown, & Würbel, 2004). However, the actual psychological mechanisms, such as exploration and social learning plus their feedbacks, through which these developmental effects are produced, are still only partially documented. Nevertheless, identifying them is vital for understanding the development of cognition as well as its evolution (Rowe & Healy, 2014; Thornton & Lukas, 2012).

Among humans, curiosity is often seen as an important contributor to creativity (Day & Langevin, 1969), decision making (Hirschman, 1980) and innovation (Carr, Kendal, & Flynn, 2016). Curiosity is defined as a motivation towards the acquisition of novel information (novelty seeking) and thus an attraction towards learning and experiencing something new (Berlyne, 1950, 1960; Collins, Litman, & Spielberger, 2004; Litman, 2005; Loewenstein, 1994). Accordingly, curiosity is reflected in approaching and exploring novel stimuli (Berlyne, 1960; Loewenstein, 1994), which makes it a potentially important ingredient of innovation and problem solving (Kummer & Goodall, 1985), for example through trial and error. Therefore, one major factor for the evolution of intelligence and culture in humans may be our curiosity, which makes us seek and explore novelty.

Curiously, although studies of animal problem solving and innovation consider a variety of mechanisms (Griffin & Guez, 2014; Tebbich, Griffin, Peschl, & Sterelny, 2016; van Schaik et al., 2016), curiosity is rarely mentioned (see Kaufman & Kaufman, 2015; but see Benson-Amram, Weldele, & Holekamp, 2013). This rarity may reflect the fact that in their natural environment individuals must be vigilant for predators and rivals and are preoccupied with planning their daily routines (Greenberg, 2003), and thus cannot afford to respond to novelty and engage in time-intensive exploration (with rare exceptions: e.g. Diamond & Bond, 1999). In wild orang-utans, Pongo spp., for instance, exploration overwhelmingly...
occurs when initiated by the observation of trusted experts (van Schaik et al., 2016; Schuppli et al., 2016). This preference for social learning may reflect the risks attached to exploration, such as injury or poisoning, especially when the items are novel, which they inevitably are for infants. Interestingly, whereas wild orang-utans avoid novelty, orang-utans in zoos seek novel stimuli (Damerius et al., 2017; Forss, Schuppli, Haiden, Zweifel, & Van Schaik, 2015). The captivity effect (reviewed in Haslam, 2013) partly reflects this difference in novelty response.

This unexpected juxtaposition of strong conservatism and seeming curiosity within the same species in different conditions raises the question of how curiosity is elicited. One possibility is that captivity offers a safe and stable environment, which includes a reduced need to find and process food and thus increased free time, reduced need to be vigilant for predators and plan travel routes and thus reduced cognitive load, and permanent gregariousness and thus more frequent opportunities for social learning. These circumstances allow individuals to approach and explore novel items and situations (Forss, Schuppli, Haiden, Zweifel, & Van Schaik, 2015; van Schaik et al., 2016), which, over time, results in larger skill repertoires (Haslam, 2013). In addition, the ability to attend to humans and their actions may increase an individual’s knowledge of affordances or stimulate different cognitive processes (Fredman & Whiten, 2008) and might therefore indirectly stimulate innovation propensity. This idea is supported by recent findings in orang-utans (Damerius et al., 2017) showing that human contact during ontogeny led to changes in the orang-utan’s attention structure that positively affected individual’s problem-solving success. Thus, it appears that captivity may unleash curiosity in animals that are decidedly uncurious in the wild.

The goal of the present study was to examine how important curiosity was in problem solving by linking individual variation in problem-solving ability to response-and-exploration styles in a large sample of orang-utans from widely varying backgrounds. In this work, we wanted to complement earlier studies that suggested enhanced curiosity in captivity (Benson-Amram et al., 2013; Damerius et al., 2017; Forss et al., 2015) in three ways. First, previous studies generally focused on the effect of single variables, either the absence of neophobia or aspects of exploration, on problem solving. However, response to novelty and exploration styles may have distinct underlying psychological substrates (Carr et al., 2016; Greenberg & Mette-Hofmann, 2001; Mette-Hofmann, 2014). We therefore used a multidimensional approach that includes a variety of measures to disentangle the various possible contributing factors. Second, most results relating curiosity to cognitive problem solving were only based on a single task (Benson-Amram et al., 2013; Damerius et al., 2017). However, given possible variability in performance across different tasks (Griffin & Guez, 2014; Herrmann & Call, 2012; Herrmann, Hare, Call, & Tomasello, 2010), one ideally includes an array of problem-solving tasks that may recruit different cognitive abilities. Third, previous studies tended to have small sample sizes and therefore lacked explanatory power and resolution (Cole, Cram, & Quinn, 2011; Thornton & Lukas, 2012). We therefore tested a sample of 61 Bornean, Pongo pygmaeus wurmbii, and Sumatran, Pongo abelii, orang-utans.

The present study was structured as follows. First, we combined a measure of the orang-utans’ attentiveness towards humans with various independent assays of response to novelty and exploration to gain broader insight into the nature and causes of interest in the social and physical environment. Second, because we included individuals housed in four Indonesian rehabilitation stations with various rearing histories, we could investigate the effects of individual experiences on their response-and-exploration styles. Third, we examined whether individual rearing histories or the response-and-exploration style most strongly affected their physical problem-solving abilities. We did so using a battery of tasks encompassing different domains of cognition: associative and reversal learning, flexibility, inhibitory control, causal reasoning and tool use.

**METHODS**

**Study Subjects and Species**

We studied 61 orang-utans housed at rehabilitation stations in the Republic of Indonesia: 45 individuals in Central Kalimantan, Borneo and 16 near Medan and Jambi, both on Sumatra (Appendix Table A1). Most were born in the wild but captured as young infants and kept as pets before being confiscated by the police and brought to the rehabilitation stations. Other adolescent or adult orang-utans came directly from the wild after being rescued when their habitat was lost to deforestation and conversion to plantations. We classified individuals into four different background groups (Wild, Station and Human, as well as Unknown; see Table 1), based on their age at arrival at the station and previous exposure to humans. Importantly, individuals in the Human category had lived a minimum of 6 months as pets. The ages of the subjects ranged from 3.5 to ca. 25 years. In the wild, age at weaning is around 6–7 years and age at first reproduction, for females, around 13–15 (Wich et al., 2004).

**Study Facilities and Housing**

Data collection occurred between June 2012 and June 2014 by L.D., Zaida Kosonen (Z.K.) and a trained assistant (Andreas Wendl) in four facilities of three organizations across Sumatra and Central Kalimantan, Borneo.

Eleven Sumatran orang-utans (four females, seven males) were studied at a quarantine station in Batu M’Belin (QBM), Medan, North Sumatra, which is run by the Sumatran Orangutan Conservation Program (SOCP). Their ages ranged from 5 to 10 years and we tested them in their home enclosures, as they were housed alone. We also studied one solitary housed male and four socially housed

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**Table 1**

Categories of subjects and their background histories

<table>
<thead>
<tr>
<th>Background</th>
<th>Human exposure</th>
<th>Age (years)</th>
<th>Years in captivity</th>
<th>Qualitative description</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild</td>
<td>Minimal</td>
<td>10–25</td>
<td>0–7</td>
<td>Entered the rehabilitation station directly from their natural habitat,\n</td>
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<td>often as adolescents or adults |</td>
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<td>Arrived at station as dependent offspring at the age of 1.5 years or younger. |</td>
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<td></td>
<td>Hence, spent minimally 80% of life in rehabilitation station</td>
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<td>Older than 1.5 years upon arrival. Background history includes a minimum of 6 months of human contact as pet</td>
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<td></td>
<td></td>
<td>No background information, but not reported to be wild. Arrived at station at ages 2–7 and therefore spent a large part of the developmental phase in captivity</td>
<td></td>
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</tbody>
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