Review

Great ape cognition and captive care: Can cognitive challenges enhance well-being?

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ABSTRACT

Given the close genetic link between humans and nonhuman great apes, the well-being of the latter in captivity is understandably controversial. Behavioural signs of boredom, anxiety and stress in captive great apes have been linked to being reared in small groups or by humans, and by having a lack of control over the environment. This review proposes a new framework for great ape enrichment, inspired by a century of cognitive research. Problem-solving tasks that are designed so challenge the evolved cognitive skills of great apes might allow subjects to have more control in inherently restricted environments. These sorts of tasks have historically been used to test the comparative cognitive abilities of great apes housed in research facilities, with few parallel assessments of well-being. However, there is great potential for 'cognitive challenge' tasks to be applied to great apes in a range of captive settings for the enhancement of well-being. This is based on recent research on farmed animals, demonstrating that they may seek cognitive challenges and benefit from their own learning success. A new definition of 'cognitive enrichment' – where an appropriate cognitive challenge results in measurable beneficial changes to well-being – is proposed to encourage research at the interface of great ape cognition and well-being. Finally, two approaches to great ape cognitive enrichment – 'low-investment' and 'high-investment' – are proposed for future research.

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1. Introduction

Broadly speaking, animal cognition refers to how sensory input is acquired, processed, stored and acted upon (Shettleworth, 2010). Comprehensive reviews of animal cognition and related terms such as perception and awareness are provided elsewhere (Bekoff et al., 2002; Broom, 2010; Shettleworth, 2010). In the current article, 'cognitive skill' will be used to refer to an animal's relative aptitude in processes such as learning, memory and causal reasoning. Assessments and descriptions of animal cognitive skill are, of course, biased by our own human cognitive skills (Chittka and Jensen, 2011). However, comparing the cognitive skills of other species to our own does provide a useful point of reference: humans usually outrank other vertebrate species in cognitive tests, and the performance of great apes nudges slightly above cetaceans and corvids on many (but not all) cognitive tests (Wasserman and Zentall, 2006).

As noted recently by Broom (2010), research at the interface of animal welfare and cognition is increasing. However to date, most research has focussed on the link between welfare and emotional processes (Paul et al., 2005; Mendl et al., 2009), and whether cognitively 'higher' species may suffer more than those lower on this scale (Kirkwood and Hubrecht, 2001; Brydges and Braithwaite, 2008). Less research has focussed on the cognitive 'needs' of particular species or taxa; in other words whether animals receive sufficient cognitive challenges in captivity to ensure a good level of well-being (Brydges and Braithwaite, 2008).

Nonhuman great apes are chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orang-utans (*Pongo pygmaeus*) (hereafter great apes). Despite a century of research, knowledge of great ape cognition, particularly of chimpanzees (Russell, 2008) has seldom been applied to the assessment and improvement of their well-being in captivity (Ross, 2010). This is ironic, since the cognitive skills of great apes are usually reported to exceed those of other primates and sometimes those of pre-linguistic children (Tomasello and Call, 1997; Tomasello and Herrmann, 2010). In this paper, a stronger link between cognition and care is proposed. First, current knowledge on great ape social and physical cognition from wild and captive studies is reviewed. Then, current approaches to the measurement and enhancement of great ape well-being are evaluated. Finally, a case is made for presenting cognitive challenges to great apes in captivity, since there is increasing evidence that appropriate cognitive challenges can enhance animal well-being.

2. What do we know about great ape cognition?

2.1. Studying great apes in the laboratory and field

The empirical study of great ape cognition spans a century, since the work of Yerkes and Köhler (Yerkes, 1916; Köhler, 1925). Historically, captive great apes have been used to model a wide range of cognitive concepts, including insightful and co-operative problem-solving, and the effect of rearing on cognitive development (Köhler, 1925; Yerkes, 1925). Scientific investigations of great ape behaviour and cognition in the wild increased exponentially during the latter half of the twentieth century. Long-term field studies by Goodall (chimpanzees), Fossey (gorillas), Kano (bonobos) and Galdikas (orang-utans) have revolutionised our understanding of wild ape behaviour and cognition, in parallel with artificial, highly controlled studies in laboratory settings (Matsuzawa, 2010). Due to space limitations, interested readers are advised to seek further information in several dedicated reviews of great ape cognition (Russon et al., 1998; Russon, 2004; Tomasello and Herrmann, 2010).

2.2. Physical cognition

A body of evidence over the past two decades suggests that great apes understand the physical world (relating to space, time, number and causation) in similar ways to humans (reviewed by Tomasello and Call, 1997; Tomasello and Herrmann, 2010). Like humans, great apes understand the material properties of objects, their quantity and order, as well as some cause–effect relationships over space and time (Vlamings et al., 2006; Albiach-Serrano et al., 2010; Manrique et al., 2010).

A main focus of cognitive research has been tool manufacture and use (*sensu* Beck, 1980). Chimpanzees habitually make and use tools in the wild (Whiten et al., 1999), and there are examples of great ape 'meta-tool use' where one tool is used to create another (Shumaker et al., 2011). Curiously, the prevalence and diversity of tool use in gorillas and orang-utans is less pronounced than in *Pan* spp., especially in the wild (Parker et al., 1999). Several explanations for this Genus difference have been suggested: gorillas and orang-utans may use their large body size and strength to

access food rather than using tools, or different social structures may lead to social learning constraints in gorillas and orang-utans (McGrew, 1989; Van Schaik et al., 1999). Leading from this, lateralisation of hand use, or 'handedness', in great apes during different tasks has received a large amount of study (reviewed by Hopkins and Morris, 1993; McGrew and Marchant, 1996). In a sample of over 700 great apes, Hopkins et al. (2011) found a population-level right-handed bias in chimpanzees, bonobos and gorillas and a left-handed bias in orang-utans, when interacting with an object.

Since physical cognitive skills are thought to have evolved in the context of foraging (Tomasello and Herrmann, 2010), the majority of laboratory experiments designed to investigate physical cognition are based on the extraction of food rewards. For example, 'trap tube' tests are commonly used to study causal reasoning and problem-solving (Call, 2010). These tests involve sliding a small, rake-like tool though a tube, usually to remove food from the tube without it falling into a trap.

Spatial cognition in nonhuman primates has been tested using two-dimensional 'virtual' mazes on a computer screen (Washburn and Rumbaugh, 1992; Washburn and Astur, 2003), and matching-to-sample real life objects with small scale models (such as real and dolls' houses) (Kuhlmeier et al., 1999). Collectively, studies reveal that chimpanzees possess impressive spatio-cognitive skills including eidetic-like (photographic) memory (Inoue and Matsuzawa, 2007). The spatio-cognitive skills of gorillas and orang-utans have been studied to a lesser extent, but increasing knowledge suggests that they also possess high spatial memory skills. For example, high levels of spatial memory when foraging have been demonstrated in zoo-housed gorillas (Gibeault and MacDonald, 2000) and orang-utans (Macdonald and Agnes, 1999), as has serial learning ability in gorillas (Ross, 2009) and orang-utans (Swartz and Himmanen, 2006). One of the most interesting current avenues of research shows that like humans, great apes are capable of 'mental time travel' and can perceive and understand concepts in the past, present and future (Martin-Ordas et al., 2010). For example, Mulcahy and Call (2006) showed that bonobos and orang-utans learned to keep a tool after using it for a food-based task, in anticipation of needing it for a future task.

2.3. Social cognition

The social cognition of great apes (knowledge of, and information transfer between, other animals) is also similar to our own. Great ape social systems are complex, and individuals hold different types of relationship in order to collaborate or compete for changing resources (Byrne and Whiten, 1988; de Waal and Lanting, 1997). In fact, the large relative brain size of primates is hypothesized to have evolved in response to social pressures (Dunbar, 1998). de Waal's (1982) famous popular science text, 'Chimpanzee Politics' documented the social lives of chimpanzees living at Arnhem Zoo, the Netherlands. This text illustrated that like humans, great apes can deceive, form alliances with and console conspecifics. More recent research shows that great apes understand the perceptions and intentions

of others (Tomasello and Herrmann, 2010); and Call and Tomasello (2008) postulate that chimpanzees have a 'theory of mind'.

A number of cognitive tasks have been designed to test the cooperative and collaborative skills of great apes. For example, the 'string-pulling task' requires two subjects to simultaneously pull on strings or handles in order to cooperatively gain a food reward (Chalmeau, 1994; Chalmeau et al., 1996). Other investigations have involved comparing the responses of different great ape species to clumped or dispersed sources of food (Hare et al., 2007; Lonsdorf et al., 2009). Collectively, these studies indicate that bonobos and chimpanzees are tolerant of their conspecifics and can collaborate when required in certain tasks, while gorillas and orang-utans have a lower level of social tolerance.

Attempts to teach spoken language to great apes (and other nonhuman primates) have failed, since they lack the appropriate anatomy for human-like speech (Arbib et al., 2008). However, a generation of intensive artificial language research (1960s–1980s) has shown that great apes are capable of acquiring some types of symbolic language (reviewed by Matsuzawa, 2010). To date, great apes have been taught to use gestural signs; arrange tokens in specific sequences (thus apparently understanding order and context); and operate lexigram keyboards (Matsuzawa, 2010). Even so, the full extent of great ape language is still debated (Cohen, 2010). In recent years, there has been a noticeable shift away from the study of apes' acquisition of artificial language, towards intra-specific communication in wild and naturalistic captive settings (Slocombe et al., 2010; Clay and Zuberbühler, 2011).

2.4. The limits of great ape cognition

Over the last two decades, the study of great ape cognition has been a highly productive field that shows no sign of slowing (Russell, 2008; Tomasello and Herrmann, 2010). However, de Waal and Ferrari (2010) warn that to date, research has focussed on the upper limits of cognition in a small number of subjects (who are usually reared in controlled environments and spend their lifetimes undertaking cognitive tests). In other words, our knowledge of great ape cognition is based on individuals who may not be representative of their species. On the contrary, Russon (2004) suggests that great ape cognition is tested in under-stimulating captive conditions (socially and environmentally), and we have yet to discover their full cognitive potential. Regardless, the knowledge we already have (upper limits of cognitive skill, and broader cognitive abilities across specific domains) should be applied to captive well-being without further hesitation.

3. Great ape well-being and enrichment

3.1. Great ape well-being in captivity

The high cognitive skills of great apes are in little doubt after almost a century of research (Tomasello and Call, 1997; Russon, 2004). Having briefly reviewed the cognition literature above, the focus of this article now shifts to the care and management of great apes in captivity, and

considers the evidence that restricted environments can lead to compromised well-being.

In comparison with most farmed and domesticated species, breeds or strains, it is extremely difficult to define the characteristics of an 'average' captive great ape. Today, several thousand great apes live in captivity, mostly in zoos, research laboratories and sanctuaries. There are approximately 1200 chimpanzees in biomedical facilities in the United States (Conlee, 2008), and 3500 in zoos and registered sanctuaries worldwide (ISIS, 2011). Within and between each type of captive condition, their well-being can range from very good to very poor and there appears to be no clear consistent relationship between housing type and well-being (Nash et al., 1999; Fernie, 2008).

A full survey on the factors affecting the well-being of captive great apes is absent from the literature (but see Fernie, 2008). Indeed, compiling it would be a substantial task. The current article focuses on behavioural indicators of compromised well-being in captive great apes that commonly appear in the literature. These are: abnormal repetitive (stereotypical) behaviours, abnormal self-directed behaviours, and abnormal feeding behaviours (Walsh et al., 1982; Brüne et al., 2006; Birkett and Newton-Fisher, 2011), and points towards more detailed reviews where necessary. Debates regarding the definitions of 'abnormal' and 'normal' behaviour are on-going within animal welfare science and will not be considered here (see Mench and Mason, 1997). Suffice it to say, abnormal behaviours in great apes are not usually observed in wild populations (Brüne et al., 2006) and are usually linked to some sort of deprivation in captivity, either in current or previous housing or rearing (Fritz, 1986; Nash et al., 1999).

Abnormal repetitive (stereotypical) behaviours in captive great apes, such as rocking and weaving, have repeatedly been linked to disruptions in early rearing (Fritz, 1986; Fritz and Howell, 1993). Nash et al. (1999) found that rocking was significantly more likely in hand-reared chimpanzees, and lone or small-group housing is also associated with stereotypical behaviour (Brent et al., 1989). Thus, many stereotypical behaviours are viewed as the 'scars' of past experience, rather than indicators of current stress or a deprived environment (Mason, 1991). Furthermore, there is conflicting evidence for whether enrichment can significantly reduce gross stereotypical behaviours such as rocking in captive animals (Shyne, 2006; Mason et al., 2007).

Self-directed behaviours such as hair-plucking are also considered to be abnormal behaviours performed by great apes, and may or may not be injurious (Novak and Suomi, 1988). One theory is that self-directed behaviours are linked with boredom. As Rumbaugh et al. (1989, p. 366) state, "*It seems that the chimpanzee, like the human, has a very busy mind, and if it is not occupied solving real problems, it will manufacture problems to solve*". Boredom-related behaviours include directing excessive attention towards self-grooming, or grooming others. Another theory is that self-directed behaviours in primates are linked with anxiety (Maestripieri et al., 1992). For example, self-directed behaviours in captive chimpanzees have been linked with social tensions (Aureli and de Waal, 1997; Baker and Aureli, 1997) and participation in relatively complex

cognitive tests (Leavens et al., 2001). Clark et al. (2011) found that hair-plucking in a captive adult female gorilla was significantly related to increased faecal glucocorticoid concentrations, an indicator of short-term stress. However, hair loss (often reported to coincide with excessive grooming) has also been associated with parasitism, nutrient deficiencies and autoimmune diseases in great apes, and may not always indicate poor psychological well-being (Suedmeyer, 1997; Mundy et al., 1998).

Finally, a range of abnormal feeding behaviours are known to occur in captive great apes. Regurgitation and re-ingestion of food has a high prevalence in captive gorillas (Lukas, 1999) and chimpanzees (Baker and Easley, 1996) and is often considered to be an indicator of sub-optimal well-being (Lukas, 1999). Coprophagy may serve a similar function to regurgitation and re-ingestion, where individuals seek to increase their feeding time (Akers and Schildkraut, 1985). However, the link between compromised well-being and coprophagy is not straightforward because great apes are also known to perform coprophagy in the wild (Krief et al., 2004; Sakamaki, 2010).

3.2. Previous attempts at enrichment for great apes

One of the most commonly cited definitions of enrichment for wild animals in captivity is "...*an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physiological well-being*" (Shepherdson, 1998, p. 1). This definition is useful since it makes the distinction between psychological and physiological well-being. It also highlights that enrichment is a broad principle that can take many forms. Enrichment has traditionally been split into five main categories (Bloomsmith et al., 1991). These are: (a) food-based; (b) occupational (including psychological 'puzzles' and physical exercise); (c) structural; (d) sensory (for example visual, auditory); and (e) social. These subtypes often overlap but most can usually be categorised by their main characteristics. A diverse range of enrichment types have been implemented on great apes with varying success rates, and this article provides illustrative examples in each category.

The majority of enrichment for great apes has been food-based and occupational (Wolfe-Coote, 2005). 'Substrate feeders' have encouraged subjects to search for edible items in substrate such as woodchip or grass. This relatively simple form of enrichment has been used to increase the duration of foraging behaviours and overall activity in chimpanzees (Lambeth and Bloomsmith, 1994; Baker, 1997). 'Probe feeders' require subjects to 'dip' their fingers or a tool into a chamber to remove sticky food items (Maki et al., 1989; Celli et al., 2003). 'Puzzle feeders' potentially provide a higher level of challenge to great apes, since they require visible or hidden food items to be removed from holes using fingers or tools. However, if devices can be rapidly emptied, subjects then return to being inactive (Bloomstrand et al., 1986; Gilloux et al., 1992; Csatádi et al., 2008). Food-based devices are also commonly monopolized by dominant individuals (Celli et al., 2003; Tarou et al., 2004; Ryan et al., 2011).

Novel objects or 'toys' are often classified as structural enrichment (Bloomsmith et al., 1991), but they could also fall into the aforementioned 'occupational' category. As a rule, novel objects engage the interest of great apes, but interest is lost quickly if objects do not change in shape, size or texture during use (Paquette and Prescott, 1988; Brent et al., 1989). Other structural enrichment for great apes include larger-scale changes to enclosure size and complexity (Brent et al., 1991).

Sensory enrichment (stimulating the visual, auditory, olfactory, gustatory and tactile senses) has been used far less than physical objects. Laboratory and zoo-housed great apes have been given the opportunity to watch tele-vised images, but have not shown significant behavioural changes beyond initial engagement with the novel image (Maple and Hoff, 1982; Brent et al., 1989; Bloomsmith and Lambeth, 2000). Olfactory and auditory enrichments for great apes have received mixed effects. While zoo gorillas were observed to explore (and presumably smell) food-scented cloths more than control cloths, there was no significant effect on other behaviour (Wells et al., 2007). Conversely, a range of food- and non food-based scents engaged the interest of chimpanzees (Struthers and Campbell, 1996; Ostrower and Brent, 2000). Audi-tory enrichment has been more successful than olfactory enrichment with captive great apes; Howell et al. (2003) found that aggression and anxiety could be reduced in laboratory chimpanzees by playing music on a radio, and instrumental music also stimulated social behaviours in laboratory chimpanzees (Videan et al., 2007).

Finally, social enrichment refers to exposure (direct or indirect) to conspecifics and/or humans. While it is gener-ally agreed that opportunities for social interactions with conspecifics enhance well-being, with the obvious corol-lary that wounding and aggression is managed within groups (Brent et al., 1989; Baker, 1996; Reimers et al., 2007), human contact including interactive play can also be beneficial for great apes (Baker, 2004). Positive rein-forcement training may also benefit great ape well-being by reducing uncertainty and associated distress involved with some husbandry practices and by providing cognitive stimulation (Perlman et al., 2010). For example, Pomerantz and Terkel (2009) reported that implementation of pos-itive reinforcement training on a group of chimpanzees was associated with a significant decrease in abnormal and stress-related behaviours, and an increase in social affilia-tive behaviours.

To conclude, enrichment strategies for great apes tend to focus on the extraction of food using a repeated motor action (for example prodding or dipping). A common characteristic of great ape enrichment is a lack of long-term engagement, once the food reward or other resource is depleted. The enriching effect of food-based 'puzzles' in future might be maintained by requiring subjects to use more than one motor action (for example prodding, twisting and shaking), by providing multiple levels of problem-solving (for example the sequential completion of several tasks leading to food), or modifying and updat-ing the puzzle at regular intervals (Meehan and Mench, 2007; Clark et al., in preparation). In addition, food-based puzzles that encourage social cognitive skills (such as

collaboration) and provide a multi-sensory experience (scents and sounds) deserve further study.

4. Cognitive challenge and animal well-being

4.1. Appropriate cognitive challenges for captive animals

Wild animals face many daily challenges to survive and these must be met using evolved cognitive skills (Meehan and Mench, 2007; Shettleworth, 2010). In contrast, captive animals tend to live in highly predictable and structured environments in which their evolved cognitive skills are challenged infrequently, or inappropriately (Wemelsfelder and Birke, 1997; Morgan and Tromborg, 2007). A practical solution is to provide more cognitively challenging enrich-ment programmes, but care should be taken to ensure the level of challenge is appropriate (Meehan and Mench, 2007). Carlstead and Shepherdson (2000, p. 344) stated that cognitive challenges should "... *put captive animals in a position where they can learn to actively control and explore some aspects of their environment*". Furthermore, Meehan and Mench (2007, p. 248) suggested that appropriate chal-lenges for captive animals are "*Problems that may elicit frustration, but are potentially solvable or escapable through the application of cognitive and behavioural skills*".

According to Meehan and Mench, 2007 (reproduced from Myers and Diener, 1995), the level of cognitive chal-lenge an animal receives compared to its level of skill can create four possible welfare outcomes for the ani-mal: flow, apathy, boredom, and anxiety. Flow is a positive emotional state of satisfaction and pleasure reported in humans (Csikszentmihalyi, 1988), and arises from a match between high challenge and high skill. Alternatively, anx-iety may arise when an animal does not possess enough skills to meet a cognitive challenge (Duncan and Wood-Gush, 1972). A match of low skill to low challenge results in apathy; a negative emotional state often attributed to cap-tive animals in environments that suppress opportunities for exploration (Wood-Gush and Vestergaard, 1989; Myers and Diener, 1995). Finally, boredom occurs when an animal possesses more skill than it can exercise on its environment (Wemelsfelder and Birke, 1997).

In order to develop what we believe are appropriate cognitive challenges for captive animals, the four-outcome model as described above suggests that we should develop cognitive challenges that require a high level of naturally occurring skill (thus facilitating the experience of 'flow'). However, while Csikszentmihalyi and Csikszentmihalyi (1988) found that flow is a self-reported phenomenon in humans, Meehan and Mench (2007) point out that there have been no attempts to measure flow in nonhuman ani-mals. Since flow is facilitated by being absorbed in a task, we might be able to infer flow by measuring how easily an animal is 'distracted' from a cognitive task. Since chal-lenges can also lead to anxiety, apathy or boredom, proxies for these welfare outcomes must be measured in order to evaluate whether a challenge is indeed appropriate. Anx-iety has been measured to a fair degree in primates, by using self-directed behaviour as a proxy (Maestripieri et al., 1992; Aureli and de Waal, 1997; Baker and Aureli, 1997). However, boredom is difficult to measure in nonhuman

animals, and has been linked to both high levels of inactivity (Dawkins, 2001) and active behaviours such as restless or stereotypical behaviour (Wemelsfelder, 1993). Overall, this discussion brings credence to Meehan and Mench's (2007) claim of 'The challenge of a challenge': challenging captive animals appropriately is a challenge for researchers themselves.

4.2. When can a cognitive challenge be classified as enrichment?

As demonstrated above, cognitive challenges can have beneficial effects on animal well-being if the level of challenge is appropriate for an animal's level of cognitive skill. But under what circumstances does *cognitive challenge* justifiably become *cognitive enrichment?* To date, the term cognitive enrichment has been used inconsistently between study systems and species, and appears to be based more intended function than the animal's actual response to challenge. In a GAP analysis by de Azevedo et al. (2007), the percentage of published studies on 'cognitive enrichment' (defined as the use of puzzles) were: laboratory 3.95% (18/456 studies); farm 0% (0/103 studies); zoo 3.23% (2/62 studies). However since this publication, the number of studies on cognitive challenges for farm animals has grown considerably (Meyer et al., 2011).

Milgram (2003) may have coined the phrase cognitive enrichment when studying the effects of learning tasks on the cognitive performance of laboratory dogs. Laboratory-based cognitive enrichment usually describes several simultaneous changes in housing, including social changes and the addition of 'toys' (Milgram et al., 2006). On the farm, cognitive enrichment usually refers to the provision of a specific and short-term problem-solving activity or device (Ernst et al., 2005; Langbein et al., 2009; Puppe et al., 2007). The most ambiguous use of the term cognitive enrichment comes from human studies, where it refers to an individual's education or job complexity, sometimes over an entire lifetime (Milgram et al., 2006). In a comprehensive survey of zoo-based enrichment, Swaisgood and Shepherdson (2005) suggested that mechanical apparatuses, puzzle feeders and interactive computer tasks are cognitively challenging. However, the term cognitive enrichment has not been used explicitly for zoo animals, and little attention has been given to the development of cognitive challenges that not only seek to provide specific opportunities for problem-solving, but also enhance well-being (Meehan and Mench, 2007; but see Citrynell, 1998).

While cognitive enrichment is diverse in form, few authors have attempted to define the actual purpose of cognitive enrichment. Milgram et al. (2006) suggested that cognitive challenges promote the use of available brain resources. Further to this, Manteuffel et al. (2009, p. 88) suggested that cognitive enrichment should stimulate "...*perceptive processes for operant learning of discriminatory cues which lead eventually to a better active control of the environment"*. Better control of the environment is advantageous for captive animals (Sambrook and Buchanan-Smith, 1997; Bassett and Buchanan-Smith, 2007), but Manteuffel's definition falls short because learning is only one aspect of cognition. In contrast, Meehan and Mench (2007, p. 253)

propose that cognitive challenges should stimulate many cognitive skills simultaneously: "...*in addition to opportunities to explore and interact with environmental elements, opportunities to solve problems, make decisions, and exercise cognitive skills are important to an animal's subjective experience and ultimately, its welfare".* In response to an inconsistent use of terminology and its perceived benefits in previous literature, this article proposes a new, more comprehensive definition of cognitive enrichment: *Cognitive enrichment is a task (or tasks) whose use (1) engages evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of wellbeing.* 'Evolved cognitive skills' are demonstrated through empirical research on the species in the wild or captivity. Task 'use' can be measured by the frequency or duration of task use over time, or the degree to which the task is solved. Using a task or tasks may be sufficient to enhance well-being, without needing to 'solve' the task as the design intended. In future, it may be possible to incorporate the concept of 'flow' into the definition of cognitive enrichment, but further research is needed to decide whether flow is measurable in nonhuman animals.

4.3. Cognitive challenges in the context of foraging

One promising area of research on farmed animals has been to integrate cognitive challenges with the acquisition of food. Ernst et al. (2005) and Puppe et al. (2007) implemented an automatic feeding system for pigs who first had to discriminate between acoustic cues calling them to various feeding stations, and then discriminate between different stimuli to receive a food reward. This system allowed pigs to be challenged several times a day, with spatial and temporal variation. Pigs, who were exposed over ten weeks to an automated feeding device, exhibited a significant reduction in belly-nosing (Puppe et al., 2007). However, since subjects received prior training in how to use the device, it could be argued that no ongoing problem-solving was required to access food rewards. Sambrook and Buchanan-Smith (1997) suggested that once control over an environmental factor is gained, repeated control is unlikely to have significant welfare benefits.

Farmed animals also appear to benefit from cognitive challenge without the need for extrinsic rewards (such as food). Langbein et al. (2009) found that dwarf goats apparently seek cognitive challenges, because they continue to solve a previously learnt cognitive problem to get a reward when the same reward is concurrently available without participating in the task. There may also be an intrinsic value to learning, as demonstrated by Hagan and Broom (2004). They found that cattle who had the opportunity to perform an operant task to receive a food reward displayed greater 'excitement' (elevated heart rate and activity level) than control animals who did not participate in the task but received the same food reward.

In the laboratory, computer game-like tasks (a computer screen combined with a joystick or buttons) have been used to test the cognitive abilities of a range of primate species (Leighty and Fragazsy, 2003). An interesting tangent to this research has been to evaluate whether

these tasks are enriching. Washburn and Rumbaugh (1992) found that engagement with computer game-like tasks (linked to food rewards) was a highly preferred activity for rhesus macaques (*Macaca mulatta*), occupying over 9 h of their day, replacing over-grooming, aggression, and stereo-typical behaviour in activity budgets. Game-like tasks were also more effective at reducing behavioural indicators of distress than 'toys' such as balls, and by housing subjects in pairs. Intriguingly, it is not clear whether engagement with computer game-like tasks was enriching because sub-jects had already learnt an association between computer interaction and food rewards from their formal cognitive testing, or because exploration and problem-solving were inherently enriching. To this end, while there is evidence of 'contrafreeloading' in these experiments (a phenomenon where individuals continue to engage with the problem-solving to receive a reward even when the equivalent reward is freely available, see Inglis et al., 1997), the previ-ously learnt link between engagement and food reward is a confounding factor that should be investigated further.

5. A new enrichment framework for captive great apes using cognitive challenges

5.1. Why is a new enrichment framework needed?

"*Working to improve captive animal care without an understanding of how animal minds work, or the scope in which they perceive and interact with their social and physical environments, is akin to drawing a map without knowledge of any landmarks or bearings*". (Ross, 2010, p. 310)

As Ross (2010) exemplifies, it is naïve to approach animal well-being without an appreciation of cognition. Of course, animal managers are unlikely to adopt a new enrichment framework that provides for cognitive needs unless it can be justified. There are at least two relevant justifications for great apes. First, a number of relationships have been demonstrated between restricted environments (i.e. those lacking cognitive challenges) and abnormal behaviours in great apes (Section 3.1). This is bolstered by the knowledge that the captive great ape population is ageing due to increased standards in health care (Tarou et al., 2002). Secondly, enrichment for great apes to date has relied heavily on food rewards, and has lacked high levels of engagement and cognitive challenge (Section 3.2).

Fortunately, we have in our scientific armoury a vast amount of knowledge on great ape cognition. Ross (2010) demonstrates how these studies have already been applied to the management of great ape social groups and rear-ing, and this article focuses on enrichment. It provides two ideas for cognitive enrichment that are complimen-tary with the new definition given above (Section 4.2); the first is a 'low-investment' approach suitable for adult sub-jects that may or may not have experienced high levels of cognitive challenge during early development. The sec-ond is a more holistic approach to enriching an animal's entire environment, beginning at an early age, known as 'high-investment'.

5.2. A low-investment approach to cognitive enrichment

'Low-investment' is used to refer to enrichment strate-gies that are relatively quick to implement, but have definable goals and measurable outcomes (Mellen and Sevenich MacPhee, 2001). The low-investment approach to cognitive enrichment is appropriate for zoos, sanctuaries and laboratories with limited financial resources, because it requires minimal preparation and no prior animal training. Indeed, animal training should be avoided so that subjects reach the "*Eureka moment*" independently and benefit from their own learning success (Hagan and Broom, 2004). Since engagement in exploration and problem-solving activities can be viewed as immediate benefits of cognitive challenge, this approach may be particularly suitable for great apes who perform high levels of self-directed or food-related abnormal behaviour. Engagement with a cognitive task may replace the performance of abnormal or undesirable behaviours in the repertoire if they are mutually exclu-sive (cannot occur at the same time). However, animal staff should not expect drastic behavioural changes, par-ticularly in stereotypical behaviours which may be difficult to remove from the repertoire and require more concerted, directed therapy (Mason and Rushen, 2006).

In 1925, Yerkes wrote "*the greatest possibility for improvement in our provision for captive primates lies with the invention and installation of apparatus which can be used for play or work*" (p. 242). Further, Markowitz (1982, pp. 197–198) wrote that we should "*... leave as many decisions as possible to the animals while providing them increased behavioral opportunities*". A sensible approach to low-investment cognitive enrichment is to borrow devices from a cognitive laboratory such as spatial tasks (mazes) or cause–effect problems (trap-tube tests). Because we have background research on how challenging these tasks are for great apes, and because they have presumably been designed to be safe and practical, they could translate well to other captive facilities. For example, two-dimensional finger mazes have been used for decades to test the cogni-tive skills of primates (for example Iversen and Matsuzawa, 2001; Tsuchida et al., 2003) and could be used to allow apes to choose to work for their food, or non-food resources in other settings. From a practical perspective, these devices could be modular in design, so that different configura-tions can be created over time. Clark et al. (in preparation) designed a modular two-dimensional finger maze for zoo-housed chimpanzees at relatively low cost, allowing potentially hundreds of novel maze arrays to be tested within the same static 0.5 m^2 frame.

Previous cognitive research on great apes indicates what types of cognitive tasks may be challenging, but indi-vidual differences in skill and motivation should always be taken into account. As stated earlier, the cognitive skills of laboratory subjects do not always reflect the species as a whole (de Waal and Ferrari, 2010). Importantly, some studies have reported a negative relationship between cog-nitive testing and well-being in captive great apes (Leavens et al., 2001; Yamanashi and Matsuzawa, 2010). Yamanashi and Matsuzawa (2010) demonstrated that three out of six chimpanzees exhibited higher rates of self-directed behaviour when making errors in cognitive tasks and

during more difficult tasks. Elder and Menzel (2001) reported that frustration (evidenced by aggression towards the device, and self-scratching) increased in a singly-housed orang-utan when the inter-trial interval was increased. However, the authors also found that levels of salivary cortisol (a measure of short-term stress) were lower during test sessions than during baseline sessions. It is important for laboratories to be transparent where possible about the welfare effects of cognitive testing, so that the wider community of captive great apes can benefit from these findings.

If resources are available then devices should be custom-made to suit individual differences in skill and motivation. This will certainly be more feasible for lone-housed great apes (for example new animals in quarantine, or those housed in biomedical facilities). As stated above, the easiest way to achieve this type of enrichment is by using modular, grid-like devices where the level of complexity can be altered easily and devices can be used re-used over time. In large social groups, several versions of a cognitive device could be provided, each with a different level of difficulty or type of reward. With the knowledge that great apes show high individual differences towards enrichment (Gilloux et al., 1992; Morimura, 2003; Tarou et al., 2004), some individuals may benefit from interacting with a device (without necessarily 'solving' the problem and accessing a physical reward), while others will be more sensitive to their own performance and reward schedule. Subject's responses to previous types of enrichment and novel objects or situations may allow animal care staff to anticipate subject's responses to cognitive enrichment before it is provided (Clark et al., in preparation). However ideally, evaluating the responses of individuals to cognitive challenge devices should be a regular and on-going process, to ensure that the level of challenge remains appropriate. Some animal care staff may worry that on-going evaluation contradicts the term 'low-investment', but evaluation is critical to determine whether a cognitive challenge is, in fact, enriching.

5.3. The high-investment approach to cognitive enrichment

Early rearing history influences a great ape's well-being in later life (Section 3.1), and intriguingly, cognitive challenges early in life can protect against the development of age-associated cognitive decline in humans and other animals (reviewed by Milgram et al., 2006). At a neuronal level, spatial cognitive challenges have been linked to increased synapse formation in the motor cortex of the brain (Jones et al., 1999). Laboratory rodents who participate in 'obstacle courses' have better problem-solving abilities, spatial awareness and co-ordination than controls (Lambert et al., 2005). The remaining question is whether the chronic effects of cognitive challenge can also improve well-being. For this we require longitudinal studies of animals, where cognitive function and indicators of well-being can be monitored over many years. It is a particularly interesting question for great apes, who live for approximately 50–60 years in captivity, which is 10–20 years above their lifespan in the wild (Tarou et al., 2002).

This leads to the idea of 'high-investment' cognitive enrichment: an approach that immerses an animal with cognitive challenges from an early age and throughout life. Far removed from the low-investment approach to cognitive enrichment, this more holistic approach requires significant changes to management, and considerable preparation including animal training. As inspiration, the 'Crystal Maze' was a popular British game show on television in the 1990s. A group of human participants volunteered themselves for a number of mental and physical challenges in dedicated 'zones' in order to win rewards. Could great ape housing be developed so that subjects have access to a number of distinct 'zones' (Clark, 2011), each with its own problem-solving opportunities? However, rather than make these challenges competitive (for example one subject wins food while the other loses), subjects would have full control over their participation and no deprivation would occur.

There are many possible approaches to holistic cognitive enrichment, requiring significant financial investment and on-going maintenance costs. One approach is the use of computer technology to provide great apes with cognitive challenges. Chimpanzees and orang-utans are able to use video images to guide their search for hidden objects (Menzel et al., 1978; Poss and Rochat, 2003), and Hirata (2007) recently showed that chimpanzees can recognize live images of themselves or objects on video screens. Integrating this type of technology into great ape exhibits will require high initial investment and maintenance, but, "*The infinite number of tasks and levels of complexity that can be programmed into a computer can provide animals with daily cognitive stimulation and the continual opportunity to solve novel problems*" (Tarou et al., 2004, p. 445).

While there are many technological possibilities, these will not be acceptable or feasible in all captive facilities. An alternative approach is something more naturalistic. Different enclosure zones could be converted into 'biomes', each with its own climate and vegetation thus offering environmental unpredictability. As zoos and sanctuaries become increasingly willing and able to build large and naturalistic exhibits (Coe and Dykstra, 2010), cognitive challenges can more closely mimic those experienced by wild great apes. For example, wild chimpanzee extractive foraging could be simulated in captivity by providing opportunities to 'dip' and 'fish' for live insect prey (Goodall, 1964), and opportunities to crack nuts and other hard-cased food items (Boesch and Boesch, 1983). To date, artificial termite mounds have been used to encourage natural behaviours including tool use in captive chimpanzees, gorillas and orang-utans (Nash, 1982; Nakamichi, 2004; Lonsdorf et al., 2009), but the presence of 'real' (and therefore temporally and spatially unpredictable) prey items has been absent.

There are other practical considerations relating to high-investment cognitive enrichment. The link between unpredictability of events and anxiety in captive primates is unclear. For example, Leavens et al. (2001) found that the rate of self-directed behaviours in laboratory chimpanzees was higher during more complex cognitive tasks, but this rate decreased when an auditory tone signalled if the subject's response was correct or

incorrect. In contrast, Bloomsmith and Lambeth (1995) found that unpredictable feeding times promoted more species-appropriate behaviour than predictable feeding times in laboratory chimpanzees. Therefore, high-investment cognitive enrichment is likely to require an initial training period so that subjects can learn the relationships between some of the different signals in their complex environment, and access to different challenge opportunities, so that they are not overtly stressful.

Finally, as demonstrated by Markowitz and Line (1989), too much control can also be detrimental if an animal becomes too engaged in a cognitive task to the detriment of other activities. The authors found that rhesus macaques pressed a control switch over 100,000 times in one week to receive food rewards, when they could have been expressing more naturalistic behaviours. A more practical option may be to provide signalled cognitive challenges in different zones, which are predictable in use but unpredictable over time (Sambrook and Buchanan-Smith, 1997). Overall, for high-investment cognitive enrichment to be a success there must be a balance between providing great apes with diverse and interesting cognitive challenges over the long-term, and not impinging on a subject's natural and important behaviours including resting and socialising.

6. Conclusions

As humans, we are somewhat blinkered when it comes to understanding how other animals 'see' their world. As our closest living relatives, we understand great apes better than any other animal, domestic animals excepted. In fact, we have dedicated almost a century of scientific activity to understanding the behaviour and cognition of great apes. This article can only give a flavour of the knowledge we have accumulated thus far. Future enrichment should incorporate cognitive challenges based on the results of cognitive testing, in which animals can participate actively. Successful cognitive enrichment should be relevant to the natural history and motivations of an animal, and responses to enrichment should be correlated with validated indicators of well-being. This article does not suggest that cognitive enrichment is a panacea for great apes in captivity. It cannot solve the behavioural problems of all great apes living in captivity, but may offset the effects of an inadequate or inappropriate environment. Cognitive enrichment should be used alongside other forms of enrichment to ensure that physical fitness and naturalistic relationships between conspecifics are maintained.

This review distils our growing knowledge of great ape cognition, and can only whet the appetite of those who are interested in the subject. Our knowledge of great ape cognition has been biased towards chimpanzees thus far (Russell, 2008), and further cognitive work should be focussed on bonobos, gorillas and orang-utans. There are plenty of collaborative opportunities for cognitive scientists, animal welfare scientists and animal care staff. In fact, research could go full circle so that well-being research helps inform the design of future cognition research. Finally, questions that could be addressed in future are: (1) Do different great ape social groupings significantly affect the success of cognitive enrichment? (2) Do

long-term cognitive challenges have significant impacts on great ape cognitive function? For example, can a programme of cognitive challenge off-set the rate of cognitive decline in ageing apes? (3) How can cognitive challenges be evaluated most effectively as forms of enrichment?

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References

Akers, J.S., Schildkraut, D.S., 1985. Regurgitation/reingestion and coprophagy in captive gorillas. Zoo. Biol. 4, 99–109.

Albiach-Serrano, A., Call, J., Barth, J., 2010. Great apes track hidden objects after changes in the objects' position and in subject's orientation. Am. J. Primatol. 72, 349–359.

Arbib, M.A., Liebal, K., Pika, S., 2008. Primate vocalization, gesture, and the evolution of human language. Curr. Anthropol. 49, 1053–1076.

Aureli, F., de Waal, F.B.M., 1997. Inhibition of social behaviour in chimpanzees under high-density conditions. Am. J. Primatol. 41, 213–228.

Baker, K.C., 1997. Straw and forage ameliorate abnormal behaviors in adult chimpanzees. Zoo. Biol. 16, 225–236.

Baker, K.C., 2004. Benefits of positive human interaction for socially-housed chimpanzees. Anim. Welf. 13, 239–245.

Baker, K.C., 1996. Chimpanzees in single cages and small social groups: Effects of housing on behavior. Contemp. Top. Lab. Anim. Sci. 35, 71–74.

Baker, K., Easley, S., 1996. Regurgitation and reingestion in captive chimpanzees. Appl. Anim. Behav. Sci. 149, 403–415.

Baker, K.C., Aureli, F., 1997. Behavioural indicators of anxiety: an empirical test in chimpanzees. Behaviour 134, 1031–1050.

Bassett, L., Buchanan-Smith, H.M., 2007. Effects of predictability on the welfare of captive primates. Appl. Anim. Behav. Sci. 102, 223–245.

Beck, B.B., 1980. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. Garland, New York.

Bekoff, M., Allen, C., Burghardt, G.M., 2002. The Cognitive Animal, Empirical and Theoretical Perspectives. MIT Press, Cambridge.

Birkett, L.P., Newton-Fisher, N.E., 2011. How abnormal is the behaviour of captive, zoo-living chimpanzees? PLoS ONE 6, e20101.

Bloomsmith, M.A., Brent, L.Y., Schapiro, S.J., 1991. Guidelines for developing and managing an environmental enrichment program for nonhuman primates. Lab. Anim. Sci. 41, 372–377.

Bloomsmith, M.A., Lambeth, S.P., 1995. Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior. Appl. Anim. Behav. Sci. 44, 65–74.

Bloomsmith, M.A., Lambeth, S.P., 2000. Videotapes as enrichment for captive chimpanzees (Pan troglodytes). Zoo. Biol. 19, 541–551.

Bloomstrand, M., Riddle, K., Alford, P.L., Maple, T.L., 1986. Objective evaluation of a behavioral enrichment device for captive chimpanzees (Pan troglodytes). Zoo. Biol. 5, 293–300.

Boesch, C., Boesch, H., 1983. Optimization of nut cracking with natural hammers by wild chimpanzees. Behaviour 3–4, 265–286.

Brent, L., Lee, D.R., Eichberg, J.W., 1989. The effects of single caging on chimpanzee behavior. Lab. Anim. Sci. 39, 345–346.

Brent, L., Lee, D.R., Eichberg, J.W., 1991. Evaluation of chimpanzee enrichment enclosure. J. Med. Primatol. 20, 29–34.

Broom, D.M., 2010. Cognitive ability and awareness in domestic animals and decisions about obligations to animals. Appl. Anim. Behav. Sci. 126, 1–11.

Brüne, M., Brüne-Cohrs, U., McGrew, W.C., Preuschoft, S., 2006. Psychopathology in great apes: concepts, treatment options and possible homologies to human psychiatric disorders. Neurosci. Biobehav. Rev. 30, 1246–1259.

Brydges, N.M., Braithwaite, V.A., 2008. Measuring animal welfare: what can cognition contribute? Annu. Rev. Biomed. Sci. 10, T91–T103.

Byrne, R.W., Whiten, A., 1988. Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans. Oxford University Press, New York.

Call, J., 2010. Trapping the minds of apes: causal knowledge and inferential reasoning about object–object interactions. In: Lonsdorf, E.V., Ross, S.R., Matsuzawa, T. (Eds.), The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, Chicago, pp. 75–86.

Call, J., Tomasello, M., 2008. Do chimpanzees have a theory of mind? 30 years later. Trends. Cogn. Sci. 12, 187–192.

Carlstead, K., Shepherdson, D., 2000. Alleviating stress in zoo animals with environmental enrichment. In: Moberg, G.P., Mench, J.A. (Eds.), The Biology of Animal Stress. CABI Publishing, New York, pp. 337–354.

Celli, M.L., Tomonaga, M., Udono, T., Teramoto, M., Nagano, K., 2003. Tool use task as environmental enrichment for captive chimpanzees. Appl. Anim. Behav. Sci. 81, 171–182.

Chalmeau, R., 1994. Do chimpanzees cooperate in a learning task? Primates 35, 385–392.

Chalmeau, R., Lardeux, K., Brandibas, P., Gallo, A., 1996. Cooperative problem solving by orangutans (Pongo pygmaeus). Int. J. Primatol. 18, 23–32.

Chittka, L., Jensen, K., 2011. Animal cognition: concepts from apes to bees. Curr. Biol. 21, R116–R119.

Citrynell, P., 1998. Cognitive enrichment: problem solving abilities of captive white-bellied spider monkeys. Primate Eye 6, 16–17.

Clark, F.E., 2011. Space to choose: network analysis of social preferences in a captive chimpanzee community, and implications for management. Am. J. Primatol. 73, 748–757.

Clark, F.E., Fitzpatrick, M., Hartley, A., King, A.J., Lee, T., Routh, A., Walker, S., George, K., 2011. The relationship between behavior, adrenal activity and environment in zoo-housed Western lowland gorillas (Gorilla gorilla gorilla). Zoo. Biol., doi:10.1002/zoo.20396.

Clark, F.E., Hitchcock, D., Sainsbury, A.W., Wathes, C.M. In preparation. Can cognitive challenges be enriching? Behavioural responses of zoo-housed chimpanzees (Pan troglodytes) to a novel cognitive challenge device, in preparation.

Clay, Z., Zuberbühler, K., 2011. Bonobos extract meaning from call sequences. PLoS ONE 6, e18786.

Coe, J., Dykstra, G., 2010. New and sustainable directions in zoo exhibit design. In: Kleiman, G., Thompson, K.V., Kirk, C. (Eds.), Wild Mammals in Captivity: Principles and Techniques for Zoo Management. , 2nd ed. University of Chicago Press, Chicago, pp. 202–215.

Cohen, J., 2010. Boxed about the ears, ape language research field is still standing. Science 328, 38–39.

Conlee, K.M., 2008. Chimpanzees in research and testing worldwide: overview, oversight and applicable laws. In: Proceedings of the Sixth World Congress on Alternatives and Animal Use in the Life Sciences, Tokyo, Japan, pp. 111–118.

Csatádi, K., Leus, K., Pereboom, J.J.M., 2008. A brief note on the effects of novel enrichment on an unwanted behaviour of captive bonobos. Appl. Anim. Behav. Sci. 112, 201–204.

Csikszentmihalyi, M., 1988. The flow experience and human psychology. In: Csikszentmihalyi, M., Csikszentmihalyi, I.S. (Eds.), Optimal Experience: Psychological Studies of Flow in Consciousness. Cambridge University Press, New York, pp. 15–35.

Dawkins, M.S., 2001. How can we recognise and assess good welfare? In: Broom, D.M. (Ed.), Coping with Challenge: Welfare in Animals Including Humans. Dahlem University Press, Berlin, pp. 67–76.

de Azevedo, C.S., Cipreste, C.F., Young, R.J., 2007. Environmental enrichment: a GAP analysis. Appl. Anim. Behav. Sci. 102, 329–343.

de Waal, F.B.M., 1982. Chimpanzee Politics. Cape Publishing, London.

de Waal, F., Lanting, F., 1997. Bonobo: The Forgotten Ape. University of California Press, Berkley.

de Waal, F.B.M., Ferrari, P.F., 2010. Towards a bottom-up perspective on animal and human cognition. Trends Cogn. Sci. 14, 201–207.

Dunbar, R.I.M., 1998. The social brain hypothesis. Evol. Anthropol. 6, 178–190.

Duncan, I.J.H., Wood-Gush, D.G.M., 1972. Thwarting of feeding behaviour in the domestic fowl. Anim. Behav. 20, 444–451.

Elder, C.M., Menzel, C.R., 2001. Dissociation of cortisol and behavioral indicators of stress in an orangutan (Pongo pygmaeus) during a computerized task. Primates 42, 345–358.

Ernst, K., Puppe, B., Schon, P.C., Manteuffel, G., 2005. A complex automatic feeding system for pigs aimed to induce successful behavioural coping by cognitive adaptation. Appl. Anim. Behav. Sci. 91, 205–281.

Fernie, A., 2008. The creation and implementation of a great ape welfare index. Ph.D. Thesis. School of Animal Studies, University of Queensland, St. Lucia.

Fritz, J., 1986. Resocialization of asocial chimpanzees. In: Benirschke, K. (Ed.), The Road to Self-Sustaining Populations. Springer-Verlag, New York, pp. 351–359.

Fritz, J., Howell, S., 1993. Psychological wellness for captive chimpanzees: an evaluative program. Hum. Innov. Alts. 7, 426–433.

Gibeault, S., MacDonald, S.E., 2000. Spatial memory and foraging competition in captive western lowland gorillas (Gorilla gorilla gorilla). Primates 4, 147–160.

Gilloux, I., Gurnell, J., Shepherdson, D., 1992. An enrichment device for great apes. Anim. Welfare 1, 279–289.

Goodall, J., 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. Nature 201, 1264–1266.

Hagan, K., Broom, D.M., 2004. Emotional reactions to learning in cattle. Appl. Anim. Behav. Sci. 85, 203–213.

Hare, B., Melis, A.P., Woods, V., Hastings, S., Wrangham, R.W., 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. Curr. Biol. 17, 619–623.

Hirata, S., 2007. A note on the responses of chimpanzees (Pan troglodytes) to live self-images on television monitors. Behav. Process. 75, 85–90.

Hopkins, W.D., Morris, R.D., 1993. Handedness in great apes: a review of findings. Int. J. Primatol. 14, 1–25.

Hopkins, W.D., Phillips, K.A., Bania, A., Calcutt, S.E., Gardner, M., Russell, J., Schaeffer, J., Lonsdorf, E.V., Ross, S.R., Schapiro, S.J., 2011. Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in Hominins. J. Hum. Evol. 60, 605–611.

Howell, S., Schwandt, M., Fritz, J., Roeder, E., Nelson, C., 2003. A stereo music system as environmental enrichment for captive chimpanzees. Lab. Anim. 32, 31–36.

Inglis, I.R., Forkman, B., Lazarus, J., 1997. Free food or earned food? A review and fuzzy model of contrafreeloading. Anim. Behav. 53, 1171–1191.

Inoue, S., Matsuzawa, T., 2007. Working memory of numerals in chimpanzees. Curr. Biol. 17, R1004–R1005.

International Species Information System (ISIS), 2011. Accessed at http://www.isis.org.

Iversen, I.H., Matsuzawa, T., 2001. Acquisition of navigation by chimpanzees (Pan troglodytes) in an automated fingermaze task. Anim. Cogn. 4, 179–192.

Jones, T.A., Chu, C.J., Grande, L.A., Gregory, A.D., 1999. Motor skills training enhances lesion-induced structural plasticity in the motor cortex of adult rats. J. Neurosci. 19, 10153–10163.

Kirkwood, J.K., Hubrecht, R., 2001. Consciousness, cognition and animal welfare. Anim. Welfare 10, S5–S17.

Köhler, W., 1925. The Mentality of Apes. Routledge, London.

Krief, S., Jamart, A., Hladik, C.M., 2004. On the possible adaptive value of coprophagy in free-ranging chimpanzees. Primates 45, 141–145.

Kuhlmeier, V.A., Boysen, S.T., Mukobi, K.L., 1999. Scale-model comprehension by chimpanzees (Pan troglodytes). J. Comp. Psychol. 113, 396–402.

Lambert, K.G., Berry, A.E., Griffin, G., Amory-Meyer, E.A., Madonia-Lomas, L.F., Love, G., Kinsley, C.H., 2005. Pup exposure differentially enhances foraging ability in primiparous and nulliparous rats. Physiol. Behav. 85, 799–806.

Lambeth, S.P., Bloomsmith, M.A., 1994. A grass foraging device for captive chimpanzees (Pan troglodytes). Anim. Welfare 3, 13–24.

Langbein, J., Siebert, K., Nürnberg, G., 2009. On the use of an automated learning device by group-housed dwarf goats: do goats seek cognitive challenges? Appl. Anim. Behav. Sci. 120, 150–158.

Leavens, D.A., Aureli, F., Hopkins, W.D., Hyatt, C.W., 2001. Effects of cognitive challenge on self-directed behaviors by chimpanzees (Pan troglodytes). Am. J. Primatol. 55, 1–14.

Leighty, K.A., Fragaszy, D.M., 2003. Primates in cyberspace: using interactive computer tasks to study perception and action in nonhuman animals. Anim. Cogn. 6, 137–139.

Lonsdorf, E.V., Ross, S.R., Linick, S.A., Milstein, M.S., Melber, T.N., 2009. An experimental, comparative investigation of tool use in chimpanzees and gorillas. Anim. Behav. 77, 1119–1126.

Lukas, K.E., 1999. A review of the nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (Gorilla gorilla gorilla). Appl. Anim. Behav. Sci. 63, 237–249.

Macdonald, S.E., Agnes, M.M., 1999. Orangutan (Pongo pygmaeus abelii) spatial memory and behavior in a foraging task. J. Comp. Psychol. 113, 213–217.

Maestripieri, D., Schino, G., Aureli, F., Troisi, A., 1992. A modest proposal: displacement activities as indicators of emotions in primates. Anim. Behav. 44, 967–979.

Maki, S., Alford, P.L., Bloomsmith, M.A., Franklin, J., 1989. Food puzzle device simulating termite fishing for captive chimpanzees (*Pan troglodytes*). Am. J. Primatol. Suppl. 1, 71–78.

Manrique, H.M., Gross, A.N., Call, J., 2010. Great apes select tools based on their rigidity. J. Exp. Psychol. Anim. B 36, 409–422.

Manteuffel, G., Langbein, J., Puppe, B., 2009. From operant learning to cognitive enrichment in farm animal housing: bases and applicability. Anim. Welfare 18, 87–95.

Maple, T.L., Hoff, M.P., 1982. Gorilla Behavior. Van Nostrand Reinhold Co., New York.

Markowitz, H., 1982. Behavioral Enrichment in the Zoo. Van Nostrand Reinhold, New York.

Markowitz, H., Line, S., 1989. Primate Research Models and Environmental Enrichment. Noyes Publications, New Jersey.

Martin-Ordas, G., Haun, D., Colmenares, F., Call, J., 2010. Keeping track of time: evidence for episodic-like memory in great apes. Anim. Cogn. 13, 331–340.

Mason, G.J., 1991. Stereotypes and suffering. Behav. Process. 25, 103–115.

Mason, G.J., Rushen, J., 2006. Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare, second ed. CABI Press, Wallingford.

Mason, G.J., Clubb, R., Latham, N., Vickery, S., 2007. Why and how should we use environmental enrichment to tackle stereotypic behaviour? Appl. Anim. Behav. Sci. 102, 163–188.

Matsuzawa, T., 2010. The chimpanzee mind: bridging fieldwork and laboratory work. In: Lonsdorf, E.V., Ross, S.R., Matsuzawa, T. (Eds.), The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, Chicago, pp. 1–22.

McGrew, W.C., 1989. Why is ape tool use so confusing? In: Standen, V., Foley, R.A. (Eds.), Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals. Blackwell Scientific Publications, Oxford, pp. 457–472.

McGrew, W.C., Marchant, L.F., 1996. On which side of the apes? Ethological study of laterality of hand use. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. University of Cambridge Press, Cambridge, pp. 255–272.

Meehan, C.L., Mench, J.A., 2007. The challenge of challenge: can problem solving opportunities enhance animal welfare? Appl. Anim. Behav. Sci. 102, 246–261.

Mellen, J., Sevenich MacPhee, M., 2001. Philosophy of environmental enrichment: past, present, and future. Zoo. Biol. 20, 211–226.

Mench, J.A., Mason, G.J., 1997. Behaviour. In: Appleby, M.C., Hughes, B.O. (Eds.), Anim. Welf. CABI Publishing, Wallingford, pp. 127–141.

Mendl, M., Burman, O.H.P., Parker, R.M.A., Paul, E.S., 2009. Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. Appl. Anim. Behav. Sci. 118, 161–181.

Menzel, E.W., Premack, D., Woodruff, G., 1978. Map reading by chimpanzees. Folia Primatol. 29, 241–249.

Meyer, S., Puppe, B., Langbein, J., 2011. Cognitive enrichment in zoo and farm animals – implications for animal behaviour and welfare. Berliner und Münchener Tierärztliche Wochenschrift 123, 446–456.

Milgram, N.W., 2003. Cognitive experience and its effect on age-dependent cognitive decline in beagle dogs. Neurochem. Res. 28, 1677–1682.

Milgram, N.W., Siwak-Tapp, C.T., Araujo, J., Head, E., 2006. Ageing. Res. Rev. 5, 354–369.

Morgan, K.N., Tromborg, C.T., 2007. Sources of stress in captivity. Appl. Anim. Behav. Sci. 102, 262–302.

Morimura, N., 2003. Cognitive Enrichment in Chimpanzees: An Approach of Welfare Entailing an Animal's Entire Resources. In: Matsuzawa T, Tomonaga M, Tanaka M. (Eds.), 2006 Cognitive development in chimpanzees, Tokyo, Japan, Springer, p. 368–391.

Mulcahy, N.J., Call, J., 2006. Apes save tools for future use. Science 312, 1038–1040.

Mundy, N.I., Ancrenaz, M., Wickings, J., Lunn, P.G., 1998. Protein deficiency in a colony of Western lowland gorillas (*Gorilla g. gorilla*). J. Zoo. Wildl. Med. 29, 261–268.

Myers, D.G., Diener, E., 1995. Who is happy? Psychol. Sci. 6, 10–19.

Nakamichi, M., 2004. Tool-use and tool-making by captive, group-living orangutans (*Pongo pygmaeus abelii*) at an artificial termite mound. Behav. Process. 65, 87–93.

Nash, V.J., 1982. Tool use by captive chimpanzees at an artificial termite mound. Zoo. Biol. 1, 211–221.

Nash, L.T., Fritz, J., Alford, P.L., Brent, L., 1999. Variables influencing the origins of diverse abnormal behaviors in a large sample of captive chimpanzees (*Pan troglodytes*). Am. J. Primatol. 48, 15–29.

Novak, M.A., Suomi, S., 1988. Psychological well-being of primates in captivity. Am. Psychol. 43, 765–773.

Ostrower, S., Brent, L., 2000. Olfactory enrichment for captive chimpanzees: responses to different odors. Lab. Primate Newslett. 36, 8–12.

Paquette, D., Prescott, J., 1988. Use of novel objects to enhance environments of captive chimpanzees. Zoo. Biol. 7, 15–23.

Parker, H.L., Miles, H.L., Mitchell, R.W., 1999. The Mentality of Gorillas and Orangutans. Cambridge University Press, Cambridge.

Paul, E.S., Harding, E.J., Mendl, M., 2005. Measuring emotional processes in animals: the utility of a cognitive approach. Neurosci. Biobehav. Rev. 29, 469–491.

Perlman, J.E., Horner, V., Bloomsmith, M.A., Lambeth, S.P., Schapiro, S.J., 2010. Positive reinforcement training, social learning, and chimpanzee welfare. In: Lonsdorf, E.V., Ross, S.R., Matsuzawa, T. (Eds.), The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, Chicago, pp. 320–332.

Pomerantz, O., Terkel, J., 2009. Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (*Pan troglodytes*). Am. J. Primatol. 71, 687–695.

Poss, S.R., Rochat, P., 2003. Referential understanding of videos in chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and children (*Homo sapiens*). J. Comp. Psychol. 117, 420–428.

Puppe, B., Ernst, K., Schön, P.C., Manteuffel, G., 2007. Cognitive enrichment affects behavioural reactivity in domestic pigs. Appl. Anim. Behav. Sci. 105, 75–86.

Reimers, M., Schwarzenberger, F., Preuschoft, S., 2007. Rehabilitation of research chimpanzees: stress and coping after long-term isolation. Horm. Behav. 51, 428–435.

Ross, S.R., 2009. Sequential list-learning by an adolescent lowland gorilla (*Gorilla gorilla gorilla*) using an infrared touchframe apparatus. Int. Stud. 10, 115–129.

Ross, S.R., 2010. How cognitive studies help shape our obligations for the ethical care of chimpanzees. In: Lonsdorf, E.V., Ross, S.R., Matsuzawa, T. (Eds.), The Mind of the Chimpanzee: Ecological and Experimental Perspectives. The University of Chicago Press, Chicago, pp. 309–319.

Rumbaugh, D.M., Washburn, D., Savage-Rumbaugh, E.S., 1989. On the care of captive chimpanzees: methods of enrichment. In: Segal, E. (Ed.), Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates. Noyes Publications, New Jersey, pp. 357–375.

Russell, N., 2008. Evidence for the social revolution: trends in great ape behavioral research between 1992 and 2006. Mind Matters: The Wesleyan Journal of Psychology 3, 17–20.

Russon, A.E., Bard, K.A., Taylor Parker, S., 1998. Reaching into Thought: The Minds of the Great Apes. Cambridge University Press, Cambridge.

Russon, A.E., 2004. Great ape cognitive systems. In: Russon, A.E., Begun, D.R. (Eds.), The Evolution of Great Ape Intelligence. Cambridge University Press, Cambridge, pp. 76–100.

Ryan, E.B., Proudfoot, K.L., Fraser, D., 2011. The effect of feeding enrichment methods on the behavior of captive Western lowland gorillas. Zoo. Biol, doi:10.1002/zoo.20403.

Sakamaki, T., 2010. Coprophagy in wild bonobos (*Pan paniscus*) at Wamba in the Democratic Republic of the Congo: a possibly adaptive strategy? Primates 51, 87–90.

Sambrook, T., Buchanan-Smith, H., 1997. Control and complexity in novel object enrichment. Anim. Welfare 6, 207–216.

Shepherdson, D.J., 1998. Tracing the path of environmental enrichment in zoos. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), Second Nature: Environmental Enrichment for Captive Animals. Smithsonian Institution, Washington, pp. 1–14.

Shettleworth, S.J., 2010. Cognition, Evolution and Behavior. Oxford University Press, Oxford.

Shumaker, R.W., Walkup, K.R., Beck, B.B., 2011. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. Johns Hopkins University Press, Baltimore.

Shyne, A., 2006. Meta-analytic review of the effects of enrichment on stereotypic behavior in zoo mammals. Zoo. Biol. 25, 317–337.

Slocombe, K., Kaller, T., Call, J., Zuberbühler, K., 2010. Chimpanzees extract social information from agonistic screams. PLoS ONE 5, e11473.

Struthers, E.J., Campbell, J., 1996. Scent-specific behavioral response to olfactory enrichment in captive chimpanzees (*Pan troglodytes*). In: Presented at the XVIth Congress of the International Primatological Society and the XIXth Conference of the American Society of Primatology, Wisconsin.

Suedmeyer, W.K., 1997. Hypothyroidism in an Orangutan (*Pongo pygmaeus pygmaeus*): Clinical Management and Long-term Monitoring. American Association of Zoo Veterinarians, Florida, pp. 71–72.

Swaisgood, R.R., Shepherdson, D.J., 2005. Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next? Zoo. Biol. 24, 499–518.

Swartz, K.B., Himmanen, S.A., 2006. Individual response strategies in list learning by orangutans. Int. J. Psychol. Psychol. Therapy 6, 233–240.

Tarou, L.R., Bloomsmith, M.A., Hoff, M.P., Erwin, J.M., Maple, T.L., 2002. The behavior of aged great apes. In: Erwin, J.M., Hof, P.R. (Eds.), Aging in Nonhuman Primates. Karger, Basel, pp. 209–231.

Tarou, L.R., Kuhar, C.W., Adcock, D., Bloomsmith, M.A., Maple, T.L., 2004. Computer-assisted enrichment for zoo-housed orangutans (*Pongo pygmaeus*). Anim. Welfare 13, 445–453.

Tomasello, M., Call, C.J., 1997. Primate Cognition. Oxford University Press, Oxford.

Tomasello, M., Herrmann, E., 2010. Ape and human cognition: what's the difference? Curr. Dir. Psychol. Sci. 19, 3–8.

Tsuchida, J., Kawasaki, K., Sankai, T., Kubo, N., Keiji, T., Koyama, T., Makino, J., Yoshikawa, Y., 2003. New type of puzzle-task finger maze learning in *Macaca fascicularis*. Int. J. Primatol. 24, 261–270.

Van Schaik, C.P., Deaner, R.O., Merrill, M.Y., 1999. The conditions for tool use in primates: implications for the evolution of material culture. J. Hum. Evol. 36, 719–741.

Videan, E.N., Fritz, J., Howell, S., Murphy, J., 2007. Effects of two types and genres of music on social behaviour in captive chimpanzees (*Pan troglodytes*). J. Am. Assoc. Lab. Anim. Sci. 46, 66–70.

Vlamings, P.H.J.M., Uher, J., Call, J., 2006. How the Great apes (*Pan troglodytes, Pongo pygmaeus, Pan paniscus*, and *Gorilla gorilla*) perform on the reversed contingency task: the effects of food quantity and food visibility. J. Exp. Psychol. Anim. Behav. Process. 32, 60–70.

Walsh, S., Bramblett, C.A., Alford, P.L., 1982. A vocabulary of abnormal behaviors in restrictively reared chimpanzees. Am. J. Primatol. 3, 315–319.

Washburn, D.A., Astur, R.S., 2003. Exploration of virtual mazes by rhesus monkeys (*Macaca mulatta*). Anim. Cogn. 6, 161–168.

Washburn, D.A., Rumbaugh, D.M., 1992. Testing primates with joystick-based automated apparatus: Lessons from the Language Research Center's Computerized Test System. Behav. Res. Meth. Instr. Comput. 24, 157–164.

Wasserman, E.A., Zentall, T.R., 2006. Comparative Cognition: Experimental Explorations of Animal Intelligence. Oxford University Press, London.

Wells, D.L., Hepper, P.G., Coleman, D., Challis, M.G., 2007. A note on the effect of olfactory stimulation on the behaviour and welfare of zoo-housed gorillas. Appl. Anim. Behav. Sci. 106, 155–160.

Wemelsfelder, F., 1993. The concept of animal boredom and its relationship to stereotyped behaviour. In: Lawrence, J.B., Rushen, J. (Eds.), Stereotypical Animal Behaviour: Fundamentals and Applications to Welfare. CABI Publishing, Wallingford, pp. 65–96.

Wemelsfelder, F., Birke, L.I.A., 1997. Environmental challenge. In: Appleby, M.C., Hughes, B.O. (Eds.), Animal Welfare. CAB International, Wallingford, pp. 35–47.

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–685.

Wolfe-Coote, S., 2005. The Laboratory Primate. Elsevier Academic Press, London.

Wood-Gush, D.G.M., Vestergaard, K., 1989. Exploratory behavior and the welfare of intensively kept animals. J. Agric. Ethics 2, 161–169.

Yamanashi, Y., Matsuzawa, T., 2010. Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: individual differences in self-directed behaviours during cognitive tasks. Anim. Welfare 19, 25–30.

Yerkes, R.M., 1916. The Mental Life of Monkeys and Apes. Scholars' Facsimiles & Reprints, New York.

Yerkes, R.M., 1925. Almost Human. Jonathan Cope, London.