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Cognitive enrichment: Positive animal welfare through skill development and expression

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Opinion Paper

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Abstract

Contemporary animal welfare science emphasises the roles of challenge, skill development and skill expression in positive animal welfare, and takes a dynamic, temporal view of affect. However, cognitive enrichment as a welfare intervention (CE originally defined by Clark 2011 and later termed $CE_{welfare}$ by Clark 2022) has largely focused on how challenge impacts welfare at a general activity budget level, rather than evidence of skill development and coping during challenge. This paper aims to realign CE with the current views of challenge and animal welfare, by proposing an updated CE definition and a new methodological approach. CE arises *when an animal is challenged to develop and express its evolved cognitive skills, and the process or outcome of coping with challenge is associated with a net positive affective state.* We argue that rule-scaffolded play (gameplay) could be a powerful subtype of CE, because games offer skill development opportunities similar to the Zone of Proximal Development in humans. Gameplay unfolds as a sequence of events, allowing us to explore how cognitive performance is temporally linked to emotional expression. We describe two broad types of CE game – Innovation and Flow – that feature relatively lower and higher rule scaffolding, respectively. We also discuss the role of frustration in CE; initial frustration is normal when animals encounter a challenge, but a Flow game aims to avoid ongoing boredom and frustration by maintaining a skill-challenge balance. We end by presenting a case study of a Flow game for marine mammals in a zoological setting.

A critical review of CE to date

Definition

A captive environment is *enriched* when an intentional change to the environment has a beneficial impact on animal welfare (Newberry 1995; Young 2013; Vicino *et al.* 2022). While enrichment categories, such as 'food-based' and 'olfactory' are relatively self-explanatory (i.e. adding, removing or modifying food sources and scents, respectively), cognitive enrichment has often felt misaligned because 'cognition' refers to mental processes (characteristics) that belong to the animal, not the environment. Our paper reviews CE (cognitive enrichment) as a welfare intervention (i.e. welfare enhancement is the goal, cognition is the mechanism). This type of CE was termed '$CE_{welfare}$' by Clark (2022) in an attempt to distinguish it from another type of CE used in laboratory animal models of human cognition and health termed 'CE_{skill}'. In CE_{skill}, enhanced cognition is the goal, general environmental (cage) changes are the mechanism, and there is no welfare component (for comprehensive reviews of CE_{skill}, see Milgram *et al.* 2006; Petrosini *et al.* 2009; Fischer 2016; Landolfo *et al.* 2025). From here on, we shorten $CE_{welfare}$ to CE for simplicity.

Rising interest in the link between cognition and welfare this century (Meehan & Mench 2007; Boissy *et al.* 2007; Mendl *et al.* 2010) led to the following operational definition of CE: "*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 well-being*" (Clark 2011; p 6). The definition aimed to hybridise two disciplines: 'evolved cognitive skills' stemming from comparative psychology and 'validated welfare measures' stemming from animal welfare science. Thus, opportunities to solve and control a challenge (task) were linked to well-being.

The 2011 CE definition aligns with three tenets of challenge laid out in the seminal paper by Meehan and Mench (2007). The tenets are: (i) environments *change* in numerous ways; (ii) environmental changes of appropriate magnitude and evolutionary or ecological relevance are likely to *challenge* (pressurise, stress) an animal; and (ii) an animal's responses to challenge are processes, not snapshots in time. Note that while Meehan and Mench (2007) use the term 'challenge', 'cognitive challenge' and 'environmental challenge' also appear synonymously across the literature (e.g. see Špinka & Wemelsfelder 2018; Rose & Lewton 2025). We add some cautionary notes to the tenets of challenge, arguing that enrichment does not always have to be challenging (e.g. it may lead to comfort instead), and being challenged does not automatically guarantee positive welfare. This can be illustrated by five possible scenarios, only one of which counts as successful cognitive enrichment (Table 1; scenario 3).

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Table 1. Five possible scenarios for an animal experiencing environmental change. Cognitive enrichment is only possible when the environment is challenging, the challenge can be coped with, and this is linked to a net positive welfare outcome

Scenario	Does the environment change *challenge* (pressure/stress) the animal?	Does the animal *cope with* the challenge?	What is the *net welfare outcome* for the animal?	Is this *cognitive enrichment*?
1	No	N/A	Neutral or positive (comfort)	No
2	No	N/A	Negative (boredom)	No
3	Yes	Yes	Positive	Yes
4	Yes	Yes	Neutral or negative (frustration)	No
5	Yes	No	Neutral or negative (frustration)	No

Table 1 illustrates that CE is not guaranteed by changing a captive environment, because the animal must perceive a challenge, cope with the challenge, and have a net positive welfare outcome. The multidimensional nature of CE may explain why a recent meta-analysis of published enrichment studies between 2005 and 2021 found that CE was the least successful type of enrichment in terms of meeting its aims (Bachetti *et al.* 2024). Even though 76% of CE attempts were described as successful by practitioners, CE was 20% less successful than food-based enrichment. The proportion of enrichment studies classified as 'cognitive' decreased from 3.5% in 2007 to 2.2% in 2024 (de Azevedo *et al.* 2007; Bachetti *et al.* 2024). De Azevedo *et al.* (2007) reviewed 744 scientific enrichment articles published between 1985–2004, and Bachetti *et al.* (2024) performed a similar analysis of 2,002 articles published between 2005–2021. Even accounting for small differences in their sampling periods (19 vs 16 years, respectively) and differences in their definition of CE ('use of puzzle boxes' and the Clark 2011 definition, respectively), published peer-reviewed enrichment studies have increased over time but the proportion within them described as CE has remained low.

Published literature search (2011–2026)

Leading from the meta-analyses of de Azevedo *et al.* (2007) and Bachetti *et al.* (2024), we sought to explore the more specific influence of the Clark CE definition (2011) on CE research (note that the Clark 2011 definition was re-amplified in a 2017 opinion paper on CE; Clark 2017). We performed a Boolean search in PubMed and Google Scholar using the search term '*cognitive enrichment*' AND '*animal*'. We only included literature with 'animal welfare' as the primary aim (i.e. not CE_{skill}), and literature published in peer-reviewed sources between November 2011 and March 2026. This means that our literature search overlooked grey literature, such as industry conference abstracts and dissertations, but we did not bias the search towards a particular captive setting or taxonomic group.

Prevalence of CE

Thirty published studies met our search criteria (Table S1; Supplementary material). The majority of CE studies (18 articles, 60.0%) were performed on primates or marine mammals. We found that 22/30 studies (73.3%) cited the original CE definition (Clark 2011). Three of these empirical studies were authored by Clark and colleagues. Studies that did not cite the original 2011 definition (26.6%) provided similar definitions, including references to problem-solving and/or having additional control over the environment. Initially, we also hoped to assess whether the CE studies in our literature search met the conditions of CE according to scenario 3 in Table 1. However, this assessment was not possible because studies seldom reported whether the putative CE presented a high enough level of challenge to animals, or the net welfare outcome. Due to positive publication biases in animal welfare science and allied fields (Van der Schot & Phillips 2013), enrichment practitioners might be deterred from using CE if it is too difficult to evidence a significant improvement in animal welfare. In a survey of 177 zoo animal care staff (Hall *et al.* 2021), respondents generally saw the value of CE but felt discouraged from using CE because they felt that it required specialist knowledge and resources.

CE subtypes and rationale

We identified five broad subtypes of CE: maze navigation (n = 9; 30.0%); object manipulation (n = 9; 30.0%); associative learning opportunities (n = 5; 16.7%); cognitive task batteries, such as match-to-sample or object discrimination tasks traditionally found in cognitive research (n = 5; 16.7%); and social group manipulation (n = 2; 6.6%). For our classification purposes, we defined a maze as a system of intersecting paths and blind alleys that must be navigated (VandenBos 2015). One hundred percent of studies in our literature search met at least one of their stated goals of CE. Our literature search showed that, despite a high level of agreement on the definition of CE, the rationale for using CE varied across studies. In some cases, CE aimed to stimulate the expression of cognitive skills that were absent, assumed to be weak, or deemed to be important for optimal biological functioning (e.g. rainbow trout [*Oncorhynchus mykiss*] were trained to associatively learn the availability of food to forage more effectively; Kleiber *et al.* 2022). While in other cases, existing or traditional forms of husbandry were evaluated as putative forms of CE (e.g. mixed-species housing of tufted capuchin monkeys [*Cebus apella*] and squirrel monkey [*Saimiri sciureus*]; Daoudi *et al.* 2017).

Summary

In summary, Clark's 2011 CE definition has been frequently cited within the past 15 years and appears to be the most common definition of CE used in peer-reviewed research on captive animal welfare. However, it is difficult to accurately report whether CE has been sufficiently challenging, coped with, or has led to sufficiently positive welfare outcomes, and subtypes of CE are difficult to compare against each other. So, after 15 years of advancement in the field of animal welfare science, CE deserves a critical appraisal, including the definition of CE itself. The remainder of this opinion paper will discuss current scholarly consensus on positive animal welfare and challenge (see *Positive animal welfare, skill development and expression*), leading to an updated definition of CE (see *An updated definition of cognitive enrichment*) and our proposal for game-based CE (see *Gameplay: The next frontier in cognitive enrichment?* and *Flow game case study*).

Positive animal welfare, skill development and expression

Improved captive animal conditions and standards, more refined and validated welfare assessment methods, and a general shift towards 'affectivism' (integrating emotion and mood into the study

of cognition and behaviour; Dukes *et al.* 2021) recently gave rise to a new expert consensus definition of positive animal welfare (Rault *et al.* 2025): '*…animal flourishing through the experience of predominantly positive mental states and the development of competence and resilience.*' This re-centres positive animal welfare interventions on how an animal experiences environmental change, aiming to provide environments that allow animals to develop and succeed in some manner. Rault *et al.* (2025) bring us closer to the concept of animals living predominantly positive lives, akin to human flourishing. In humans, to 'flourish' means to function optimally, and to experience personal growth and resilience (Keyes 2002; Fredrickson 2004). Competence, resilience and flourishing concepts in animals are in stark contrast to the Five Freedoms paradigm of animal welfare, a checklist of freedoms from hunger/thirst, discomfort, pain/disease, and fear (Farm Animal Welfare Council 1979) that dominated the field of animal welfare science for many decades (McCulloch 2013; Mellor 2016).

Rault *et al.* (2025) did not directly define 'competence', but indicated that competence is acquired through exploration, play and practising decision-making. We suggest that competence could be conceptualised more directly as having the skills necessary to cope with challenge (coping is discussed later in this section). Competence is *gained* when skills are developed and *expressed* when skills are applied to a specific challenge. In the current paper, we make a clear distinction, where possible, between skill development (becoming more competent) and skill expression (expressing competence).

There is evidence that both skill development and skill expression are linked to enhanced animal welfare. First, animals may be intrinsically motivated to seek opportunities for challenge and therefore skill development and expression (Wood-Gush & Vestergaard 1989; Hughes 1997; Meehan & Mench 2007). Second, there are a few reports of animals having strong, positive emotional responses when a challenge is suddenly and unexpectedly overcome. This is known as the Eureka effect or Eureka moment in domestic cattle (*Bos taurus*) (Hagen & Broom 2004) and domestic dogs (*Canis lupus familiaris*) (McGowan *et al.* 2014) and is potentially analogous to the 'victory squeal' in common bottlenose dolphins (*Tursiops truncatus*) (Ridgway *et al.* 2014, 2015; Dibble *et al.* 2016) although this requires further study. Third, great apes and monkeys can exhibit strong, negative emotional responses when they regress or fail on cognitive tasks, indicating that performance and emotion can be consciously linked (e.g. Yamanashi & Matsuzawa 2010; Judge *et al.* 2011). Although not tested, this might suggest primates could also experience positive emotional responses to progression and success, in other words, the Eureka effect. And fourth, boredom in animals is a negative affective state linked to sterile, monotonous environments (e.g. Meagher & Mason 2012; Russell *et al.* 2024). Burn (2017) argued that boredom in animals arises from monotony and under-stimulation, and Meagher (2019) asserted that opportunities to experience appropriate cognitive challenge may stave off boredom.

Animal welfare has often been defined as the subjective ability to cope with the environment (Broom 1988). Wechsler (1995) views coping as a response to aversive situations, but we take a wider and less negatively skewed view that coping refers to dealing with a challenge, regardless of its valence or direction towards punishment avoidance/reward-seeking (Mendl *et al.* 2010). In addition, coping can be viewed as both a process (an attempt to cope) and an outcome (whether coping is successful or not). If an animal is presented with a challenge it is not equipped to cope with, the difference between skill level and challenge level leads to a skill-challenge imbalance, causing either boredom and apathy (skill exceeds challenge) or frustration and anxiety (challenge exceeds skill) (Meehan & Mench 2007; based on the human skill-challenge balance; Meyers & Diener 1995). It is therefore quite straightforward to integrate concepts of coping, skill development and expression: the process of coping with challenge requires skills to be developed and expressed, and inadequate skill development or expression leads to an inability to cope.

An updated definition of cognitive enrichment

Our desire to update the 2011 CE definition was motivated by CE research trends (see *A critical review of CE to date*) and two further points. First, we wanted to acknowledge the changing theoretical and empirical priority landscape of animal welfare science over the past 10–15 years, which has brought coping, flourishing and measuring richer positive emotional experiences to the fore (see *Positive animal welfare, skill development and expression*). CE has arguably not kept pace with these changes. Second, our personal experience of CE in zoos, sanctuaries and research facilities has led us to integrate the concept of cognitive *processes* (Mendl *et al.* 2010) with evaluating CE across a series of timepoints. We will now explain five issues with the original CE definition and provide solutions that may bring CE back up to speed.

Linking CE to cognitive challenge

Issue

Although the original definition was inspired by Meehan and Mench's (2007) challenge framework, it does not explicitly mention *challenge*.

Solution

A more conditional definition (i.e. 'CE arises *when X, Y and Z happen*') avoids the 'near-miss' scenarios illustrated in Table 1.

Origins of challenge

Issue

CE was originally defined quite narrowly as a '*task*'. A task is normally associated with high levels of experimental control, which could be off-putting to many captive settings.

Solution

A challenge does not have to be a task. It can be spontaneously induced by changes of a biotic (e.g. social) and abiotic (e.g. climatic) origin or artificially induced by a '*game*' (see *Gameplay: The next frontier in cognitive enrichment?*).

The natural or artificial origin of CE is not important, as long as an animal's response can be evaluated against the operational definition.

Cognitive skills

Issue

We agree with a criticism of the original 2011 definition (Jaakkola 2024) that '*engaging cognitive skills*' does not provide a clear enough distinction between CE and cognition in everyday life. Jaakkola used the simple example of eating food from a bowl, which engages several cognitive skills in an attempt to solve a problem (hunger) and control some aspect of the environment (how much food to eat and when to leave).

Solution

Our updated definition asserts that CE requires an animal to '*develop and express its evolved cognitive skills*'. In line with Rault *et al.* (2025), this acknowledges how skill development (i.e. becoming more competent) and skill expression (i.e. expressing competence) are aspects of cognitive operation that may go beyond an animal's everyday baseline.

Challenge solution and coping

Issue

The original definition mentions opportunities to solve problems and have control over the environment. With hindsight, the word 'opportunity' is ambiguous, and it is unclear whether an overall solution is necessary in CE. As discussed in *Positive animal welfare, skill development and expression*, finding a final solution to a challenge may be associated with an acute positive affective state in animals, but high engagement and making progress towards finding a solution may also be beneficial. Animals may progress or find the solution to a problem through hard work or by accident (i.e. innovation; Reader & Laland 2003).

Solution

Therefore, we have replaced '*solve*' and '*control*' in the original definition with '*cope*'. We also refer to coping as a '*process*' rather than a discrete event, to align with the concepts of challenge as a process (Meehan & Mench 2007) and cognitive processes (Mendl *et al.* 2010).

Positive affective state

Issue

The original CE definition did not actually specify that well-being should be in the positive direction. For completeness, we have added 'positive' to the definition. Furthermore, '*validated indicators of welfare*' implied that CE is only suitable for species with a rich empirical literature on validated behavioural (and perhaps physiological) welfare indicators, which could be off-putting to many animal settings (Jaakkola 2024).

Solution

CE should aim for '*a net positive affective state*' compared to the animal's baseline, in a range of species. This aligns CE with the concept of affective balance (Webb *et al.* 2019) and predominantly positive affective states (Rault *et al.* 2025).

Updated definition

CE arises when an animal is challenged to develop and express its evolved cognitive skills, and the process or outcome of coping with challenge is associated with a net positive affective state.

In summary, our updated definition asserts that:

(i) CE inherently branches from cognitive challenge;
(ii) CE has a necessary cognitive component, a necessary welfare component, and these components are inherently interlinked;
(iii) In line with the contemporary view of positive animal welfare, CE involves skill development and expression;
(iv) CE excludes environmental changes that do not involve the development and/or expression of cognitive skills and may instead induce comfort, and also excludes environmental changes that are challenging but cannot be coped with; and
(v) CE requires a net positive affective state, meaning that overall, there are more positive experiences (responses) than negative ones.

Gameplay: The next frontier in cognitive enrichment?

In this section, we propose an approach to CE whereby animals play games. This approach complements our updated definition of CE and therefore supports clearer and more detailed measurements of animal responses to CE over time.

Defining games and gameplay

CE has previously taken many forms, but descriptions have not always been easy to interpret. For example, describing CE as a 'puzzle feeder' or 'puzzle box' is common in the literature, but there are vast differences in the physical structures of these objects and, consequently, how they may be used and coped with. Rather than subtypes of CE on their physical shape or type of reward (i.e. food), we categorised CE into five subtypes in our literature search (Section 1, Table S1; Supplementary material) that unified them but were still largely focused on the physical structure of the challenge rather than its mechanisms. So, in future, we propose a new CE sub-category called 'game'. For our purposes, a game for animals is defined as "*An externally constructed, non-threatening challenge with an objective goal, rules, mechanics, and rewards that develops cognitive skill*" (Clark 2025). We have chosen the word game rather than 'puzzle' to connect with a rich human experimental psychology literature on games (for a review, see Allen *et al.* 2024). The key reasons why a game (as we conceptualise it) works well as a subtype of CE are as follows:

A game fosters both skill development and expression (competence)

Humans play games for general stimulation, leisure/occupation/distraction, social connection and external rewards (see Lazzaro 2009). But from a psychological research perspective, games have typically been used to *develop* a participant's skill over a particular period of time (e.g. to improve working memory over a period of several hours or days). Existing and newly developed skills are also *expressed* during gameplay. Psychologists have also recognised the value of games in extending participant engagement and performance (Allen *et al.* 2024). Traditional cognitive tasks that test a participant's skill at a particular point in time (e.g. to find if working memory exists at a particular threshold) can be 'gamified' to extend their duration and therefore shift from skill testing to skill development (Lumsden *et al.* 2016; Suh *et al.* 2018). In contrast to a traditional task, where a skill is often scored as present or absent during a single trial, game performance can be assessed in more flexible, non-binary ways.

A game imposes measurable parameters

A game's parameters are substantially known and measurable, thus making it a powerful tool for research (Allen *et al.* 2024; Clark 2025). And unlike a task, a game tends to have layers or combinations of rules that change as gameplay unfolds, dependent or independent of the player's performance. Game parameters are consistent with the zone of proximal development (ZPD) theory from human developmental psychology (Vygotsky 1978). ZPD theory posits that skill development (in children) is facilitated by creating a 'scaffold' environment that provides just the right level of

support to help them reach a high level of potential and agency. The supportive element of the ZPD is crucial: a person would not develop to such a high level completely independently. Examples of scaffolding are rules, training and rewards, and demonstrating solutions or 'teaching'. In adults, the ZPD is similar to the human skill-challenge balance (*Positive animal welfare, skill development and expression*) and avoiding boredom and cognitive overload facilitates a psychological state called 'flow' (Nakamura & Csikszentmihalyi 2002; Csikszentmihalyi *et al.* 2014). While the ZPD supports reaching a high level of potential, it is important to note ZPD does not support 'life or death' activities and does not lead to maximum possible skill development and expression. A state of maximum performance known as 'clutch state' in humans occurs during high-endurance sporting activities; it cannot be sustained long-term due to high energetic demands and is associated with maximum physiological arousal and negative affective state (Swann *et al.* 2019).

To our knowledge, ZPD theory is yet to be applied to animal enrichment. This is surprising because, as previously discussed, a skill-challenge balance has already been identified as beneficial for animal welfare because it minimises the negative affective states of boredom and frustration (for a review, see Meehan & Mench 2007). If we apply ZPD theory to animal CE, we can think of a game as having an inbuilt scaffold designed and controlled by the practitioner, supporting the animal with rules and feedback and matching the level of challenge to their current skill level.

Games involve two forms of play

Using simple and accessible language, games are 'played', but it is important to distinguish between two possible types of play during game-based CE. First, 'gameplay' is how an animal directly interacts with a game, through a tangible or digital interface. This type of play is linked to functional skill development or 'training for the unexpected' (Held & Špinka 2011; Burghardt 2005). Second, 'joyful' ('luxury') play, often involving one's own body, toys, or social partners, is an established positive animal welfare indicator (Burghardt 2005; Yeates & Main 2008; Nelson *et al.* 2023, although see Ahloy-Dallaire *et al.* 2018 for a counter-argument).

Given that several lines of evidence already link skill development and intrinsic reward or affective state in animals (see *Positive animal welfare, skill development and expression*), it is probable that gameplay in some animal taxa will be associated with emotional responses indicating how well the animal perceives itself coping with challenge. The evolution of high technical skills in humans has been linked to the evolution of positive feelings as a form of intrinsic reward (Broaden and Build theory; Fredrickson 1998, 2004), so if we assume some evolutionary continuity, skill development in some taxa may also be moderated by their affective state. In humans, there is still debate over two prevailing theories of the evolution of 'happiness' or positive affect: hedonism (a more immediate drive towards behaviours that cause pleasure and/or avoid pain) and eudaimonism (a longer-term drive towards the satisfaction of self-development and full functionality: Ryan & Deci 2001; Delle Fave *et al.* 2011; Mauss & Ford 2026). Rather than one happiness theory being correct, hedonism and eudaimonism may be expressed across different time-frames. An interesting future research question is whether an animal's current (in-the-moment) and retrospective experiences of CE differ. Welfare indicators during CE might be more hedonistic (pleasure-like), whereas welfare indicators after CE might be more eudaimonic (satisfaction-like).

Pre-existing CE games

Can any existing forms of CE be classified as games? Some existing types of CE (Table S1; Supplementary material) may fit the definition of a game, but we were unable to perform a full assessment due to varying data availability. A probable example of a CE game is a 'puzzle feeder' (we re-classified this to 'object manipulation') for laboratory-housed guppies (*Poecilia reticulata*) (Varracchio *et al.* 2024). The challenge was externally constructed (created by a human), had an objective goal (access food reward by pushing a coloured lid off a food container), had rules and mechanics (related to the predictabilities of the lid colour, movement, etc) and had rewards that promoted cognitive skill development (because the correct gameplay action was linked to food reward). The skills being developed in this case were the ability to learn the association between lid colour/location and food reward, and how to physically remove the occluding lid. In contrast, mixed-species housing of tufted capuchins and squirrel monkeys in a zoo (Daoudi *et al.* 2017) does not meet the definition of a game as defined by Clark (2025) because there were very few measurable challenge 'parameters' other than two species being placed in the same physical space. One or both species may have created and abided by instinctual or social norm rules for inter-species interaction (e.g. if *A* approaches too closely, *B* will retreat), but it would be difficult to measure and manipulate any of these rules externally.

Animal gameplay has been vastly overlooked in comparison to human gameplay (Clark 2025). The concept of 'Game Theory' has been popular within the field of behavioural ecology and refers to relatively simple decision-making contests where a player (human or animal) must monitor and use the decisions of their competitor to make optimal decisions (Colman 1999). The games used to study Game Theory have been relatively simple; rather than being taught set rules, players learn to play and improve performance as they go, according to binary win-lose feedback. In contrast, animals have also been trained to play far more complex human games with rich yet abstract feedback. For example, two rhesus macaques (*Macaca mulatta*) recently learned the rules of the commercial computer game Pac-Man and eventually played a full game (competing against the computer), navigating around virtual obstacles with over 90% accuracy (Yang *et al.* 2022). The most direct evidence of the emotional impact of gameplay comes from research on rats (*Rattus* spp). Rats have apparently been taught to play the social game 'hide and seek', adopting either a hider or seeker role against a human competitor (Reinhold *et al.* 2019; Concha-Miranda *et al.* 2020; Bagi *et al.* 2022). Spontaneous 'joy jumps' during the game were interpreted as an indicator of high positive affect (Reinhold *et al.* 2019), but seeker rats who found a hiding human were rewarded with social play and tickling (Concha-Miranda *et al.* 2020), so it is difficult to ascertain whether rats were responding emotionally to the challenge of the game or by its extrinsic rewards.

Innovation and flow games

To advance game-based CE, we believe it is worthwhile pursuing CE games that fall somewhere between simple contests (e.g. Game Theory games) and extremely sophisticated human games with intense pre-training (e.g. Pac-Man). There is an underexplored middle ground where an animal can develop skills semi-independently during the process of gameplay (i.e. within its ZPD; *Defining games and game-play*). We divide games into those with a relatively low-intensity ZPD and more emphasis on expressing a diversity of skills ('Innovation games'), and those with a relatively high-intensity ZPD

and emphasis on steady skill development and maintaining a skill-challenge balance ('Flow games') (Figure 1).

Innovation games

Innovation refers to inventing a novel behaviour to reach a win state or using an existing behaviour on a novel problem to win suddenly (innovation as conceptualised by Reader & Laland 2003; Tebbich *et al.* 2016). The justification for an innovation game is that finding sudden solutions to abstract problems (Figure 1, top) can cause acute bursts of positive emotion and/or positive physiological arousal in animals, the so-called 'Eureka effect' (*Positive animal welfare, skill development and expression*). While we acknowledge evidence of this effect is currently restricted to cattle, dogs and possibly dolphins, it is a promising CE avenue to explore. The Eureka effect in humans has been studied by comparing participant responses on tasks that do and do not naturally converge towards a logical solution; in other words, comparing the emotional effect of an expected and unexpected solution (Lu & Singer 2023). The same experimental design could be applied to animals and is supported by evidence that Japanese macaques (*Macaca fuscata*) showed increased behavioural signs of arousal or 'surprisal' when they encountered an unexpected reward during cognitive testing (Iki & Adachi 2025). Interestingly, the behavioural sign of arousal in the macaque study was self-scratching, which is typically used to indicate negative arousal (anxiety) in primates (Maestripieri *et al.* 1992). Two further research questions are whether the Eureka effect is more intense in animals exposed to a higher level of challenge relative to their everyday baseline, and whether animals that can acquire a game solution via social learning (direct observation, then emulation or imitation) have a weaker Eureka moment than asocial innovators.

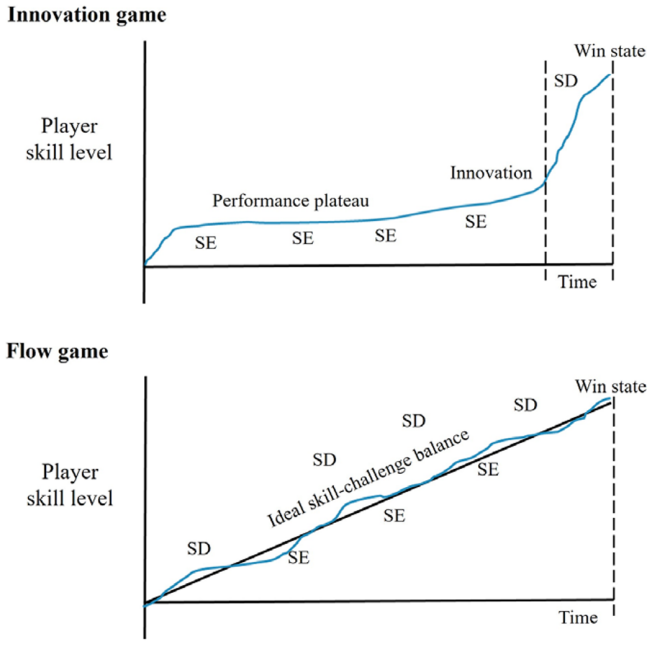


Figure 1. A graphical representation of skill development in an Innovation (top) vs a Flow game (bottom). SE = skill expression. SD = skill development. In an Innovation game, animal performance will plateau when existing skill expression exceeds new skill development. In a Flow game, high engagement and performance occur when skill and challenge are balanced. There are frequent alternations between skill expression and skill development, and no sudden shifts in skill level or challenge level.

An Innovation game has a low-intensity ZPD because it encourages the animal to try out many possible behavioural solutions and therefore express many pre-existing skills to overcome a challenge. Imagine the following example for a pig: a novel wheel apparatus contains food occluded behind a rotating plate (resembling an old rotary telephone; Clark *et al.* 2025). The intended solution is to rotate the plate until food is exposed through a single hole. The pig may attempt many different behaviours in a trial-and-error process to find the win state to this very novel challenge, such as general nosing, pressing and pulling. It should be understood that spontaneous innovation to any challenge is never guaranteed. The ability to innovate is not universal across the animal kingdom, and even within innovating species, some individuals in a group do not innovate (Reader & Laland 2003; Ramsey *et al.* 2007; Brosnan & Hopper 2014). This being said, the capacity to innovate continues to be reported in unsuspected and previously understudied species (e.g. bat-eared foxes [*Otocyon megalotis*]; Petelle *et al.* 2023; orchard bees [*Osmia cornuta*]; Collado *et al.* 2021). Linked to *Pre-existing CE games*, we highly recommend evaluating existing innovation tasks used in comparative cognition research as putative CE.

Flow games

As discussed in *Gameplay: The next frontier in cognitive enrichment?*, Flow is a psychological state in humans that integrates high focus and skill development with positive affect (Nakamura & Csikszentmihalyi 2002; Csikszentmihalyi *et al.* 2014). Flow state has not been definitively evidenced in animals to date, but evidence of high task engagement and a motivation to forego extrinsic rewards has begun to shape an exciting new direction of research (Clark 2023; Hintze & Yee 2023). For now, we suggest working towards the measurement of one or more indicators of Flow evidenced in humans: high focus, disinterest in the wider environment and extrinsic reward, easeful movements, and positive emotion. As in humans, Flow games for animals should create a skill-challenge balance (see *Positive animal welfare, skill development and expression*), thereby avoiding frustration/anxiety and boredom/apathy (Table 1; Section 4.1, bottom box). A Flow game has relatively high-intensity ZPD scaffolding because skills are developed gradually within quite narrow parameters.

A Flow game should adaptively respond so that the skill-challenge balance is maintained during play. The analogy of a tightrope is useful here. Maintaining a skill-challenge balance (staying on the tightrope) and avoiding frustration/anxiety and boredom/apathy (falling off the tightrope) requires constant, active challenge adjustments. If the game design is too simplistic, surplus skill development will naturally pull the player off the tightrope and towards boredom. In contrast, a game that has elements that are perceptually or cognitively inappropriate will pull the player towards frustration.

Computerised systems that can perform frequent 'tightrope' calibrations will be very beneficial for Flow games. Fortunately, computer technology can recognise individual animals housed in groups and offer customised tasks using dynamic difficulty adjustment (Calapai *et al.* 2022, 2023; see *Flow game case study*). However, we fully acknowledge that computerised systems are a substantial investment and are not feasible for most captive settings. A low-tech alternative is to present different levels of a modular analogue game over time, based on an animal's current performance (for example, providing a harder module if the animal is performing at a high level). The ability to recognise and rapidly respond to an animal's gameplay performance is crucial for this to be effective, and the rules of the game need to be explicit to both the player and the practitioner. Referring to the tightrope analogy once again, this may also involve rapid recognition of behavioural indicators of frustration and

boredom/disengagement if relevant, in addition to the rate at which the animal is progressing through levels of challenge. While the low-tech approach to flow games might sound difficult in practice, animal cognition researchers are experienced in rapidly presenting tasks to animals during blocks of trials and responding to their immediate performance, so this experience could be leveraged by incorporating flow games into studies of animal cognition.

Choosing Innovation versus Flow

We encourage CE practitioners to explore options for Innovation and Flow games – either through the extension and modification of existing CE and cognitive tasks, or through novel designs. CE practitioners should consider whether their target species/individual is likely to innovate and how sensitive it may be to reward loss or failure in a game. For example, even though great apes can innovate, not all individuals in a group usually do so (Manrique *et al.* 2013). Great apes can also develop high emotional sensitivity to response errors, reward loss, or inconsistent task feedback but this can vary per individual (Elder & Menzel 2001; Yamanashi & Matsuzawa 2010), which could make a Flow game more suitable than an Innovation game, as long as the game is responsive to individual performance. Conversely, an Innovation game may be more suitable for settings with low experimental control and low technology.

To end this section, we cover some more general CE game design principles. As a first step, it is wise to work with species that have already undergone extensive cognitive research, such as rats and mice, chickens, corvids, dogs, pigs and cows, primates, dolphins, and sea lions (Farrar *et al.* 2020), so that game design is based on cognitive evidence. CE game design should be compatible with a target species' sensory system, anatomy, ultimate (evolved) motivations, and proximate motivations (Meehan & Mench 2007; Clark 2011). If existing cognitive tasks will be gamified (i.e. adding more measurable parameters, rules and opportunities to develop skill), we caution that humans can develop disordered, addictive gaming behaviour towards very high levels of gamification. This includes commercial electronic gambling machines (i.e. slot machines) that encourage rapid and repetitive actions and have ambiguous performance indicators such as losses disguised as wins (Murch & Clark 2016). Even though making risky decisions is a naturalistic strategy for animals to encounter and exploit new resources (De Petrillo & Rosati 2021), 'unskilled gambling' (i.e. risking resources for little or no beneficial reward pay-off) can readily occur in rodents, primates and pigeons in a laboratory setting (Laude *et al.* 2014; Hall *et al.* 2019; Zentall 2023). This being said, there is a lack of research on precisely how gambling could become addictive to the point of harming welfare in animals (Clark 2025), and our approach to CE throughout this paper has emphasised close animal monitoring and being prepared to modify challenge if it has negative welfare outcomes.

Cognitive enrichment game evaluation

Fine temporal resolution

CE evaluation has previously focused on CE as an environmental 'event' rather than a process (Table S1; Supplementary material) and has also focused on fairly broad behavioural effects. As previously discussed, this does not align with how animals naturally encounter and deal with challenges (Meehan & Mench 2007) and does not capture all of an animal's meaningful cognitive and emotional responses happening in sequence. For example, between-group CE experiments (enriched group vs control group) and within-group CE experiments (baseline vs enrichment vs post-enrichment) have evaluated how total durations, frequencies or averages of behaviours such as exploration, aggression and play are affected by CE presence/absence (between-group example: zebra fish [*Danio rerio*]; Gatto *et al.* 2024; domestic cats [*Felis catus*]; Gourkow & Phillips 2016; within-group example: black rhinoceros [*Diceros bicornis*]; Krebs & Watters 2017). Although it is important to assess the lingering effects of enrichment that extend beyond its physical presence (e.g. Fairhurst *et al.* 2011; Woodward *et al.* 2019), it is also important to pay closer attention to what happens during CE presence to reflect the increasing integration of cognition, emotion and mood in animal welfare. In particular, the 'Affective Balance' model portrays welfare as a dynamic sum or accumulation of positive and negative experiences over time (Webb *et al.* 2019; Kremer *et al.* 2020; Paul & Mendl 2025) and requires a fine scale of analysis. For example, instantaneous sampling at 10-min intervals could easily miss a sudden 'Eureka moment' in an Innovation game.

To illustrate how future CE game evaluation could work in practice, imagine the following game scenario (Innovation or Flow). A chimpanzee (*Pan troglodytes*) plays a maze game, and all responses (gameplay and off-game behaviour) are plotted across time (Figure 2). The Bayesian brain framework of animal welfare (Lecorps & Weary 2024) predicts that prior game performance should impact future emotional response. Visualising responses to a CE game on a timeline thus allows us to use Bayesian framework to assess temporal relationships, such as whether negative emotions follow a losing streak or sudden loss, and positive emotions follow a winning streak or sudden win.

The functional role of frustration in cognitive enrichment

Although game-based CE broadly aims to avoid frustration by scaffolding (Innovation and Flow games) and maintaining a skill-challenge balance (Flow games), we expect that all CE will induce at least a small amount of initial frustration. We previously described how environmental change can either challenge or comfort an animal (or lead to boredom, see *A critical review of CE to date*). To expand on this, challenge activates an animal's physiological stress response (Wiepkema & Koolhaas 1993; Moburg & Mench 2000; Broom & Johnson 2019; Wu *et al.* 2025). Even though 'stress' often has negative connotations and is conflated with poor animal welfare (Morgan & Tromborg 2007), stress in response to challenge is normal and functional. And at a behavioural level, Meehan and Mench (2007) discussed how frustration is normal and functional when an animal is challenged because it represents motivation to alter its conditions (see also Toates 1986; Wiepkema & Koolhaas 1993). Meehan and Mench (2007) proceeded to argue that while initial frustration is to be expected when an animal perceives a challenge, the challenge must either be solvable or escapable so that this frustration can ultimately be removed.

It is ethically important to acknowledge whether the animal and/or the practitioner has control over an animal's experience of frustration. An animal may or may not have control over removing its experience of frustration; it may happen actively by solving or escaping the challenge, or passively by the environment changing. Given the physiological and behavioural 'normalcy' of stress and frustration, we imagine that most CE practitioners will be ethically satisfied if CE causes some initial frustration and it can easily be reduced or removed. This also aligns with Rault *et al.*'s (2025) definition of positive animal welfare which is 'predominantly' but not exclusively a positive affective state, allowing for some negative emotions to arise over time. And in human flow, the Affective Change hypothesis (Baumann & Scheffer 2010) emphasises that experiencing positive and negative affective states in close temporal

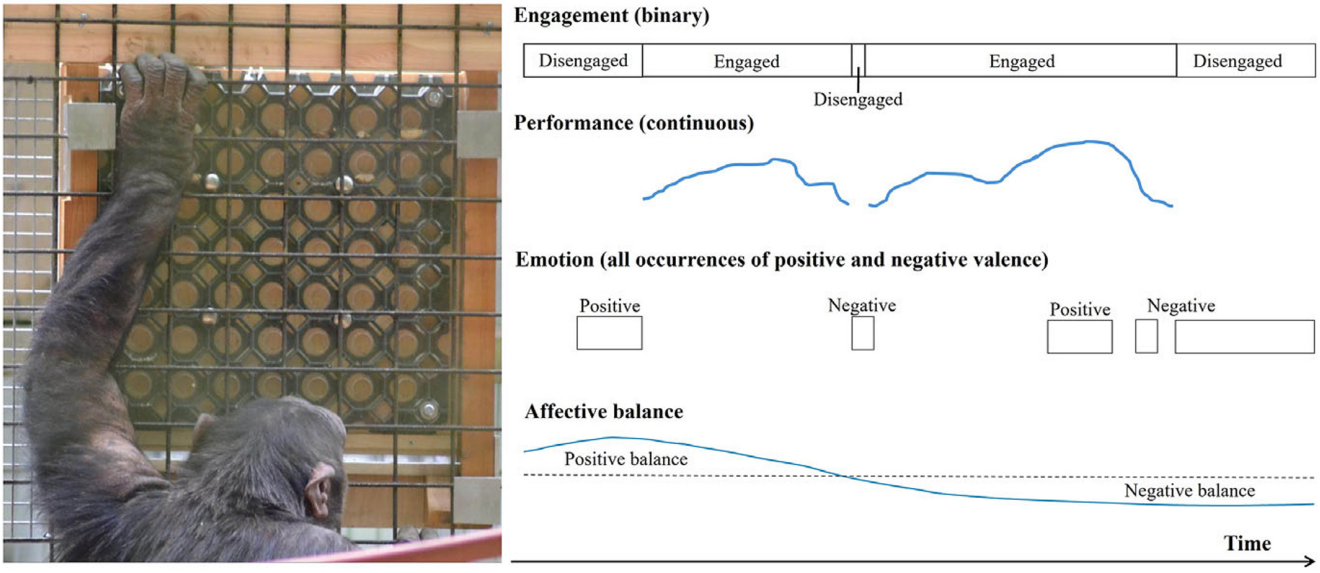


Figure 2. Game engagement, performance and emotion synchronised across time during a cognitive enrichment session for a chimpanzee (*Pan troglodytes*). The Engagement domain refers to whether the chimpanzee is using the game or not. The Performance domain is a deeper measurement of how well the chimpanzee is coping with the challenge and progressing towards the win state. The Emotion domain refers to any behavioural response that may reflect emotion, such as game-directed aggression or self-scratching. And finally, the Affective Balance domain represents the sum of positive and negative emotions across time. Critically, all responses are accurately plotted on the timeline to examine cause-effect relationships across multiple domains.

proximity (the alternation between 'seeing difficulty' and 'mastering difficulty') helps a person reach an overall positive experience.

The fine-scale temporal analysis we proposed above (Figure 2) is useful because it allows us to observe not only the frequency of frustration events, but their timing and context. But how much frustration is too much? Currently, the field of animal affect (also known as affective neuroscience; Panksepp 2004) has not been able to produce a full cost-benefit analysis of negative *versus* positive emotions for any species. For example, we cannot say for a given species that one frustrating event is outweighed by three joyful play events. The Affective Balance model (Figure 2, bottom) is currently a rough binary method based on emotional valence (i.e. score 1 for a positive emotion, score minus 1 for a negative emotion), which clearly has limitations (Webb *et al.* 2019). But it is worth remembering that humans also differ in the extent to which positive emotions are valued and weighed against negative emotions (Affect Valuation theory: Tsai *et al.* 2006; Willroth *et al.* 2023).

If an animal cannot solve CE, this could be assessed as 'distress' or a failure to cope (Broom & Johnson 2019). Distress is associated with a lack of skill or control (Wu *et al.* 2025), whereas eustress is associated with challenges that can be overcome because skills are developed and expressed. We hope that by using fine-scale assessment, CE would never reach a point of animal distress because the practitioner would already be prepared to modify the challenge if necessary. This could be through rule simplification, rule reduction, enhanced positive feedback, positive reinforcement training, or demonstrating solutions.

Although one CE exposure is associated with acceptable brief initial frustration, repeated CE exposures over time could add up to repeated instances of frustration. Our counter-argument is that animals should regularly encounter challenges (Toates 1986; Moberg & Mench 2000) and making challenge a life-long process may actually decrease frustration across the lifespan, as the animal gains competence and resilience (Rault *et al.* 2025). Clark (2011) used the analogy of a British television game show 'The Crystal Maze' where a team of human contestants voluntarily took part in challenges in different game zones based on their respective strengths (e.g. motor skills, memory, strategy) and motivations. A vision of animal enclosures containing voluntary gameplay zones is ambitious, even for the most major zoos and research centres. But if ambition eventually becomes reality, the concept of CE could evolve into *cognitive husbandry* (i.e. CE has evolved into CH), a lifelong commitment to avoid loss of brain and cognitive function in captive environments (Clark *et al.* 2023).

Flow game case study

Over the past five years, bottlenose dolphins and California sea lions (*Zalophus californianus*) at the US Navy Marine Mammal Program (MMP) in San Diego, California have been using a flow CE game. Both species have previously exhibited high levels of focus towards cognitive tasks (Branstetter *et al.* 2012; Banks *et al.* 2018), and the MMP has highly trained animals and computerised enrichment capabilities. The Enclosure Video Enrichment (EVE) system was designed to offer computerised gameplay that is cognitively challenging yet practical and cost-effective for long-term use (Winship *et al.* 2023; Sill *et al.* 2025). Over the past five years, EVE has been incrementally evaluated and expanded to allow individual animals to advance to increased levels of challenge difficulty within the same game and advance to new games with new gameplay rules. Data collection with this system was approved by the MMP Institutional Animal Care & Use Committee (IACUC) Protocol #139-2020.

Animals at MMP had previously been trained to focus on their trainers and ignore external stimuli during cognitive and behavioural research; therefore, animals did not spontaneously focus on the EVE computer screen and could not spontaneously use the system without prior training. For sea lions, the EVE interface sits above water and consists of four circular buttons arranged in a

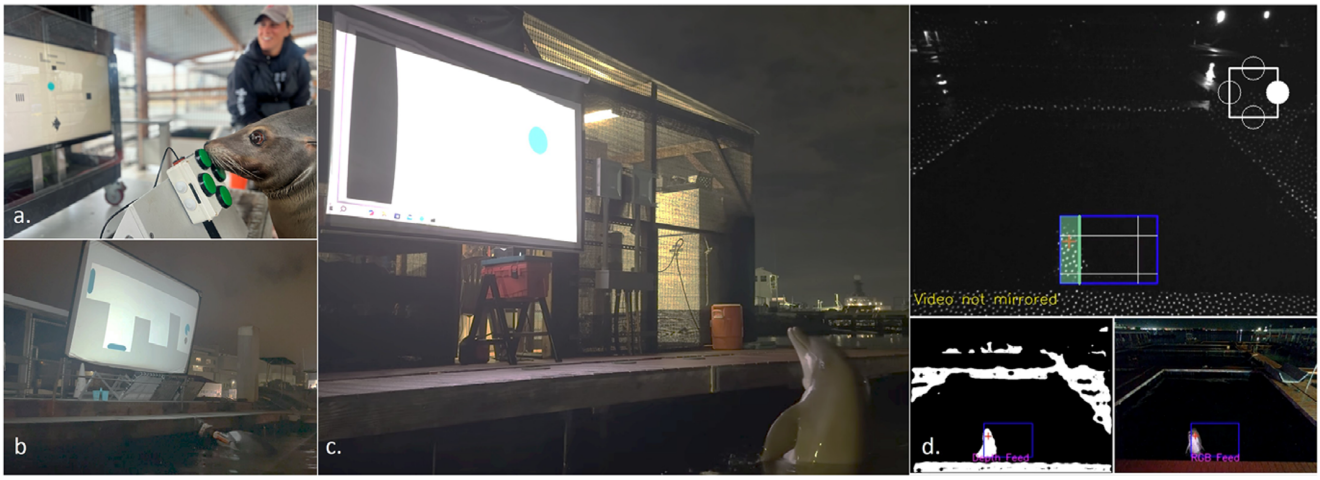


Figure 3. The presentation of EVE for California sea lions (*Zalophus californianus*) and bottlenose dolphins (*Tursiops truncatus*) at the Marine Mammal Program. A sea lion (a) selects which game to play from four presented options, choosing a task by moving the blue circle via the four-button controller by pressing a button with the muzzle. In (b), a dolphin moves the cursor to contact an image of a shell on the screen. In (c) a dolphin plays a cursor training game by moving its body to drive the cursor while for (d) the animal's location is translated by a custom computer vision programme into 'button presses.'

diamond array corresponding to up, down, left and right cursor movements (for full method, see Winship *et al.* 2023; Figure 3[a]). For dolphins, the screen is presented above water, with either a joystick affixed with a biteplate mounted to the side of the enclosure (Figure 3[b]) or a computer vision controller viewing the animal from above (Sill *et al.* 2025; Figures 3[c], [d]). Both species learned to interact with EVE's physical interface to control the movement of a blue circular cursor towards a black square target. This took around one year with approximately two 10-min sessions per week.

The training process itself was designed to be a game (the Cursor Taining Game, CTG; Winship *et al.* 2023) where cursor use was incrementally shaped and rewarded with a reward tone and extrinsic reward (fish, ice, or verbal 'cheering' from a trainer). Overall, the CTG was deemed to be cognitively enriching for both species. For example, voluntary engagement remained high during training, one sea lion engaged in long (> 30-min) gameplay sessions reinforced by ice or cheering only (Winship *et al.* 2023), and EVE eventually became a reinforcer in its own right to reward voluntary participation in husbandry procedures and moving between enclosures (Winship *et al.* 2024). Two further EVE system games 'Maze' and 'Match to sample' (Roberts *et al.* 2023) have offered different types and levels of challenge complexity, such as cursor movement restrictions and screen freezes, or a 'time out' signalled by the screen darkening following an incorrect response.

Anecdotally, dolphins can consistently engage with EVE far longer than engaging with standard cognitive tests or toy enrichment objects, and there are early indications that the skill-challenge balance does maximise their engagement, as predicted by human flow theories (Nakamura & Csikszentmihalyi 2002; Csikszentmihalyi *et al.* 2014; Clark 2023). For example, a female dolphin played one level of an EVE game continuously for 17 min when play performance was moderate (neither high wins nor high losses) with no intermittent fish reinforcement during the trial. Normal total gameplay was 13 min per session, but in this instance, play duration was 23 min with no signs of disengagement (K Winship, personal communication 2026). Future research on EVE aims to manipulate various game conditions to explore their effects on animal performance and affective state. Human flow state is associated with a loss of sense of time (Nakamura & Csikszentmihalyi 2002; Csikszentmihalyi *et al.* 2014; Clark 2023), so we plan to leverage parallel research on sea lion rhythmic ability and timing at MMP (e.g. Cook *et al.* 2013, 2025; Rouse *et al.* 2016) to embed interval timing tasks within EVE's games.

Animal welfare implications

Aligning CE with challenge, coping, and more positive affective states complements contemporary viewpoints in animal welfare science, and in doing so, we hope to reignite interest in CE research. We believe that games are a very promising subtype of CE that have the potential to drive more positive welfare outcomes than previous CE designs. This is because games have clear parameters that are scientifically measurable, and gameplay is a temporal process that can be approached using Bayesian statistics. We fully acknowledge that our proposal is ambitious and that research on CE games will likely be targeted towards primates, marine mammals and farmed animals. However, in time, CE games should be evaluated for captive animals more widely across laboratories, farms and zoos. Demonstrating gameplay abilities in animals will also shed light on their complex cognitive and emotional lives, thus helping to lobby for better overall care standards and protective legislation.

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References

Ahloy-Dallaire J, Espinosa J and Mason G 2018 Play and optimal welfare: Does play indicate the presence of positive affective states? *Behavioural Processes* **156**: 3–15. https://doi.org/10.1016/j.beproc.2017.11.011

Allen K, Brändle F, Botvinick M, Fan JE, Gershman SJ, Gopnik A and Schulz E 2024 Using games to understand the mind. *Nature Human Behaviour* **8**: 1035–1043. https://doi.org/10.1038/s41562-024-01878-9

Bachetti ÉD, Viol LY, Viana-Junior AB, Young RJ and de Azevedo CS 2024 Global overview of environmental enrichment studies: what has been done and future directions. *Animals* **14**: 1613. https://doi.org/10.3390/ani14111613

Bagi B, **Brecht M and Sanguinetti-Scheck JI** 2022 Unsupervised discovery of behaviorally relevant brain states in rats playing hide-and-seek. *Current Biology* **32**: 2640–2653. https://doi.org/10.1016/j.cub.2022.04.068

Banks PN, **Finneran JJ**, **Mulsow J and Xitco MJ** 2018 Dolphins maintain high echolocation vigilance for eight hours without primary (food) reinforcement. *Journal of the Acoustical Society of America* **144**: 660–666. https://doi.org/10.1121/1.5049585

Baumann N and Scheffer D 2010 Seeing and mastering difficulty: The role of affective change in achievement flow. *Cognition and Emotion* **24**: 1304–1328. https://doi.org/10.1080/02699930903319911

Boissy A, **Arnould C**, **Chaillou E**, **Désiré L**, **Duvaux-Ponter C**, **Greiveldinger L and Veissier I** 2007 Emotions and cognition: a new approach to animal welfare. *Animal Welfare* **16**: 37–43.

Branstetter BK, **Finneran JJ**, **Fletcher EA**, **Weisman BC and Ridgway SH** 2012 Dolphins can maintain vigilant behavior through echolocation for 15 days without interruption or cognitive impairment. *Plos One*. https://doi.org/10.1371/journal.pone.0047478

Broom DM 1988 The scientific assessment of animal welfare. *Applied Animal Behaviour Science* **20**: 5–19. https://doi.org/10.1016/0168-1591(88)90122-0

Broom DM and Johnson KG 2019 *Stress and Animal Welfare: Key Issues in the Biology of Humans and Other Animals*, *Volume* **19**. Springer Nature: Cham, Switzerland.

Brosnan SF and Hopper LM 2014 Psychological limits on animal innovation. *Animal Behaviour* **92**: 325–332. https://doi.org/10.1016/j.anbehav.2014.02.026

Burghardt GM 2005 *The Genesis of Animal Play: Testing the Limits*. MIT Press: New York, NY, USA. https://doi.org/10.7551/mitpress/3229.001.0001

Burn CC 2017 Bestial boredom: A biological perspective on animal boredom and suggestions for its scientific investigation. *Animal Behaviour* **130**: 141–151. https://doi.org/10.1016/j.anbehav.2017.06.006

Calapai A, **Cabrera-Moreno J**, **Moser T and Jeschke M** 2022 Flexible auditory training, psychophysics, and enrichment of common marmosets with an automated, touchscreen-based system. *Nature Communications* **13**: 1648. https://doi.org/10.1038/s41467-022-29185-9

Calapai A, **Pfefferle D**, **Cassidy LC**, **Nazari A**, **Yurt P**, **Brockhausen RR and Treue S** 2023 A touchscreen-based, multiple-choice approach to cognitive enrichment of captive rhesus macaques (*Macaca mulatta*). *Animals* **13**: 2702. https://doi.org/10.3390/ani13172702

Clark FE 2011 Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science* **135**: 1–12. https://doi.org/10.1016/j.applanim.2011.10.010

Clark FE 2017 Cognitive enrichment and welfare: Current approaches and future directions. Animal Behavior and *Cognition* **4**: 52–71. https://doi.org/10.12966/abc.05.02.2017

Clark FE 2022 Bridging pure cognitive research and cognitive enrichment. *Animal Cognition* **25**: 1671–1678. https://doi.org/10.1007/s10071-022-01636-2

Clark FE 2023 In the zone: Towards a comparative study of flow state in primates. *Animal Behavior and Cognition* **10**: 62–88. https://doi.org/10.26451/abc.10.01.04.2023

Clark FE 2025 Levelling up the Study of Animal Gameplay. *Neuroscience & Biobehavioral Reviews* **16**: 106016. https://doi.org/10.1016/j.neubiorev.2025.106016

Clark FE, **Burdass J**, **Kavanagh A and King A** 2025 Palaeognath birds innovate to solve a novel foraging problem. *Scientific Reports* **15**: 4512. https://doi.org/10.1038/s41598-025-88217-8

Clark FE, **Greggor AL**, **Montgomery SH and Plotnik JM** 2023 The endangered brain: actively preserving ex-situ animal behaviour and cognition will benefit in-situ conservation. *Royal Society Open Science* **10**: 230707. https://doi.org/10.1098/rsos.230707

Collado MÁ, **Menzel R**, **Sol D and Bartomeus I** 2021 Innovation in solitary bees is driven by exploration, shyness and activity levels. *Journal Of Experimental Biology* **224**: jeb232058. https://doi.org/10.1242/jeb.232058

Colman AM 1999 *Game Theory and its Applications: In the Social and Biological Sciences*. Psychology Press: London, UK.

Concha-Miranda M, **Hartmann K**, **Reinhold A**, **Brecht M and Sanguinetti-Scheck JI** 2020 Play, but not observing play, engages rat medial prefrontal cortex. *European Journal of Neuroscience* **52**: 4127–4138. https://doi.org/10.1111/ejn.14908

Cook P, **Rouse A**, **Wilson M and Reichmuth C** 2013 A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. *Journal of Comparative Psychology* **127**: 412. https://doi.org/10.1037/a0032345

Cook P, **Hood C**, **Rouse A and Reichmuth C** 2025 Sensorimotor synchronization to rhythm in an experienced sea lion rivals that of humans. *Scientific Reports* **15**: 12125. https://doi.org/10.1038/s41598-025-95279-1

Csikszentmihalyi M, **Csikszentmihalyi M**, **Abuhamdeh S and Nakamura J** 2014 Flow. In: Csikszentmihalhi M (ed) *Flow and the Foundations of Positive Psychology: The Collected Works of Mihaly Csikszentmihalyi* pp 227–238. Springer: Dordrecht, The Netherlands. https://doi.org/10.1007/978-94-017-9088-8_15

Daoudi S, **Badihi G and Buchanan-Smith HM** 2017 Is mixed-species living cognitively enriching? Enclosure use and welfare in two captive groups of tufted capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*). *Animal Behavior and Cognition* **4**: 51–69. https://doi.org/10.12966/abc.06.02.2017

de Azevedo CS, **Cipreste CF and Young RJ** 2007 Environmental enrichment: A GAP analysis. *Applied Animal Behaviour Science* **102**: 329–343. https://doi.org/10.1016/j.applanim.2006.05.034

De Petrillo F and Rosati AG 2021 Decision making in animals: Rational choices and adaptive strategies. In: Kaufman AB, Call J and Kaufman JC (eds) *The Cambridge Handbook of Animal Cognition* pp 770–791. Cambridge University Press: Cambridge, USA. https://doi.org/10.1017/9781108564113.043

Delle Fave A, **Brdar I**, **Freire T**, **Vella-Brodrick D and Wissing MP** 2011 The eudaimonic and hedonic components of happiness: Qualitative and quantitative findings. *Social Indicators Research* **100**: 185–207. https://doi.org/10.1007/s11205-010-9632-5

Dibble DS, **Van Alstyne KR and Ridgway S** 2016 Dolphins signal success by producing a victory squeal. *International Journal of Comparative Psychology* **29**. https://doi.org/10.46867/ijcp.2016.29.00.14

Dukes D, **Abrams K**, **Adolphs R**, **Ahmed ME**, **Beatty A**, **Berridge KC**, **Broomhall S**, **Brosch T**, **Campos JJ**, **Clay Z and Clément F** 2021 The rise of affectivism. *Nature Human Behaviour* **5**: 816–820. https://doi.org/10.1038/s41562-021-01130-8

Elder CM and Menzel CR 2001 Dissociation of cortisol and behavioral indicators of stress in an orangutan (*Pongo pygmaeus*) during a computerized task. *Primates* **42**: 345–357. https://doi.org/10.1007/bf02629625

Fairhurst GD, **Frey MD**, **Reichert JF**, **Szelest I**, **Kelly DM and Bortolotti GR** 2011 Does environmental enrichment reduce stress? An integrated measure of corticosterone from feathers provides a novel perspective. *PLoS One* **6**: e17663. https://doi.org/10.1371/journal.pone.0017663

Farm Animal Welfare Council 1979 *Five Freedoms. UK Ministry of Agriculture, Fisheries and Food*. FAWC: London, UK.

Farrar BG, **Altschul DM**, **Fischer J**, **Van Der Mescht J**, **Placì S**, **Troisi CA**, **Vernouillet A**, **Clayton NS and Ostojić L** 2020 Trialling meta-research in comparative cognition: claims and statistical inference in animal physical cognition. *Animal Behavior and Cognition* **7**: 419. https://doi.org/10.26451/abc.07.03.09.2020

Fischer A 2016 Environmental enrichment as a method to improve cognitive function. What can we learn from animal models? *Neuroimage* **131**: 42–47. https://doi.org/10.1016/j.neuroimage.2015.11.039

Fredrickson BL 1998 What good are positive emotions? *Review of General Psychology* **2**: 300–319. https://doi.org/10.1037/1089-2680.23

Fredrickson BL 2004 The broaden–and–build theory of positive emotions. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**: 1367–1377. https://doi.org/10.1098/rstb.2004.1512

Gatto E, **Varracchio C**, **Bertolucci C and Lucon-Xiccato T** 2024 Puzzle feeder as a cognitive enrichment strategy determines long-term welfare improvements in a teleost fish. *Applied Animal Behaviour Science* **279**: 106401. https://doi.org/10.1016/j.applanim.2024.106401

Gourkow N and Phillips CJ 2016 Effect of cognitive enrichment on behavior, mucosal immunity and upper respiratory disease of shelter cats rated as frustrated on arrival. *Preventive Veterinary Medicine* **131**: 103–110. https://doi.org/10.1016/j.prevetmed.2016.07.012

Hagen K and Broom DM 2004 Emotional reactions to learning in cattle. *Applied Animal Behaviour Science* **85**: 203–213. https://doi.org/10.1016/j.applanim.2003.11.007

Hall BA, **McGill DM**, **Sherwen SL and Doyle RE** 2021 Cognitive enrichment in practice: a survey of factors affecting its implementation in zoos globally. *Animals* **11**: 1721. https://doi.org/10.3390/ani11061721

Hall K, **Smith M**, **Russell JL**, **Lambeth SP**, **Schapiro SJ and Brosnan SF** 2019 Chimpanzees rarely settle on consistent patterns of play in the hawk dove, assurance, and prisoner's dilemma games, in a token exchange task. *Animal Behavior and Cognition* **6**: 48. https://doi.org/10.26451/abc.06.01.04.2019

Held SD and Špinka M 2011 Animal play and animal welfare. *Animal Behaviour* **81**: 891–899. https://doi.org/10.1016/j.anbehav.2011.01.007

Hintze S and Yee JR 2023 Animals in flow–towards the scientific study of intrinsic reward in animals. *Biological Reviews* **98**: 792–806. https://doi.org/10.1111/brv.12930

Hughes RN 1997 Intrinsic exploration in animals: motives and measurement. *Behavioural Processes* **41**: 213–226. https://doi.org/10.1016/s0376-6357(97)00055-7

Iki S and Adachi I 2025 Monkeys increase scratching when encountering unexpected good fortune. *Scientific Reports* **15**: 8386. https://doi.org/10.1038/s41598-025-92251-x

Jaakkola K 2024 Minding the Minds: A Primer on Cognitive Challenge for Marine Mammals in Human Care. *Animals* **14**: 949. https://doi.org/10.3390/ani14060949

Judge PG, **Evans DW**, **Schroepfer KK and Gross AC** 2011 Perseveration on a reversal-learning task correlates with rates of self-directed behavior in non-human primates. *Behavioural Brain Research.* **222**: 57–65. https://doi.org/10.1016/j.bbr.2011.03.016

Keyes, CL (2002). The mental health continuum: From languishing to flourishing in life. *Journal of health and social behavior*, 207–222.

Kleiber A, **Le-Calvez JM**, **Kerneis T**, **Batard A**, **Goardon L**, **Labbé L**, **Brunet V**, **Ferreira VH**, **Guesdon V**, **Calandreau L and Colson V** 2022 Positive effects of bubbles as a feeding predictor on behaviour of farmed rainbow trout. *Scientific Reports* **12**: 11368. https://doi.org/10.1038/s41598-022-15302-7

Krebs BL and Watters JV 2017 Simple but temporally unpredictable puzzles are cognitive enrichment. *Animal Behavior and Cognition* **4**: 119–134. https://doi.org/10.12966/abc.09.02.2017

Kremer L, **Holkenborg SK**, **Reimert I**, **Bolhuis JE and Webb LE** 2020 The nuts and bolts of animal emotion. *Neuroscience & Biobehavioral Reviews* **113**: 273–286. https://doi.org/10.1016/j.neubiorev.2020.01.028

Landolfo E, **Berretta E**, **Balsamo F**, **Petrosini L and Gelfo F** 2025 Cognition enhances cognition: a comprehensive analysis on cognitive stimulation protocols and their effects on cognitive functions in animal models. *Journal of Neuroscience Methods* **7**: 110316. https://doi.org/10.1016/j.jneumeth.2024.110316

Laude JR, **Stagner JP and Zentall TR** 2014 Suboptimal choice by pigeons may result from the diminishing effect of nonreinforcement. *Journal of Experimental Psychology: Animal Learning and Cognition.* **40**: 12. https://doi.org/10.1037/xan0000010

Lazzaro N 2009 Why we play: affect and the fun of games. *Human-Computer Interaction: Designing for Diverse Users and Domains* **15**: 679–700.

Lecorps B and Weary D 2024 Animal affect, welfare and the Bayesian brain. *Animal Welfare* **33**: e39. https://doi.org/10.1017/awf.2024.44

Lu Y and Singer W 2023 Dynamic signatures of the Eureka effect: an EEG study. *Cerebral Cortex.* **33**: 8679–8692. https://doi.org/10.1093/cercor/bhad150

Lumsden J, **Edwards EA**, **Lawrence NS**, **Coyle D and Munafò MR** 2016 Gamification of cognitive assessment and cognitive training: a systematic review of applications and efficacy. *JMIR Serious Games* **4**: e5888. https://doi.org/10.3389/conf.fpubh.2016.01.00007

Maestripieri D, **Schino G**, **Aureli F and Troisi A** 1992 A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour* **44**: 967–997. https://doi.org/10.1016/S0003-3472(05)80592-5

Mauss IB and Ford BQ 2026 The pursuit of happiness: pitfalls and promises. *Trends in Cognitive Sciences*, in press

McCulloch SP 2013 A critique of FAWC's five freedoms as a framework for the analysis of animal welfare. *Journal of Agricultural and Environmental Ethics* **26**: 959–975.

McGowan RT, **Rehn T**, **Norling Y and Keeling LJ** 2014 Positive affect and learning: exploring the "Eureka Effect" in dogs. *Animal Cognition* **17**: 577–587. https://doi.org/10.1007/s10071-013-0688-x

Meagher RK 2019 Is boredom an animal welfare concern? *Animal Welfare* **28**: 21–32. https://doi.org/10.7120/09627286.28.1.021

Meagher RK and Mason GJ 2012 Environmental enrichment reduces signs of boredom in caged mink. *PloS One.* **7**: e49180. https://doi.org/10.1371/journal.pone.0049180

Meehan CL and Mench JA 2007 The challenge of challenge: can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science* **102**: 246–261. https://doi.org/10.1016/j.applanim.2006.05.031

Mellor DJ 2016 Moving beyond the 'Five Freedoms' by updating the 'Five Provisions' and introducing aligned 'Animal Welfare Aims'. *Animals* **6**: 59. https://doi.org/10.3390/ani6100059

Mendl M, **Burman OH and Paul ES** 2010 An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences*, **277**: 2895. https://doi.org/10.1098/rspb.2010.0303

Meyers DG and Diener E 1995 Who is Happy? *Psychological Science* **6**: 10–19.

Milgram NW, **Siwak-Tapp CT**, **Araujo J and Head E** 2006 Neuroprotective effects of cognitive enrichment. *Ageing Research Reviews* **5**: 354–369. https://doi.org/10.1016/j.arr.2006.04.004

Moberg GP and Mench JA 2000 *The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare*. CABI Publishing: Wallingford, UK.

Morgan KN and Tromborg CT 2007 Sources of stress in captivity. *Applied Animal Behaviour Science* **10**: 262–302.

Murch WS and Clark L 2016 Games in the brain: neural substrates of gambling addiction. *The Neuroscientist* **22**: 534–545.

Nakamura J and Csikszentmihalyi M 2002 The concept of flow. In: Snyder CR and Lopez SJ (eds) *Handbook of Positive Psychology* pp 89–105. Oxford University Press: Oxford, UK. https://doi.org/10.1093/oso/9780195135336.003.0007

Nelson XJ, **Taylor AH**, **Cartmill EA**, **Lyn H**, **Robinson LM**, **Janik V and Allen C** 2023 Joyful by nature: approaches to investigate the evolution and function of joy in non-human animals. *Biological Reviews* **98**: 154–163. https://doi.org/10.1111/brv.12965

Newberry RC 1995 Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science* **44**: 229–243. https://doi.org/10.1016/0168-1591(95)00616-z

Panksepp J 2004 *Affective Neuroscience: The Foundations of Human and Animal Emotions*. Oxford University Press: Oxford, UK.

Paul ES and Mendl MT 2025 Tackling challenges in the study of animal emotions: a review. *Cognition and Emotion* **39**: 1190–1209. https://doi.org/10.1080/02699931.2025.2534728

Petelle MB, **Jacobs PJ and le Roux A** 2023 Innovative problem-solving in a small, wild canid. *Animal Cognition* **26**: 405–413. https://doi.org/10.1007/s10071-022-01678-6

Petrosini L, **De Bartolo P**, **Foti F**, **Gelfo F**, **Cutuli D**, **Leggio MG and Mandolesi L** 2009 On whether the environmental enrichment may provide cognitive and brain reserves. *Brain Research Reviews* **61**: 221–239. https://doi.org/10.1016/j.brainresrev.2009.07.002

Ramsey G, **Bastian ML and Van Schaik C** 2007 Animal innovation defined and operationalized. *Behavioral and Brain Sciences.* **30**: 393–407. https://doi.org/10.1017/s0140525x07002373

Rault JL, **Bateson M**, **Boissy A**, **Forkman B**, **Grinde B**, **Gygax L and Jensen MB** 2025 A consensus on the definition of positive animal welfare. *Biology Letters* **21**: 20240382.

Reader SM and Laland KN 2003 *Animal Innovation*. Oxford University Press: Oxford, UK. https://doi.org/10.1093/acprof:oso/9780198526223.001.0001

Reinhold AS, **Sanguinetti-Scheck JI**, **Hartmann K and Brecht M** 2019 Behavioral and neural correlates of hide-and-seek in rats. *Science* **365**: 1180–1183.

Ridgway SH, **Moore PW**, **Carder DA and Romano TA** 2014 Forward shift of feeding buzz components of dolphins and belugas during associative learning reveals a likely connection to reward expectation, pleasure and brain dopamine activation. *Journal of Experimental Biology.* **217**: 2910–2919. https://doi.org/10.1242/jeb.100511

Ridgway S, **Samuelson Dibble D**, **Van Alstyne K and Price D** 2015 On doing two things at once: dolphin brain and nose coordinate sonar clicks, buzzes and emotional squeals with social sounds during fish capture. *Journal of Experimental Biology* **218**: 3987–3995. https://doi.org/10.1242/jeb.130559

Roberts DL, **Eskelinen HC**, **Winship KA**, **Ramos AM and Xitco MJ** 2023 Effects of failure on California sea lion (*Zalophus californianus*) gameplay strategies and interest in a cognitive task: Implications for cognitive

enrichment in pinnipeds. *Journal of Zoological and Botanical Gardens* **4**: 240–255. https://doi.org/10.3390/jzbg4010021

Rose PE and Lewton J 2025 Key concepts for enhancing zoo animal welfare: Coping, comfort, choice, control, challenge, and compassion. *Journal of Applied Animal Welfare Science* **2**: 497–514.

Rouse AA, **Cook PF**, **Large EW and Reichmuth C** 2016 Beat keeping in a sea lion as coupled oscillation: implications for comparative understanding of human rhythm. *Frontiers in Neuroscience* **10**: 257. https://doi.org/10.3389/fnins.2016.00257

Russell AL, **Randall LV**, **Eyre N**, **Kaler J and Green MJ** 2024 Novel enrichment reduces boredom-associated behaviors in housed dairy cows. *JDS Communications* **5**: 452–456. https://doi.org/10.3168/jdsc.2023-0475

Ryan RM and Deci EL 2001 On happiness and human potentials: A review of research on hedonic and eudaimonic well-being. *Annual Review of Psychology*. **52**: 141–166. https://doi.org/10.1146/annurev.psych.52.1.141

Sill N, **Du M**, **Allemand L**, **Bratis J**, **Winship K and Xitco M** 2025 *Adapting enclosure video enrichment for Navy dolphins.* Presented at the International Animal Trainers Association Conference, Chicago, IL, USA.

Špinka M and Wemelsfelder F 2018 Environmental challenge and animal agency. *Animal Welfare* pp 39–55. CAB International: Wallingford, UK.

Suh A, **Wagner C and Liu L** 2018 Enhancing user engagement through gamification. *Journal of Computer Information Systems* **58**: 204–213. https://doi.org/10.1080/08874417.2016.1229143

Swann C, **Jackman PC**, **Schweickle MJ and Vella SA** 2019 Optimal experiences in exercise: A qualitative investigation of flow and clutch states. *Psychology of Sport and Exercise* **40**: 87–98. https://doi.org/10.1016/j.psychsport.2018.09.007

Tebbich S, **Griffin AS**, **Peschl MF and Sterelny K** 2016 From mechanisms to function: an integrated framework of animal innovation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**: 20150195. https://doi.org/10.1098/rstb.2015.0195

Toates FM 1986 *Motivational Systems*. Cambridge University Press: Cambridge, UK.

VandenBos GR 2015 *APA Dictionary of Psychology*, Second *Edition.* American Psychological Association: USA. https://doi.org/10.1037/14646-000

Tsai J, **Knutson B and Fung HH** 2006 Cultural variation in affect valuation. *Journal of Personality and Social Psychology* **90**: 288–307. https://doi.org/10.1037/0022-3514.90.2.288

Van der Schot AA and Phillips C 2013 Publication bias in animal welfare scientific literature. *Journal of Agricultural and Environmental Ethics* **26**: 945–958. https://doi.org/10.1007/s10806-012-9433-8

Varracchio C, **Gatto E**, **Bertolucci C and Lucon-Xiccato T** 2024 Do captive fish need cognitive enrichment? A test with a puzzle feeder in guppies. *Ethology* **130**: e13442. https://doi.org/10.1111/eth.13442

Vicino GA, **Sheftel JJ and Radosevich LM** 2022 Enrichment Is simple, that's the problem: Using outcome-based husbandry to shift from enrichment to experience. *Animals* **12**: 1293. https://doi.org/10.3390/ani12101293

Vygotsky LS 1978 *Mind in Society: The Development of Higher Psychological Processes*. Harvard University Press: USA.

Webb LE, **Veenhoven R**, **Harfeld JL and Jensen MB** 2019 What is animal happiness? *Annals of the New York Academy of Sciences* **1438**: 62–76. https://doi.org/10.1111/nyas.13983

Wechsler B 1995 Coping and coping strategies: a behavioural view. *Applied Animal Behaviour Science* **43**: 123–134. https://doi.org/10.1016/0168-1591(95)00557-9

Wiepkema PR and Koolhaas JM 1993 Stress and animal welfare. *Animal Welfare* **2**: 195–218. https://doi.org/10.1017/S0962728600015876

Willroth EC, **Young G**, **Tamir M and Mauss IB** 2023 Judging emotions as good or bad: Individual differences and associations with psychological health. *Emotion*, **23**: 1876–1890. https://doi.org/10.1037/emo0001220

Winship KA, **Ramos A and Xitco Jr MJ** 2023 The introduction of a novel computerized apparatus to California sea lions (*Zalophus californianus*). *Aquatic Mammals*. **49**: 73–86. https://doi.org/10.1578/am.49.1.2023.73

Winship K, **McClain A**, **Ramos A**, **Dunham J and Xitco Jr M** 2024 Health and Welfare Benefits of Computerized Cognitive Enrichment in California Sea Lions (*Zalophus californianus*) at the US Navy Marine Mammal Program. *Animals* **14**: 1120. https://doi.org/10.3390/ani14071120

Wood-Gush DG and Vestergaard K 1989 Exploratory behaviour and the welfare of intensively kept animals. *Journal of Agricultural Ethics* **2**: 161–169. https://doi.org/10.1007/bf01826929

Woodward MA, **Winder LA and Watt PJ** 2019 Enrichment increases aggression in zebrafish. *Fishes* **4**: 22. https://doi.org/10.3390/fishes4010022

Wu F, **Tilbrook A**, **Maloney SK and Blache D** 2025 The intricate relationship between stress and animal welfare: from historical perspective to new avenues. *Biological Reviews* **100**: 2528–2581. https://doi.org/10.1111/brv.70057

Yamanashi Y and Matsuzawa T 2010 Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: individual differences in self-directed behaviours during cognitive tasks. *Animal Welfare* **19**: 25–30. https://doi.org/10.1017/s0962728600001123

Yang Q, **Lin Z**, **Zhang W**, **Li J**, **Chen X**, **Zhang J and Yang T** 2022 Monkey plays Pac-Man with compositional strategies and hierarchical decision-making. *Elife* **11**: e74500. https://doi.org/10.7554/elife.74500

Yeates JW and Main DC 2008 Assessment of positive welfare: A review. *The Veterinary Journal* **175**: 293–300. https://doi.org/10.1016/j.tvjl.2007.05.009

Young RJ 2013 Environmental enrichment. In: Hosey G, Melfi V and Pankhurst S (eds) *Zoo Animals: Behaviour, Management, and Welfare*. Oxford University Press: Oxford, UK. https://doi.org/10.1093/hesc/9780199693528.003.0008

Zentall TR 2023 An animal model of human gambling behavior. *Current Research in Behavioral Sciences* **4**: 100101. https://doi.org/10.1016/j.crbeha.2023.100101