Bestial boredom: a biological perspective on animal boredom and suggestions for its scientific investigation

Charlotte C. Burn

The Royal Veterinary College, North Mymms, Hertfordshire, UK

Corresponding author: Dr C Burn, The Royal Veterinary College, North Mymms, AL9 7TA, UK

Highlights

- Chronic boredom is distressing and damaging in humans yet barely studied in animals
- Animals in barren conditions seek even aversive stimulation, as with boredom
- Causal, ontogenetic, adaptive and phylogenetic explanations for boredom are offered
- Biological signs of boredom include indicators of suboptimal arousal
- Measurement of altered time perception will aid identification of animal boredom

Abstract

Boredom has likely adaptive value in motivating exploration and learning, and many animals may possess the basic neurological mechanisms to support it. Chronic inescapable boredom can be extremely aversive, and under-stimulation can harm neural, cognitive and behavioural flexibility. Wild and domesticated animals are at particular risk in captivity, which is often spatially and temporally monotonous. Yet biological research into boredom has barely begun, despite having important implications for animal welfare, the evolution of motivation and cognition, and for human dysfunction at individual and societal levels. Here I aim to facilitate hypotheses about how monotony affects behaviour and physiology, so that boredom can be objectively studied by ethologists and other scientists. I cover valence (pleasantness) and arousal (wakefulness) qualities of boredom, because both can be measured, and I suggest boredom includes 'negatively valenced suboptimal arousal, caused by monotony'. Because the suboptimal arousal during boredom is aversive, individuals will resist low arousal. Thus, behavioural indicators of boredom will seemingly paradoxically include signs of increasing drowsiness, alongside bouts of restlessness, avoidance and sensation-seeking behaviour. Valence and arousal are not, however, sufficient to fully describe boredom. For example, human boredom is further characterised by a perception that time 'drags', and this effect of monotony on time-perception can too be behaviourally assayed in animals. Sleep disruption and some abnormal behaviour may also be caused by boredom. Ethological research into this emotional phenomenon will deepen understanding of its causes, development, function, and evolution, and will enable evidence-based interventions to mitigate human and animal boredom.

Key words: Animal behaviour; Animal cognition; Animal welfare; Boredom; Environmental Enrichment; Motivation; Novelty; Psychobiology; Time perception.

Introduction

Chronic inescapable boredom is neither trivial nor benign. In Charles Dickens' (1853) novel Bleak House, where the relatively modern word 'boredom' was coined, he described chronic boredom as 'desolation', a 'malady', and a 'monster'. Boredom is an unpleasant emotion including sub-optimal arousal levels and a thwarted motivation to experience almost anything different or more arousing than the behaviours and sensations currently possible (adapted from Mason & Burn, 2011, in press). It arises when we perceive that there is 'nothing to do' or are 'tired of doing the same thing' (Larson & Richards, 1991), and is accompanied by a sense of time dragging (Didier-Weil, 1990; Droit-Volet & Meck, 2007; Wahidin, 2006). Fahlman, Mercer-Lynn, Flora, and Eastwood (2013) suggest boredom includes five components they labelled as Disengagement, High Arousal, Low Arousal, Inattention and Time Perception. Boredom differs from other related states including frustration (Mason & Burn, 2011, in press), depression, stress, and apathy (Goldberg, Eastwood, Laguardia, & Danckert, 2011). Inescapable boredom is highly distressing (Martin, Sadlo, & Stew, 2006), and a major torment for human prisoners (in the US and UK, respectively: Hunt, 2006; Wahidin, 2006). Human boredom can be triggered externally by monotonous, meaningless situations. This can cause work absenteeism, cognitive impairment, apathy (Harris, 2000), risk-taking, alcoholism (Wegner & Flisher, 2009) and abnormal behaviours (such as head-banging or rocking) (Mendez & Mirea, 1998). Similarly, boredom proneness exists as a personality trait, predictive of addiction, aggression, depression, impulsivity, sensation-seeking, dangerous driving and juvenile delinquency (Dahlen, Martin, Ragan, & Kuhlman, 2005; Harris, 2000; Mercer-Lynn, Flora, Fahlman, & Eastwood, 2013; Newberry & Duncan, 2001). Toohey (2011) (p.1) suggests "Predictability, monotony and confinement are all key" to triggering boredom. Although he was mostly writing about human boredom, those three factors typify captive life for non-human animals, so boredom could be a prevalent and chronic animal welfare problem (Mason & Burn, 2011; Wemelsfelder, 2005). Boredom is socially and economically important, and it has been studied in human sociological and psychological fields. However, investigation of its biological basis is just beginning.

Here I aim to help stimulate biological research into boredom in wild and captive animals. This paper consists of two main sections. First, I summarise the still rather scant empirical evidence and, using Tinbergen's (1963) framework, explore theoretical arguments for boredom-like states in animals. Second, to enable identification of potential behavioural and physiological indicators of boredom, I characterise boredom in terms of its likely behavioural and physiological manifestations, suggesting how it might be measured in future research. I cover the valence (pleasantness) and arousal (wakefulness) qualities of boredom, using this framework to predict many likely indicators of boredom. However, not every indicator fits into that framework so I also include other likely hallmarks of boredom, such as manifestations of perceived slow passage of time, abnormal behaviour and sleep disruption. Being able to scientifically study objective indicators of boredom has wide relevance, enabling use of animal models of human boredom, research into the ethology and evolution of boredom, and scientific evaluation of the efficacy of interventions to combat human and animal boredom.

Why might we expect non-human animals to experience boredom?

A dog left home alone for several hours each day energetically extracts the foam from a well-chewed corner of the sofa, then whines, yawns and lies awake awhile before getting up again (Lund & Jørgensen, 1999); Alex, the African Grey parrot, having shown great prowess in naming colours and quantities of numerous objects, starts to stare at the ceiling, to offer nonsensical answers to questions, repeatedly preens himself, and requests to go to his cage or be given water, food or novel treats (Pepperberg, 2013); a laboratory rat sniffs through the bars of its unenriched cage, digs briefly at the sawdust, sniffs the cage walls and nips at a passing cagemate (Abou-Ismail, Burman, Nicol, & Mendl, 2010); and a farmed pig with no substrate to chew sits and stares, then stands inactive awhile, before suddenly chewing a penmate's tail (Studnitz, Jensen, & Pedersen, 2007). To the naïve observer, each of these animals' behaviour may be reminiscent of that of a bored human. Indeed, the little evidence to date suggests the homology may go deeper than mere superficial resemblance.

It is important to note that, as with any emotion, boredom is private to the individual experiencing it. Therefore, we cannot be certain that other individuals – human or otherwise – experience it exactly as we ourselves do. The term 'Boredom' has historically been rather taboo in serious animal behaviour science, being labelled as 'anthropomorphic', or dismissed as trivial compared with some other welfare issues (Wemelsfelder, 2005). Moreover, boredom is sometimes assumed to be unique to humans (e.g. Anderson, 2004). Thus it has been largely neglected despite its likely prevalence and malignance. However, there are both empirical and theoretical reasons, as well as ethical ones, to encourage biological exploration of animal boredom.

Existing empirical studies of animal boredom

The few studies explicitly aiming to investigate animal boredom include observations that propensity for behavioural diversity is significantly reduced in pigs (*Sus scrofa*) kept in impoverished environments for 5 months compared with pigs who received manipulable substrate (Wemelsfelder, Hunter, Mendl, & Lawrence, 2000). This is consistent with boredom, but also with other explanations, including apathy, depression, or cognitive impairment. Taking a different approach, monotony causes many species to seek novelty, even novel stimuli they would normally avoid (reviewed in Berlyne, 1960; Kirkden, 2000; Mason et al., 2013; Stevenson, 1983). For example, despite normally shunning bright light, rats (*Rattus norvegicus*) increasingly pressed levers for flashes of light the longer they were kept in darkness (in Berlyne, 1960). Similarly, rats given only their preferred food for three days and then offered a choice, selected a non-preferred food, even choosing one previously associated with sickness (Galef & Whiskin, 2003). Thus, even initially positive monotony becomes aversive with time.

More recently, clear hypotheses regarding a key hallmark of boredom – motivation for general stimulation (Meagher, Campbell, & Mason, in press; Meagher & Mason, 2012) – have been tested in fur-farmed mink (*Mustela vison*). Compared with mink in environmentally enriched cages,

those in standard cages were significantly more likely to approach diverse stimuli, ranging from rewarding cues to (normally) aversive ones. Standard-housed mink also consumed more snacks and spent more time lying awake inactive, as is reported in bored humans (Moynihan et al., 2015).

Together, this profile of behaviours enabled Meagher and Mason (2012) to differentiate boredom from depression or apathy as explanations for the awake inactivity so prevalent in standard-housed mink.

Hypothetical ethological explanations for animal boredom

The above examples all originate from studies of captive animals, quite understandably as captive animals are subject to inescapable monotonous situations more than wild ones are. Yet, as captivity is a relatively recent challenge in evolutionary terms, one might ask why the ability to experience boredom would have evolved. As so few studies have explicitly investigated animal boredom, the hypothetical explanations I offer draw on indirect evidence regarding human boredom or from indirectly relevant phenomena in non-human animals (e.g. impulsivity, neophilia [attraction to novelty], or sensation-seeking). I offer suggestions rather than answers. With this limitation acknowledged, I briefly explore how and why animals might experience boredom, using Tinbergen's (1963) four levels of explanation as a framework.

Causation of boredom

Causation refers to the immediate internal and external mechanisms that trigger individual behaviour – or in this case a behaviourally relevant emotion. Causal explanations comprise myriad mechanisms, ranging from environmental cues to endocrine, neurological and other physiological signals. As indicated earlier, a key external trigger for boredom in captive animals will be barren environments, which may be spatially and/or temporally monotonous. Boredom thus occurs when both external and internal stimulation are insufficient to maintain optimal arousal (Berlyne, 1960).

The neural mechanisms producing boredom have seemingly not been investigated even in humans, but the brain's arousal systems will be relevant. Arousal is non-unitary, instead being distributed across several different, interconnected brain structures (Calderon, Kilinc, Maritan, Banavar, & Pfaff, 2016; Jones, 2003). Within the brainstem, arousal is supported by six systems: (1) long glutaminergic nucleus gigantocellularis neurones in the reticular formation, which receive cortical and multisensory peripheral stimulation and have both ascending (cortical) and descending (autonomic, neuroendocrine, and motor) projections; (2) cholinergic ponto-mesencephalic neurons, which facilitate awakening and REM sleep; (3) the mesolimbic dopamine pathway, which helps elicit all motivations and reward-directed behaviour; (4) the adjacent nigrostriatal dopamine system, which increases arousal and reward-directed behaviour, and is involved in time perception (Jahanshahi, Jones, Dirnberger, & Frith, 2006; Simen & Matell, 2016); (5) the serotonergic raphe nuclei, most active during awake relaxation; and (6) the noradrenergic locus coeruleus, most active during stress or panic. Activity in these systems is influenced by, and relayed to, the cortex and/or the body via further arousal systems within midbrain structures including the hypothalamus, thalamus, and basal forebrain {Jones, 2003 #4276;Calderon, 2016 #4278}. Most of these systems are highly conserved among vertebrates, with similar organisation in mammals, birds and reptiles at least (Calderon et al., 2016). Thus, many vertebrates could have the neurological apparatus to produce boredom-like states.

Boredom might thus result from discrepancy between the activations of different arousal systems. For example, because boredom often occurs when stimulation is lacking, but when general motivation for stimulation remains high, arousal systems reliant on sensory information may be relatively inactive, while the mesolimbic dopamine pathway may be highly active. Also, the locus coeruleus shifts from phasic to tonic firing, becoming less active, as non-human primates disengage from a task and start performing non-task-related behaviours (Aston-Jones & Cohen, 2005), possibly indicating task boredom. The insular cortex — integrating emotional, interoceptive and temporal perceptions — is also likely to be highly active during boredom (Wittmann & Butler, 2016; Wittmann

et al., 2011). That boredom might result from dissonance between arousal systems is consistent with observations that both stimulant and depressant drugs can relieve human boredom (Boys et al., 1999; Howard & Zibert, 1990), perhaps by resolving the discrepancy between motivation for arousal versus low actual arousal.

Whether these systems are sufficient for animals to show boredom-like aversion to monotony remains to be discovered. Indeed, perhaps convergent mechanisms could exist in invertebrates, such as octopuses. Octopuses are highly exploratory, neophilic, with remarkable cognitive abilities (Hochner, Shomrat, & Fiorito, 2006; Mather & Anderson, 1999), and the term 'boredom' has been tentatively used as impetus for providing environmental enrichment to captive octopuses (Anderson & Wood, 2001; Mather, 2001).

Ontogeny of boredom

Ontogeny refers to changes in 'behavioural machinery' during development and maturation (Tinbergen, 1963). At a neurological level, most animals require species-appropriate stimulation to develop and maintain behavioural flexibility and learning abilities (e.g. Wurbel, 2001). The propensity for boredom could motivate animals to seek appropriate types and intensities of stimulation to aid this in an age appropriate manner. This seems true in humans, with young children easily bored by adult activities, while repeating games like 'peek-a-boo', or moving objects in and out of containers, many times over (Piaget, 2013); and with teenagers notoriously susceptible to boredom, shifting attention towards socially relevant memes, sexual information, and self-image (Danesi, 1994). Similar phenomena may occur in non-human animals also; for example, motivation for different types of play changes with age in several species (Pellis & Iwaniuk, 2004). Also, boredom-relevant behaviour including risk-taking, psychoactive drug consumption, novelty seeking, and impulsivity all increase in adolescent rodents compared with juveniles or adults (Laviola, Macrì, Morley-Fletcher, & Adriani, 2003; Macrì, Adriani, Chiarotti, & Laviola, 2002).

Much ontogenetic research explores the relative contribution of genes versus environment to the development of individual behavioural phenotypes. In humans, boredom proneness is probably highly heritable, because twin studies reveal high heritability in gambling (Winters & Rich, 1998) and drunk driving (Anum, Silberg, & Retchin, 2014). The field of animal personality ('behavioural syndromes') might be ripe to explore boredom proneness, discovering whether similar correlations between boredom proneness and other traits exist in animals as in humans (Dahlen et al., 2005; Harris, 2000), and the extent of genetic *versus* environmental contribution. For example, boldness and proactive coping styles in animals are associated with neophilia (Carere, Caramaschi, & Fawcett, 2010), impulsivity and aggressiveness (e.g. Coppens, de Boer, & Koolhaas, 2010), so bolder or more proactive animals might also show other correlates of boredom proneness, e.g. sensation-seeking and overestimation of waiting-times. Also, humans with ADHD are highly boredom prone (e.g. Kass, Wallace, & Vodanovich, 2003), so animal models of putative ADHD should also show this proneness.

Adaptive value of boredom

Boredom appears to have entirely negative corollaries when prolonged and inescapable, but to have adaptive value, it must have positive evolutionary fitness effects when it can be acted upon.

Boredom might provide the motivation to stay within optimal levels of arousal for learning or maximal task performance. The Yerkes-Dodson law predicts a U-shaped relationship between arousal and performance, which is often corroborated (e.g. Anderson, 1994), but see Wu et al. (2010) for example. Boredom can arise when tasks are too easy or too difficult, especially if successful learning is not involved (e.g. Acee et al., 2010), so it encourages switching attention to more rewarding activities. Boredom might also spark creativity and innovation in animals, as in humans (Mann & Cadman, 2014). Indeed, captivity can seemingly stimulate innovative behaviours unknown in the wild, such as tool use in otherwise non-tool-using species ranging from elephants to rooks (Haslam, 2013; Tebbich, Seed, Emery, & Clayton, 2007), which could be a creative response to the monotony of captivity. It remains to be discovered whether indicators of boredom precede

innovation in real time, and whether signs of boredom proneness are more (or less) common in more innovative individuals or species. More innovative species are significantly more neophilic (Reader, 2003), so they may show more boredom indicators when faced with monotony.

Boredom could also prompt exploration and niche diversification within lifetimes, promoting learning and preventing animals from becoming behaviourally inflexible in the face of likely environmental changes. For example, boredom could help motivate some adolescent animals to leave their natal homes and seek new territory, stimulate omnivores to sample new foods even when familiar food is plentiful, or drive innovative species to experiment with new materials when their more immediate needs are fulfilled. In each case, risk comes with new behaviour, but so does opportunity. In the field, it could be useful for conservationists and behavioural ecologists to know whether indicators of boredom in wild animals can predict the onset of risky behaviour.

The negative fitness consequences of animals being unable to escape monotony, or to exercise, explore and/or learn, would usually be difficult to ascertain in wild animals, because they are rarely constrained. However, we know from captive animals without sensory or cognitive stimulation to an extreme, that neural pathways can fail to develop, and those already present can weaken; the brains of animals in barren environments even become physically smaller (e.g. Wurbel, 2001). This manifests as an increasingly inflexible and limited behavioural repertoire, such as the highly perseverative stereotypical behaviour seen in animals kept in barren conditions (Mason & Rushen, 2006). This is unlikely to reach such a pathological degree in the wild, so we would not expect natural selection to have prevented extreme synaptic die-off from happening, but even mild behavioural inflexibility could be detrimental to fitness in some wild animals, especially in highly variable niches.

It is worth noting that boredom may primarily be problematic for relatively normal captive animals: those still capable of flexible, responsive behaviour. This is because, if under-stimulation is severe and prolonged enough to cause central nervous system damage, boredom may advance into

apathy or brain damage, as can happen in human prisoners (Shalev, 2008). Boredom may gradually become irrelevant to apathetic or depressed animals who no longer seek, or respond normally to, stimulation (Meagher & Mason, 2012).

Phylogeny of boredom

Phylogenetic explanations apply at the species level, including how characteristics differ across diverse species. Boredom is most likely in generalist species, given the proposed adaptive and developmental value of boredom as a motivator to explore and learn. Discovering whether this is true will require systematically comparing the frequency of boredom indicators across a range of species, using appropriate phylogenetic analysis to control for species relatedness. This is yet to be done, but generalist traits do correlate positively with boredom-relevant traits including neophilia and innovation at the species level (reviewed in Reader, 2003). Further suggestive evidence comes from captivity, where it seems to be particularly neophilic, generalist species (Kirkden, 2000; Mason et al., 2013; Stevenson, 1983) that proactively seek – even aversive – stimulation in barren environments.

From an evolutionary psychology perspective, exploration of which species respond to monotony with boredom-like behaviour could help answer fundamental questions such as 'which brain structures facilitate boredom?' (Calderon et al., 2016), 'are more 'intelligent' species more prone to boredom?' (Mason et al., 2013), and 'which species are most at risk from the monotony common in captivity?' (Mason et al., 2013).

How to measure animal boredom

There will not be single unambiguous indicators of boredom, as with other emotional states, but instead several indicators must be used together to form a profile consistent with boredom (Mason & Mendl, 1993). The indicators chosen for any particular study will depend on the species, the relevant timescale (some indicators best reveal welfare over months, others over seconds),

ethical considerations (e.g. invasiveness), and feasibility (e.g. environmental, time and financial constraints).

Increasingly in animal studies (Mendl, Burman, & Paul, 2010), emotions are classified according to a 'dimensional model', each usually described in terms of valence (pleasantness) and arousal (Russell, 1978; Russell, 1980). Classic examples of emotions that map onto these dimensions include fear having high arousal and negative valence, or relaxation having low arousal and positive valence (Russell, 1978; Russell, 1980). The valence-arousal model oversimplifies true emotional complexity, but it aids animal research because the valence and arousal significance of much behaviour and physiology is quite well understood, enabling predictions about how to measure certain emotions using objective indicators of both valence and arousal (Mendl et al., 2010). I use this as a starting point for identifying potential indicators of animal boredom. However, there are other important qualities of human boredom that do not fit the model, so I also include some of these (altered time perception, disrupted sleep, and abnormal behaviour). First I outline theoretical reasons for suggesting certain indicators, and then offer practical examples.

Theoretical considerations

Valence and arousal qualities of boredom

There is little dispute that boredom is negatively valenced (e.g. Eastwood, Frischen, Fenske, & Smilek, 2012; Martin et al., 2006), so that will not be discussed further, except to highlight that it predicts animals will attempt to avoid or mitigate boredom-inducing situations. However, whether arousal during boredom is high or low has been debated. Berlyne (1960) argued that boredom comprises high arousal, stating that "...sensory deprivation becomes aversive when internal factors cause a rise in arousal and the lack of stimulation renders the cortex incapable of keeping arousal within bounds" (p.190). To illustrate, he pointed out that "Lying motionless in a quiet dark room... is extremely trying... when one is healthy and has had enough sleep" (p.189). In contrast,

questionnaire respondents usually classify boredom as comprising relatively low arousal (Burn, 2011; Russell, 1980).

Thus boredom is paradoxically characterised both by high and by low arousal (Fahlman et al., 2013), and perhaps this is not surprising now that the multifactorial nature of arousal in the brain has been revealed (Jones, 2003). As boredom occurs when arousal inputs are low, but arousal motivation is high, the behavioural and physiological outputs will reflect this conflict. This predicts alternation between attempts to raise arousal via motor restlessness or sensation-seeking, and low arousal drowsiness, with drowsiness gradually prevailing if the under-stimulation continues. As Berlyne (1960) said "... a human being or an animal in the throes of agonizing boredom... shows restlessness, agitation, and emotional upset... [But] lack of stimulation also has a tendency to put people to sleep" (p.189). Indeed, it also fits Wemelsfelder's (2005) (p. 85) description of a typical bored animal's behaviour: "Over time the animal appears to become both more lethargic and more irritably reactive..."; it can "never truly relax", and may "wander around, sniffing or nibbling different substrates but never staying with any for long". An important note, is that emotional arousal is not the same as motor activity (Oxendine, 1970), so even highly active restlessness may barely raise arousal by other measures.

Boredom must be distinguishable from other aversive states of suboptimal arousal that may exist (e.g. exhaustion in the face of a challenge), so one could specify that boredom is caused by monotony (rather than, say, duration or intensity of energy expenditure *per se*). Monotony can be spatial, as in barren environments, or temporal, as in repetitive tasks. Boredom appears unique among negative emotions in being caused by monotony, which is useful because monotony can be experimentally manipulated enabling comparisons to be made between, for example barren *versus* enriched environments, or repetitive *versus* varied tasks. In captivity, monotony generally is synonymous with under-stimulation, and attempts to relieve it often rely on environmental enrichment, so comparing barren with enriched conditions is likely to be a useful experimental

paradigm. However, boredom can also be induced under highly stimulating situations if that stimulation is perceived as irrelevant and predictable. This cause of boredom is described by factory workers and school children (Anderson, 2004), and might be relevant to working animals performing repetitive tasks. For example, Alex, the African Grey parrot, was reportedly most likely to baulk at tasks in the 'bored' manner described above when tasks were repetitive or simpler than preceding tasks, or when rewards lacked novelty (Pepperberg, 2013). Either way, captive animals are often rendered passive recipients of stimulation, rather than having choice and control over their experiences and behavioural options (Wemelsfelder, 2005).

A final note on this is that some apparent monotony is relevant and meaningful for animals (e.g. bamboo browsing in the Giant panda, *Ailuropoda melanoleuc*a), or can be relaxing (e.g. repetitive gardening tasks for humans: Pitt, 2014). Individuals in such situations would not show signs of boredom; they would approach the situations, rather than avoid them, and would not seek out alternative sources of stimulation.

Altered time perception, sleep disruption and abnormal behaviour

Some important qualities of boredom do not fit into the valence-arousal model. A key example is altered time-perception, which has a complex relationship with both valence and arousal: perceived duration appears to lengthen both during periods of extreme eventfulness and of extreme uneventfulness, and usually, but not always, with negative valence (Droit-Volet & Meck, 2007; Flaherty, 1991). The notion that 'time drags' during boredom is pervasive across human cultures (Didier-Weil, 1990; Droit-Volet & Meck, 2007; Flaherty, 1991; Wahidin, 2006), and is a key quality of boredom (Fahlman et al., 2013). Slow perceived time passage has been demonstrated in experimental manipulations in humans both in boredom as an acute state (e.g. Hawkins & Tedford, 1976) and as a personality trait (Danckert & Allman, 2005). The relationship even works in reverse, so humans perceive the same experience as more boring if a manipulated clock indicates that it lasted longer than it really did (Sackett, Meyvis, Nelson, Converse, & Sackett, 2010).

Another 'misfit' characteristic might include disrupted sleep, as a consequence of boredom that persists across a sleep-wake cycle. The associated suboptimal arousal may cause animals to sleep earlier than they would otherwise do, but not being tired, the animals' sleep may be relatively brief and/or superficial. Bored animals may rest more, but sleep less, because their environment is insufficiently stimulating to keep them awake or properly tire them out.

Finally, abnormal behaviour, especially stereotypic behaviour, most frequently occurs in negatively valenced situations, but has a complex relationship with arousal (Mason & Rushen, 2006). People often intuitively attribute abnormal behaviour to boredom (e.g. Blackshaw, 1988; Litva, Robinson, & Archer, 2010). However, more highly stereotypic mink initially showed fewer boredom indicators than non-stereotypers in barren environments (Meagher & Mason, 2012), and when the work was replicated, no relationship was found (Meagher, Campbell, & Mason, In Press). Different abnormal behaviours, despite sharing many behavioural and neurological features, can have diverse causative factors (Mason, 1991; Mason & Rushen, 2006). Some might well be caused by boredom, but others are caused by more specific frustrations, such as inadequate diets or lack of appropriate nests (Mason & Burn, in press). Such specific causes may need ruling out before boredom can be concluded as the cause. This limits use of abnormal behaviour as an indicator of boredom. However, if a study seeks to explore whether abnormal behaviour results from boredom, this could be tested by observing whether the behaviour is predicted by other indicators of boredom and is reduced by diverse arousing stimuli (Mason & Burn, in press).

It is worth clarifying that only abnormal or stereotypic behaviours that are responsive to external stimuli are likely to be useful indicators of boredom, because if they become habitual or reflect brain dysfunction, they no longer differ between situations (Mason & Rushen, 2006).

Practical examples of boredom indicators

All the above makes it possible to scientifically identify animal boredom, so I provide examples of promising indicators in Tables 1-3. I attempt to briefly summarise evidence for each indicator in the

tables but, as explained above, direct evidence of links with animal boredom is lacking for most indicators because research into the subject is only just beginning. Where direct evidence appears absent, I illustrate the potential relevance of the indicator by using indirect evidence from animals or humans. Specifically, evidence comes from (a) comparisons of animals in more versus less monotonous environments, and (b) human research on waiting experiences, sensory deprivation, sensation-seeking, and task-related boredom. Where effects of environmental enrichment on animals is cited, I have excluded research that only tested social housing or 'comfort' enrichment, because these would be expected primarily to relieve welfare issues other than boredom (e.g. provision of shelters or nesting material could relieve specific frustrations or stress); instead I include studies testing diverse stimulating enrichments, such as toys, novel objects, puzzle feeders, and exercise apparatus, more likely to relieve boredom. In many cases, evidence is compatible with boredom but other explanations cannot be dismissed without further research. However, its inclusion demonstrates feasibility and offers useful empirical observations upon which to build further research. None of the indicators uniquely identify boredom; those in Table 1 can indicate certain other aversions or frustrations, while those in Table 2 can indicate non-boredom related fatigue or relaxation. It is the combined presence of several indicators in monotonous situations that would indicate boredom.

Aversion to monotony

Potential indications that animals perceive monotonous situations as aversive are shown in Table 1. These generally fall into two categories: (1) indicators of aversion to the monotonous situation *per se*, such as preference tests and cognitive bias tests; and (2) indicators that the animal is proactively attempting to create stimulation, such as via sensation-seeking, restlessness and psychoactive drug consumption. Escape behaviour is intermediate between these two types of indicators; indeed escape is a unifying theme as the animal attempts to avoid low arousal either by seeking external stimulation, or by proactively attempting to increase arousal levels internally, e.g. via restlessness.

Suboptimal arousal

Indicators of the drowsiness, rather than the aversion, aspect of suboptimal arousal are covered in Table 2. These will periodically be disrupted by the above bouts of restlessness, escape-attempts or sensation-seeking. These activity bouts might resemble an extinction curve, with intense initial activity, followed by waning as the animal finds they are ineffective in raising arousal. Nevertheless, over a prolonged period (several hours, depending on the species and situation) the overall arousal of a bored animal will decline. The animal will show increasing awake inactivity, and will ultimately fall asleep earlier than in more engaging conditions (Mavjee & Horne, 1994).

The predictions for *decreased* Hypothalamic-pituitary-adrenal (HPA) and Sympathetic-adrenomedullary (SAM) activity are notable, because lower activity is commonly interpreted as indicating reduced stress and better welfare. For example, glucocorticoids are often referred to as 'stress hormones', and situations that reduce their chronically elevated concentrations are commonly perceived as benefiting animals (Möstl & Palme, 2002). Boredom may be an exception to this general rule, because glucocorticoids are catabolic, usually associated with raised arousal, so they might decline in monotonous situations; here higher, rather than lower, concentrations might indicate better welfare. Ultimately, whether this prediction is true depends on which brain arousal systems are active versus inactive during boredom (Jones, 2003). Indeed, some repetitive tasks increase SAM activity (Weber, Fussler, O'Hanlon, Gierer, & Grandjean, 1980), so either they did not cause boredom, or there could be different types of boredom reflecting the precise discrepancy between arousal systems.

Brain imaging may be another revealing avenue for future research. Until recently it has been invasive for animals, but now positive reinforcement training allows non-invasive electroencephalography (EEG) (Törnqvist et al., 2013) and functional magnetic resonance imaging (Berns, Brooks, & Spivak, 2012) in non-sedated, behaviourally normal dogs. The covert processing that such techniques can reveal may help separate measures of mental arousal versus physical

activity. For example, human EEGs have long revealed that active concentration is predominantly associated with fast beta waves (16-35Hz), while resting states progress through slower alpha (8-13Hz; awake resting), then theta (4-7Hz; drowsiness), and finally delta waves (1-4Hz; sleep), with increasing synchrony across brain activity (e.g. Boksem, Meijman, & Lorist, 2005; Lorist et al., 2009; Yeo, Li, Shen, & Wilder-Smith, 2009). Eye blink rate, which increases with drowsiness, can sometimes be counted visually or it, together with blink duration, can be quantified via EEG (Steele, Cutmore, James, & Rakotonirainy, 2004; Yeo et al., 2009).

Lastly, regarding indicators of suboptimal arousal, yawning is a classic behavioural hallmark of boredom in humans across cultures (Toohey, 2011), and it appears to occur in many vertebrates including mammals, birds, reptiles and possibly even fish (Baenninger, 1997). Yawning and sighing might be expected to occur among generally slowed respiration during boredom. It has rarely been used in scientific studies of boredom, despite its likely relevance and the fact that it will normally be quite easily quantifiable, so it could play a useful role in future research. Yawning also increases with fatigue (Guggisberg, Mathis, Herrmann, & Hess, 2007) (but see Baenninger, 1997) and even ambient temperature (Gallup, Miller, & Clark, 2009), so experimental designs will need to rule out conflicting explanations.

Measuring altered time perception, sleep disturbance and abnormal behaviour

Evidence for the non-valence-arousal indicators of boredom is summarised in Table 3. Investigating how monotony affects animals' time perception is an exciting new avenue for research, but it first requires validation using human verbal report as gold standard, to help refine paradigms for use in animals. This is because even human investigations have rarely tested effects of boredom on timing, and usually test timescales too short to be relevant (e.g. seconds) (Wittmann et al., 2011). Also, they have sometimes yielded surprising results. For example, subjective estimation of durations is greatly affected by whether humans know in advance that they must estimate the duration (so they consciously attend to the time passage, perhaps like a trained animal would),

versus whether they are only asked to estimate it in retrospect (Block, Hancock, & Zakay, 2000). Humans report time to drag (they under-produce durations [e.g. stopping at 8s when asked to produce a 10s interval], and over-estimate them [e.g. estimating the 8s interval lasted 10s]) within a monotonous experience; however, if asked retrospectively how long the monotony lasted, they sometimes underestimate duration compared with more complex experiences (Block, 1978). Time drags during monotony, but there is little to remember afterwards. Further analysis of this is outside the scope of this paper, but there are well developed models of temporal encoding within the brain (e.g. Buhusi & Meck, 2005; Droit-Volet & Meck, 2007; Simen & Matell, 2016), which will help refine predictions and paradigms.

This said, time perception can already be objectively measured in animals. 'Fixed Interval' or 'Peak Procedure' methods assess perception of concurrent (rather than remembered) time, and involve training animals to expect a certain event after a predictable time period. Suitable events must provoke distinctive responses in the animal, e.g. clear anticipatory behaviour, such as pecking a key in starlings trained to expect a reward (Bateson & Kacelnik, 1995). Once training is complete, the onset of the anticipatory behaviour can be compared between conditions that should or should not promote boredom; animals should start to perform the anticipatory behaviour earlier under monotonous conditions.

Alternative paradigms include 'time discrimination' or 'temporal bisection' tasks (e.g. Meck, 1996). Here, animals learn that if a stimulus lasted a short time, they must perform a behaviour ('A') for a reward, and if it lasted a long time, they must perform behaviour 'B' instead. They could then be exposed to intermediate stimulus durations under monotonous versus stimulating conditions, with the prediction that they will more frequently perform behaviour A under the monotonous condition (Block et al., 2000). Monotony could decrease animals' reward expectation, as indicated in cognitive bias tests under differential environmental enrichment treatments (Bateson & Matheson,

2007; Brydges, Leach, Nicol, Wright, & Bateson, 2011; Douglas, Bateson, Walsh, Bédué, & Edwards, 2012), so judgement bias and time perception explanations should be distinguishable.

A third insight into an animal's perception of time passage could be to simulate 'clock-watching' behaviour. Humans become more conscious of time passage when bored, more frequently seeking feedback on it by, for example, looking at clocks (Eastwood et al., 2012; Pulce, 2005). Animals would need learn that a simple salient clock, like a sand-timer or a slider, predicts time until an awaited event, and the experimental paradigm would need the animal to behave distinctively when checking the 'clock', e.g. peering around a barrier at it. They should perform this behaviour more frequently in monotonous situations, and the frequency should increase with absolute duration.

Regarding measurement of sleep, this is usually done by recording when animals have adopted a sleep posture with their eyes closed for a defined minimum amount of time (Abou-Ismail et al., 2010) – sleep itself is a subjective state, so animals sometimes appear asleep when still aware of their surroundings. Sleep postures are thus a proxy for actual sleep, but use of non-invasive brain imaging also opens new possibilities for objectively distinguishing between different sleep phases and sleep quality (Hänninen, Mäkelä, Rushen, de Passillé, & Saloniemi, 2008). Boredom can lead to disrupted sleep in humans (Lei et al., 2009) and possibly in rats (Abou-Ismail et al., 2010) (Table 3).

Finally, bearing in mind the aforementioned caveats about using abnormal or repetitive behaviour to indicate boredom, some predictions can be made. When such behaviour indicates boredom, rather than specific frustration, individual animals may perform more than one type of abnormal behaviour in their attempts to generate some, any, stimulation. This seems true in humans, where bored individuals may exhibit any or all of leg-joggling, drumming fingers, pacing, hair-twirling, rocking or even their own idiosyncratic behaviour (e.g. Fazzi et al., 1999; Mendez & Mirea, 1998; Newberry & Duncan, 2001). Similarly, because boredom includes motivation to experience 'something, anything, else' (Mason & Burn, in press), boredom-induced abnormal

behaviour should decrease in response to diverse stimulating interventions, including novel objects, sensory experiences, exercise apparatus or more, whether positive or negative (Berlyne, 1960; Meagher & Mason, 2012).

Conclusions

Boredom is not the trivial annoyance it is sometimes dismissed as. Animal boredom is biologically plausible: animals avoid monotony and seek stimulation, and there is gathering evidence for its mechanism in vertebrates, its role in ontogeny, and its adaptive value in maintaining behavioural flexibility, especially in generalist species. Behavioural and physiological indicators will signify aversion to monotony and suboptimal arousal, as well as perceived slowing of time. Biological study of boredom is so scarce that some research will first need validation in humans, using self-reported boredom as a gold standard (Burn, 2011), before extrapolating to animals.

Too often animal boredom has been dismissed as an anthropomorphic concept, or as a luxury compared with other more widely accepted welfare issues such as pain or stress (Wemelsfelder, 2005). However, given the intense distress that prolonged boredom can cause in humans, and the cognitive damage that under-stimulation can ultimately lead to, it is potentially a severe and highly prevalent animal welfare issue neglected too long. The time is ripe to embrace animal boredom as a topic of genuine scientific and moral interest, allowing us to explore the biological basis of boredom in animal models, and to evaluate interventions to combat boredom and its associated problems in humans and animals alike.

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Table 1. Suggested indicators of negative valence caused by monotony in animals and humans.

Indicator or test	Predicted effect of a monotonous versus a more stimulating situation	Examples of evidence from humans	Examples of evidence from non- human animals
Preference test, consumer demand test	Animals should avoid the monotonous situation	NF	Mink living in a consumer demand apparatus were least motivated to push a weighted door to access an empty compartment compared with six other options; they pushed significantly heavier weights to access a compartment containing novel objects (Mason, Cooper, & Clarebrough, 2001). Similarly, mice living for several days in a consumer demand apparatus consisting of a standard cage and a cage consisting of a mixture of comfort and stimulating enrichment pushed significantly greater weight to access the enriched cage, especially if they had been previously reared with enrichment (Latham & Mason, 2010).
Conditioned place preference or Pavlovian conditioning	Animals should avoid places or cues that they associate with the monotonous situation	Workers (n=292) who had higher job boredom scores (5-point likert scales on e.g. 'how monotonous is your job/how slowly does your job pass?') showed significantly higher absenteeism rates (% days missed) (Kass, Vodanovich, & Callender, 2001).	NF
Cognitive bias/ Judgement bias	Animals should show a more negative ('pessimistic') perception towards an ambiguous stimulus when living	Boredom proneness is associated with more negative expectations about the future (e.g. reviewed in Farmer & Sundberg, 1986)	A pessimistic-like cognitive bias has been shown in response to an absence of, or removal of, stimulating environmental enrichment in starlings (Bateson & Matheson, 2007), rats (Brydges

	in the monotonous situation		et al., 2011), and pigs (Douglas et al., 2012).
Escape behaviour	Animals should perform more escape behaviour in the monotonous situation	In humans, boredom is a reported cause of work absenteeism, e.g. workers reporting higher job boredom ratings missed a greater proportion of working days (Kass et al., 2001).	NF
Sensation- seeking behaviour and distractibility	Animals in the monotonous situation should more readily approach stimuli regardless of whether they are positive, neutral or negative, and be more distractible in general	With regards to distractibility, humans performing a 3h visual attention task increasingly paid attention to irrelevant distracting stimuli over time (Boksem et al., 2005).	Mink without stimulating environmental enrichment approached 10 stimuli more readily than mink with enrichment (Meagher & Mason, 2012).
Restlessness	Animals should perform more bouts of self-directed behaviour, stretching, destructive behaviour and repetitive displacement activity in the monotonous situation	Humans in emergency waiting rooms without visual art paced up and down, got out of their seats, and stretched significantly more than those in rooms with art (Nanda et al., 2012); Humans on a 1h monotonous task reported that rhythmic leg or finger movements helped them cope with the boredom (Pattyn, Neyt, Henderickx, & Soetens, 2008).	An orang-utan performed more self-scratching and destructive behaviour while waiting for a reward when delays to the reward presentation were longer (Elder & Menzel, 2001).
Psychoactive drug consumption	Animals should consume psychoactive drugs more in the monotonous situation	Humans self-report boredom as a major trigger for taking a variety of psychoactive drugs ranging from relaxants to stimulants (e.g. Boys et al., 1999; Howard & Zibert, 1990).	Studies often show that rats in socially and environmentally complex cages consume less morphine (e.g. Alexander, Coambs, & Hadaway, 1978), amphetamine (Bardo, Klebaur, Valone, & Deaton, 2001) or cocaine (Gipson, Beckmann, El-Maraghi, Marusich, & Bardo, 2011) than isolated conspecifics (but see the opposite for ethano consumption: Rockman, Gibson,

			& Benarroch, 1989), but the effects of social isolation and monotony are yet to be separated.
Polyphagia	A possible form of sensation-seeking or – if extreme – abnormal behaviour, animals in the monotonous situation should eat more frequently, even excessively	Humans in three different conditions consumed more snacks when they self-reported increased boredom (Moynihan et al., 2015)	Mink without environmental enrichment consumed more food rewards than mink with environmental enrichment (Meagher & Mason, 2012)
Polydipsia	As with polyphagia, animals in the monotonous condition should drink and urinate more frequently, even excessively	NF	Three laboratory rabbits drank and urinated excessively; no health abnormalities were found, and provision of toys and manipulanda successfully reduced the behaviour (Potter & Borkowski, 1998).

Examples of suggestive evidence to date are offered from human and/or animal studies – many of these did not set out to investigate boredom, so the evidence they provide requires replication. NF – No evidence found to date.

Table 2. Suggested indicators of suboptimal arousal levels in animals and humans.

Indicator or test	Predicted effect of a monotonous versus a more stimulating situation	Examples of evidence from humans	Examples of evidence from non-human animals
Hypothalamic-pituitary- adrenal (HPA) activity	Measures of HPA activity, e.g. cortisol or corticosterone, should decrease over time in the monotonous situation	In men (women were not tested), salivary cortisol was significantly lower following a boring – excessively easy – computer game than after an appropriately challenging or difficult game (Keller, Bless, Blomann, & Kleinböhl, 2011).	An orang-utan showed reduced salivary cortisol when delays to a reward were longer (Elder & Menzel, 2001). Pigs reared in barren environments had lower diurnal salivary cortisol concentrations than those reared in larger straw-provisioned pens (de Jong et al., 2000).
Sympathetic- adrenomedullary (SAM) activity	Measures of SAM activity, e.g. heart rate, adrenaline or noradrenaline, should decrease over time in the monotonous situation	As reviewed in Thackray (1981) most, but not all, studies of human performance during sustained vigilance, sensory deprivation or repetitive tasks showed that boredom or monotony were accompanied by reduced heart rate, blood pressure, oxygen consumption, urinary adrenaline and noradrenaline.	NF
Awake inactivity	Animals should spend a greater proportion of time inactive but awake in the monotonous situation; they may appear drowsy and have a 'glazed' appearance to their eyes.	People reported more sleepiness and had slower reaction times when in more boring situations (Mavjee & Horne, 1994).	Mink in standard cages spent significantly more time lying inactive with their eyes open than mink in enriched cages (Meagher & Mason, 2012);
Electroencephalographic (EEG) activity	Animals should show increasing synchrony, especially increased	Humans performing a 3h visual attention task reported increasing fatigue and showed increasing theta	Beta activity increases in cats, dogs and monkeys during task performance or reward anticipation;

	presence of slow alpha and theta waves, and decreased fast beta, during the monotonous situation	and lower-alpha EEG band power (Boksem et al., 2005); those performing a 2h repetitive task showed increased power and stronger synchronisation, although this was not frequency specific (Lorist et al., 2009); drowsy periods during a 1h monotonous driving simulation were classified as showing a higher proportion of alpha than beta activity (Yeo et al., 2009).	further, the cat studies showed it to reduce during habituation to stimuli and preceding incorrect trials, suggesting inattention (reviewed in Wróbel, 2000)
Respiratory patterns	Respiratory rate should decrease and become more variable as animals yawn and sigh more in the monotonous situation	Human yawning is believed to indicate boredom across human cultures (Toohey, 2011), but empirical evidence is scarce: humans asked to record their own yawning rate reported greater frequencies and durations of yawning while watching a 30 min monotonous screen than a 30 min rock video (Provine & Hamernik, 1986).	In animals, lions and mandrills yawned most when inactive but awake (Baenninger, 1987), and yawning rate correlated positively with stereotypic performance in horses (Fureix, Gorecka-Bruzda, Gautier, & Hausberger, 2011), both of which are consistent with boredom, but other explanations cannot be ruled out.
Eye blink rate	Blink rate should increase in the monotonous situation	In humans, blink rate increased during a situation mimicking slowed passage of time during a repetitive task (Steele et al., 2004); drowsy periods during a 1h monotonous driving simulation were classified as showing blink durations longer than 0.5s (Yeo et al., 2009).	NF

Examples of suggestive evidence to date are offered from human and/or animal studies – many of these did not set out to investigate boredom, so the evidence they provide requires replication. NF – No evidence found to date.

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Table 3. Suggested indicators of other key characteristics of boredom in animals and humans.

Indicator or test	Predicted effect of a monotonous versus a more stimulating situation	Examples of evidence from humans	Examples of evidence from non- human animals
Time perception	Time should be perceived as passing more slowly in the monotonous situation, indicated using e.g. interval timing paradigms, duration reproduction paradigms, 'clockwatching behaviour' and/or onset of anticipatory behaviour	Humans listening to 'boring' stories reported them as being relatively longer than 'interesting' stories (Hawkins & Tedford, 1976); People with ADHD, who are often also highly boredom prone, show signs of time dragging, such as shorter duration reproductions, e.g. indicating that they perceive 10s to have passed after only 8s (reviewed in Noreika, Falter, & Rubia, 2013).	Rats in peak interval (Paule et al., 1999) or temporal bisection (Meck, 1983) tasks showed behaviour consistent with time dragging (faster internal clock speed) when given metamphetamine, which increases dopamine release; this is consistent with the proposed increase in midbrain dopaminergic activity, with its corresponding motivation for increased arousal, during boredom (although metamphetamine itself does not cause boredom).
Disrupted sleep	Across sleep-wake cycles, animals should sleep less (despite being awake inactive more) in the monotonous situation	Boredom was a cause of disturbed sleep cited both by patients and nurses in a hospital (Lei et al., 2009)	Rats in standard cages had fewer apparent sleeping bouts and shorter total durations of sleep than those in cages with a mixture of comfort enrichment and novel, stimulating enrichment (Aboulsmail et al., 2010).
Abnormal and repetitive behaviour	Animals should increase performance of diverse abnormal or repetitive behaviours in the monotonous situation (unless the behaviour has become highly perseverative)	Boredom or under- stimulation are reported as causing many abnormal or repetitive behaviours in humans (e.g. Fazzi et al., 1999; Mendez & Mirea, 1998; Newberry & Duncan, 2001)	A meta-analysis of 54 published studies found that 90% of stereotypic behaviour measurements in zoo mammals were reduced by stimulating environmental enrichment provision (Shyne, 2006).

Examples of suggestive evidence to date are offered from human and/or animal studies – many of these did not set out to investigate boredom, so the evidence they provide requires replication.