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Effects of Anthropogenic Change on Animal Cognition and Emotion

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A thesis submitted for the degree of Doctor of Philosophy in the School of Biological Sciences and Institute for Global Food Security, Queens University Belfast

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Cognition reigns but does not rule.

Paul Valéry

Abstract

Human activity is driving global biodiversity loss. However, the effects on animal cognition and emotion are less studied. In this thesis, I argue that anthropogenic change impacts animals' mental states, with implications for both individuals (welfare) and populations (conservation). My first experiment explores the transition from keeping dairy cattle at pasture to housing them indoors full-time. Using a repeated-measures crossover design, I gave cows three weeks of overnight pasture access and three weeks of indoor housing. Treatment did not influence judgements of ambiguous stimuli – a cognitive measure of emotional wellbeing. Nevertheless, behavioural welfare indicators (lying, walking, and anticipatory behaviour) suggested that subjects had more comfortable, rewarding lives at pasture. Next, I review attention bias, another potential cognitive indicator of animal wellbeing. Attention to threat proves a promising method to quantify the emotional impacts of anthropogenic stressors. I then investigate a second example of human-induced environmental change: oceanic microplastic pollution. Microplastic exposure prevented hermit crabs from approaching and entering a new shell, which was better than their current shell. These results suggest that microplastics disrupt animal cognition (resource assessment and evaluation). Finally, I apply emotion theory to animal contests, and argue that emotions underpin virtually all non-reflexive behaviour. Because emotions generalise across contexts, my novel approach suggests that human activity has broader psychological impacts than usually recognised. These findings highlight how anthropogenic change can influence animal cognition and emotion, with practical applications for welfare and conservation.

Contents

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Crump, A., Jenkins, K., Bethell, E. J., Ferris, C. P., Kabboush, H., Weller, J., & Arnott, G. (2021). Optimism and pasture access in dairy cows. *Scientific Reports, 11*(1), 1-11. [Chapter Two]

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Crump, A., Arnott, G., & Bethell, E. J. (2018). Affect-driven attention biases as animal welfare indicators: Review and methods. *Animals, 8*(8), 136. [Chapter Four]

Glossary

Affect-driven attention bias (ADAB): An attention bias towards or away from emotional information that is influenced by the observer's affective state. Often labelled "attention bias" in the animal welfare literature.

Affective state: A temporary valenced state, e.g. emotions or moods.

Anthropocene: Proposed current geological epoch, covering the period in which humans have substantially modified Earth's ecosystems, biogeochemical cycles, and biodiversity. Possible start dates range from the megafauna extinctions that began around 50,000 years ago to the first atomic bomb test in 1945.

Arousal: Affective dimension of intensity or activation. Continuum from low to high.

Assessment: Evaluating the fitness costs and benefits of a stimulus.

Attention: The selective allocation of cognitive resources to particular information.

Attention bias: The preferential allocation of attentional resources towards one form of information over another.

Attention bias task (ABT): An experimental paradigm that presents subjects with stimuli and records how their attention is allocated. Examples covered here include looking time, emotional Stroop, dot-probe, emotional spatial cueing, and visual search tasks.

Attention to emotion: Attention allocated towards emotional stimuli.

Attention to threat: Attention allocated towards threatening stimuli.

Avoidance of threat: Attention allocated away from threatening stimuli.

Cognition: The mechanisms animals use to gather, process, store, and learn from information (e.g. judgement and attention).

Cognitive bias: In the animal welfare literature, an umbrella term for cognitive processes influenced by affective states, e.g., attention and judgement biases.

Compassionate conservation: Umbrella term for biodiversity conservation that accounts for the interests of individual animals, as well as the population as a whole.

Contest: Direct inter-individual interaction that determines access to an indivisible resource.

Decision: Based on judgements, the cognitive process of selecting a motor action.

Disengagement (of attention): The allocation of attention away from a stimulus previously attended to.

Emotion: Stimulus-directed affective state. Consists of behavioural, physiological, and cognitive components, and may occur outside awareness (cf. “Feeling”).

Engagement (of attention): The initial allocation of attention towards a stimulus. Limited attentional resources mean engagement to one stimulus may draw resources away from other tasks.

Experience effect: The tendency of previous contest outcomes to impact subsequent contest outcomes. In particular, previous contest winners typically initiate, escalate, and win subsequent contests (winner effects); previous contest losers typically avoid and lose subsequent contests (loser effects).

Feeling: Subjective, experiential element of affective states. Because animals’ feelings cannot be reported directly, we rely on indirect indicators that can be objectively measured, e.g. behaviour, physiology, and cognitive biases.

Incidental affective state: Affective state influencing an objectively irrelevant cognitive process.

Integral affective state: Affective state influencing an objectively relevant cognitive process.

Judgement: Based on sensory information and personal experience, cognitive inferences about the state of the world.

Judgement bias: A cognitive bias where affective state influences judgements about the affective value of ambiguous stimuli. Positive affective states are associated with optimistic judgements; negative affective states are associated with pessimistic judgements.

Judgement bias task: A task that uses judgements of ambiguous stimuli as an indicator of affective state. Typically, subjects are trained to react differently to two stimuli to achieve relatively positive- and negative-valence outcomes. Responses to subsequent presentations of ambiguous “probe” stimuli indicate whether subjects judge them more positively (optimistic responses) or negatively (pessimistic responses).

Learning: Previous exposure modifying behavioural responses to a stimulus.

Loser effect: The tendency of previous contest losers to avoid and lose subsequent contests.

Microplastic: Plastic particle < 5 mm in length or diameter.

Microplastic pollution: The introduction of microplastics to the environment.

Mood: Long-lasting affective state that reflects the cumulative impact of emotion over preceding days, weeks or months.

Motivation: Drives arising from internal signals that compel behaviour to meet basic biological needs, e.g., hunger and thirst.

Overt attention: A measurable proxy for attention, such as movements of the eye with respect to stimuli.

Personality: Behavioural and psychological traits with inter-individual variation but intra-individual consistency across time and contexts.

Primary microplastic: Industry-made microplastic particles.

Resource-holding potential (RHP): Multicomponent trait representing an animal’s ability to win contests. All else being equal, contestants with higher RHPs defeat rivals with lower RHPs.

Resource value (RV): The fitness benefit of a resource.

Secondary microplastic: Microplastic formed from the degradation of industry-made plastics > 5 mm in diameter.

Trait affect: Affect stable within individuals over time. A personality trait that does not encompass transient emotions or moods.

Valence: Affective dimension of "pleasantness". Continuum from negative (punishments) to positive (rewards).

Vigilance: Scanning the environment for potential threats (may occur in the absence of threatening stimuli).

Welfare: Three elements are often recognised: physical health and biological functioning, ability to lead a natural life, and psychological wellbeing. Prioritising the latter, I view good welfare as maximising positive affective states whilst minimizing negative ones.

Winner effect: The tendency of previous contest winners to initiate, escalate, and win subsequent contests.

Abbreviations and acronyms

5-CSRTT: Five-choice serial reaction time task.

ABT: Attention bias task.

ADAB: Affect-driven attention bias.

AIC: Akaike information criterion.

BCE: Before the Common Era.

COVID-19: Coronavirus disease 2019.

CRAN: Comprehensive R Archive Network.

CTRL: Control group.

D: Day.

Defra: Department for the Environment, Food, & Rural Affairs.

DM: Dry matter.

GLIM: Generalised linear mixed effects model.

GLM: General linear mixed effects model.

H: Hour.

HIREC: Human-induced rapid environmental change.

IQR: Inter-quartile range.

IRR: “Various Coefficients of Interrater Reliability and Agreement” R package.

K_F: Fleiss’ Kappa coefficient of agreement.

Km: Kilometre.

m: Metre.

M: Middle stimulus in a judgement bias task.

Min: Minute.

ML: Maximum likelihood.

N: Negative stimulus in a judgement bias task.

NN: Near-negative stimulus in a judgement bias task.

NP: Near-positive stimulus in a judgement bias task.

N-Unr: Unrewarded stimulus in a judgement bias task.

P: Positive stimulus in a judgement bias task.

PAS: Pasture access treatment.

PAS-first: Herd at pasture first.

PAS-second: Herd at pasture second.

PEN: Indoor housing treatment.

PLAS: Microplastic treatment.

P-Rew: Rewarded P stimulus in a judgement bias task.

P-Unr: Unrewarded P stimulus in a judgement bias task.

REML: Restricted maximum likelihood.

Rew: Rewarded stimulus in a judgement bias task.

RHP: Resource-holding potential.

RV: Resource value.

S: Second.

SD: Standard deviation.

Unr: Unrewarded stimulus in a judgement bias task.

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1 | General introduction

1.1 | The Anthropocene

Humans have modified virtually every habitat on Earth – often drastically (Ellis & Ramankutty 2008). Our ancestors' hunting and burning contributed to 65% of megafauna genera going extinct between 50,000 and 12,500 years ago (Barnosky *et al.* 2004). With the advent of agriculture around 10,000 BCE, a few plant and animal species underwent rapid morphological change, spread across the globe, and replaced lowland ecosystems (Ellis 2011, Ellis *et al.* 2013, Larson *et al.* 2014). In the last 250 years, the Industrial Revolution increased greenhouse gas emissions, population growth, urbanisation, and habitat destruction (Martinez 2005, Mays *et al.* 2008). From the mid-20th century, accelerating anthropogenic trends – increasing greenhouse gas emissions, global temperatures, land conversion, and pollution – exceeded natural variation earlier in the Holocene (Steffen *et al.* 2006, 2015). Many researchers believe that human activity defines a new geological epoch: the Anthropocene (Crutzen 2002, 2006, Crutzen & Stoermer 2000, Lewis & Maslin 2015, Steffen *et al.* 2015, Zalasiewicz *et al.* 2011; cf. Gibbard & Walker 2014).

As we transform the environment to suit our needs, we often fail to consider the needs of other species. Animals are adapted to the ecosystems that they evolved in (Robertson & Blumstein 2019). Human-induced rapid environmental change (HIREC) modifies or removes such environments (Hobbs *et al.* 2009, Radeloff *et al.* 2015, Sih *et al.* 2011). This favours species with existing traits suitable for the new conditions (e.g. invasive species or animals predisposed to domestication; Sih *et al.* 2011). Also favoured are taxa that express multiple phenotypes from a single genotype (i.e. phenotypic plasticity; Hendry *et al.* 2008), and those preadapted to rapid evolutionary change (e.g. species with short generation times and large genetic variation; Hendry *et al.* 2011). In a meta-analysis of over 3,000 effect sizes covering 68 systems, Hendry *et al.* (2008) found that phenotypic change is greater in anthropogenic contexts than natural contexts. However, HIREC has left other species with phenotypes poorly suited to present conditions, insufficient phenotypic plasticity to cope, and rates of evolution too slow to adapt (Sih *et al.* 2011). This evolution-environment mismatch impacts both the welfare of individual animals and the survival of populations.

1.1.1 The Anthropocene and Animal Welfare

There is no universal definition of “animal welfare” (Mellor 2016), but most conceptions coalesce around three themes (Fraser 2008, Fraser *et al.* 1997). First, animals with good welfare are physically healthy and functioning well (Lund & Algers 2003). This “biological functioning” viewpoint is common in industry and among veterinarians (Lund 2006, Te Velde *et al.* 2002). Second, animals with good welfare perform natural behaviours and lead natural lives (Browning 2020, Špinka 2006, Yeates 2018). This “natural lives” viewpoint thrives among the general public and animal rights advocates (Lund 2006, Te Velde *et al.* 2002). Third, animals with good welfare have many positive experiences and rarely suffer (Boissy *et al.* 2007, Dawkins 1990, Duncan 2004, Fraser & Duncan 1998, Robbins *et al.* 2018). I adopt this “psychological wellbeing” perspective and conceptualise welfare in terms of minimising suffering and maximising opportunities for positive experiences (see subsection 1.3.1).

How has HIREC impacted animals’ psychological wellbeing? Welfare scientists typically focus on animals under human care, particularly domesticated species. In terms of population size, these are some of the Anthropocene’s biggest winners. Humans and livestock constitute

96% of global mammal biomass (Laurance 2019). Based on these figures, however, only the biological functioning approach might suggest that the animals themselves have good welfare. Natural living proponents contend that anthropogenic trends, such as factory farming, laboratory experimentation, and designer breeding, are unnatural and, hence, impair welfare (Browning 2020, Yeates 2018). What about the psychological wellbeing perspective?

Despite often improving animal health, reproduction, and productivity, anthropogenic change has myriad negative impacts on mental wellbeing. Many captive animals are kept in environments that they are not adapted to cope with (Morgan & Tromborg 2007), which can lead to chronic stress (Wiepkema & Koolhaas 1993). In zoos, for example, taxa with large home ranges spend longer performing locomotor stereotypies than related species with smaller range sizes, suggesting that their space is insufficient (e.g. carnivores: Clubb & Mason 2003, 2007, Kroshko *et al.* 2016; and primates: Pomerantz *et al.* 2013). As well as human environments not meeting animals' needs, inbreeding and artificial selection can produce morphologies detrimental to psychological wellbeing. Many breeds of pedigree dog (*Canis lupus familiaris*), for instance, suffer painful and debilitating conditions that have arisen from inbreeding (Calboli *et al.* 2008, Leroy 2011) and selection for cosmetic traits (e.g. Asher *et al.* 2009, Packer *et al.* 2015, Steinert *et al.* 2019). From the psychological wellbeing perspective, good welfare also requires promoting positive experiences (Boissy *et al.* 2007, Webb *et al.* 2018, Yeates & Main 2008). Many captive environments restrict rewarding opportunities for personal agency (Špinka 2019), social interactions (Rault 2012), and highly motivated behaviours (Jensen & Pedersen 2008).

1.1.2 The Anthropocene and Biodiversity Loss

HIREC poses five major ecological threats (Sih *et al.* 2011). First, habitat degradation, fragmentation, and loss (Tilman *et al.* 1994). This is currently the greatest threat to biodiversity (Pimm & Raven 2000). As well as reducing the environment's carrying capacity, habitat loss prevents gene-flow between populations (Laurance *et al.* 2008). Second, invasive species (Hulme 2009, Lockwood *et al.* 2007, Salo *et al.* 2007). Native species have not co-evolved with invaders, leaving them potentially vulnerable to novel competitors, predators, and pathogens (Sih *et al.* 2010). Examples include invasive goats (*Capra aegagrus hircus*) overgrazing and outcompeting Galapagos giant tortoises (*Chelonoidis nigra*; Carrion *et al.* 2011), and invasive red foxes (*Vulpes vulpes*) extirpating Australian marsupials (e.g. eastern bettong, *Bettongia gaimard*; Radford *et al.* 2018). Third, unsustainable harvesting (Reeve 2014). Unlike other extinction drivers, this directly reduces wild population sizes (e.g. overhunting: Ripple *et al.* 2016; overfishing: Burgess *et al.* 2013; exotic pet trade: Tella & Hiraldo 2014). Fourth, pollution (Nabi *et al.* 2018). This includes both chemical contaminants and, more broadly, changes in environmental parameters, such as light and noise. For example, microplastic pollution impacting marine animal behaviour, development, and survival (Au *et al.* 2015, Cole *et al.* 2015, Crump *et al.* 2020b), and coastal light pollution attracting turtle hatchlings inland (Truscott *et al.* 2017, Tuxbury & Salmon 2005). Fifth, climate change (IPCC 2007, Thomas *et al.* 2004). Habitable environments are becoming too warm (Dirnböck *et al.* 2011), biological events are shifting earlier in the year (Both *et al.* 2006, Forister & Shapiro 2003, Pulido 2007), and species with temperature-dependent sex determination are developing skewed sex ratios (Morjan 2003). Synergistic effects between these five extinction drivers – such as habitat fragmentation preventing range shifts under climate change – can prove especially deadly (Barnosky *et al.* 2011, Brook *et al.* 2008, Stork 2010).

Leading biologists have concluded that, through the five extinction drivers, humanity is causing Earth's sixth mass extinction event (Barnosky *et al.* 2011, Chapin *et al.* 2000). We have lost 322 terrestrial vertebrates in the last 500 years (Ceballos *et al.* 2010, Collen *et al.* 2009). Thirty-two percent of the remaining species are declining in population size and geographical range (Ceballos *et al.* 2017). Taxa with small ranges, large territories, large body size, and slow reproduction are especially vulnerable (Cardillo *et al.* 2008, Davidson *et al.* 2009, Lee *et al.* 2011, Öckinger *et al.* 2010). Invertebrates have been less studied, but two-thirds of monitored populations have declined by at least 45% (Dirzo *et al.* 2014). Even conservative estimates indicate an overall extinction rate 100 to 1,000 times greater than the background rate (Barnosky *et al.* 2011, Ceballos *et al.* 2015). This "Anthropocene defaunation" is not only a consequence of environmental change, but also a cause. Biodiversity loss disrupts crucial ecosystem functions, with huge economic and social costs (Dirzo *et al.* 2014, Hooper *et al.* 2018).

1.1.3 Summary

Humans are changing the world. I argue that this anthropogenic change can compromise animal welfare and contribute to biodiversity loss. However, the effects on animal behaviour are poorly understood (Sih *et al.* 2011, Wong & Candolin 2015). The psychological states underpinning behaviour – even less so. In this thesis, I explore the effects of anthropogenic change on two mental faculties: animal cognition and emotions.

1.2 | Cognition

I follow Shettleworth's (1998, p. 5) broad definition of cognition: "the mechanisms by which animals acquire, process, store and act on information from the environment". This is notably similar to Ulric Neisser's conception in *Cognitive Psychology*, the field's foundational text. For Neisser (1967, p. 6), "'cognition' refers to all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered, and used." Shettleworth's and Neisser's conception encompasses perception, attention, judgement, decision-making, memory, and learning. It not only accepts animals into the cognition club; it makes rejecting them inconceivable. The definition is vague, but various prominent researchers (e.g. Destrez *et al.* 2013b, Meehan & Mench 2007, Mendl *et al.* 2009) have accepted this as the price for inclusivity and experimental accessibility.

Other researchers define cognition differently, and the term has no generally agreed meaning (Bayne *et al.* 2019). Perception researchers, for instance, debate whether processes are perceptual or cognitive (e.g. Firestone & Scholl 2016), despite perceptual psychology being a cognitive science. Others distinguish between cognition and associative learning (e.g. Buckner 2015). This approach neglects the potential complexity of associations (Ginsburg & Jablonka 2019) and encourages endless associative arguments for putatively cognitive abilities (Byrne & Bates 2006, Heyes 2012). According to Broom and Fraser (2015, p. 362), cognition means "having a representation in the brain", whether the representational subject is present or not. Again, this conception excludes processes that cognition usually encompasses (e.g. resource value assessments; Arnott & Elwood 2008). Specifying both function (*having a representation*) and mechanism (*in the brain*) is also counterintuitive. Does a representation count without a brain (Parise *et al.* 2020)? What is a representation anyway (Ramsey 2017)? Conservative definitions of cognition inevitably raise such issues, because cognition is not a natural kind (Allen 2017). There is no biologically meaningful line between "cognitive" and non-cognitive. Hence, I treat cognition as information-gathering and processing (Shettleworth 1998).

In this thesis, I focus on two phases of cognitive processing: information-gathering (including perception, interoception, and attention) and acting on information (including judgements and decision-making). First, information-gathering. Animals cannot respond to a stimulus without detecting it. Perception is the sensory process of acquiring information from the external environment (e.g. sight, sound, and smell), whilst interoception is the acquisition of internal information (e.g. hunger, thirst, and fatigue; Paul *et al.* 2020). However, information-gathering is constrained: animals do not have infinite cognitive resources to collect all potential information from their environment (Leavell & Bernal 2019). Attention describes the selective allocation of resources to particular information (Bar-Haim *et al.* 2007, Crump *et al.* 2018, Yiend 2010). For example, humans have an attention bias to threat – we prioritise attending threatening stimuli over non-threatening stimuli (Bar-Haim *et al.* 2007).

Second, acting on information. In human psychology, judgements are inferences about the state of the world, whereas decision-making is the process of action selection (Goldstein & Hogarth 1997). Mendelson *et al.* (2016) applied this framework to animals (Figure 1; see also Blumstein & Bouskila 1996). Based on information perceived and interoceived, judgements include cognitive processes like discrimination (distinguishing between different stimuli), categorisation (assigning similar stimuli to a set and distinguishing between sets), and assessment (evaluating the fitness benefits and costs of stimuli; Mendelson *et al.* 2016). Judgement researchers typically investigate how accurate judgements are, and how quickly they are updated (Tenenbaum *et al.* 2011). Based on these judgements, decisions include cognitive processes like preference (ranking stimuli), choice (selecting a course of action), and drive (investment expended; Mendelson *et al.* 2016). Decision-making researchers investigate the fitness benefits of decisions (Varian 2014). These cognitive processes are manifested in action (i.e. behaviour).

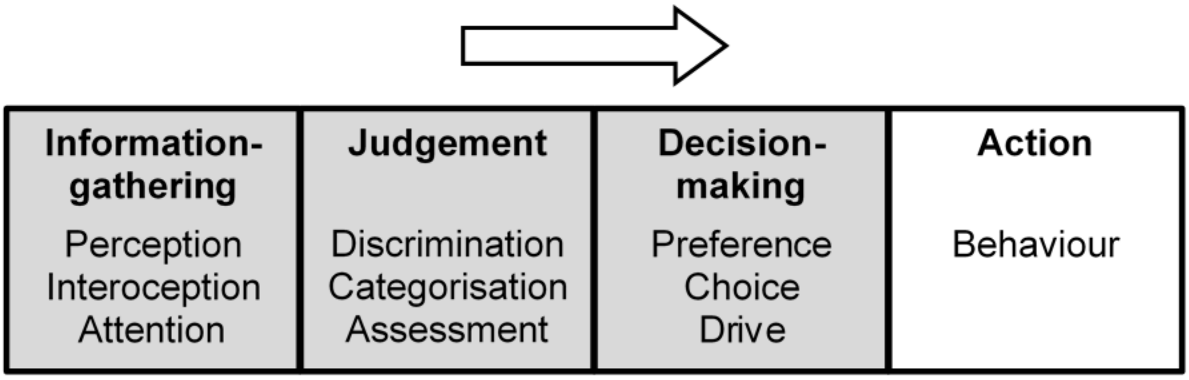


Figure 1. The cognitive processes (grey boxes) that underpin animal behaviour (white box; Mendelson *et al.* 2016).

Animals have evolved these cognitive abilities – gathering and acting on information – to overcome challenges specific to their environments (Morand-Ferron *et al.* 2016, Pritchard *et al.* 2016). However, HIREC presents animals with challenges and environments not faced during evolutionary history, which they may not be adapted to (Cox & Lima 2006). First, perceptual, interoceptive, and attentional systems may leave animals unable to gather information effectively in new environments. Second, under novel conditions, judgements can be inaccurate and decision-making can fail to maximise fitness. Conversely, behaviour is an interface with the environment. Modifying behaviour can bridge the gap between animals' existing traits and the new environment's adaptive optimum (Sih *et al.* 2011, Tuomainen & Candolin 2011). Cognition provides a means for animals to alter their behavioural responses to HIREC within a single lifetime (Sih *et al.* 2011). Generalists able to exploit novel environments have achieved unprecedented success in the Anthropocene (e.g. black rats, *Rattus rattus*, and brown rats, *R. norvegicus*: Feng & Himsworth 2014). I argue that HIREC can impair cognition, and cognition can facilitate adaptation to HIREC.

1.2.1 Cognition and Animal Welfare

HIREC may interact with animals' cognitive abilities during each phase of the cognitive process, and subsequently impact welfare. Cognition can also indicate animal welfare; I discuss this in subsection 1.3.1.

First, information-gathering. On the one hand, captive animals often cannot avoid or escape perceptual stimuli that they have evolved to find aversive (Morgan & Tromborg 2007). Persistent negative states result, such as human presence stressing zoo animals (Hosey 2000, Davey 2007, Fernandez *et al.* 2009). On the other hand, providing valuable resources scarce in evolutionary time can induce extremely positive states, as animals' perceptual and reinforcement systems have evolved to reward their acquisition. Sugar is an obvious example. However, the resulting over-consumption causes obesity (e.g. humans: Ludwig *et al.* 2001; rats: Kanarek & Orthen-Gambill 1982), compromising welfare in the longer-term. Artificial selection raises another welfare issue – a disconnect between domesticated phenotypes and interoception. For example, under extreme selection to maximise milk production, today's high-yielding dairy cows (*Bos taurus*) cannot eat enough during lactation to maintain a positive energy balance (Butler 2005). As a result, cows are hungry for weeks after parturition – a major welfare issue.

Second, acting on information. An example of impaired judgement arises from unnatural group sizes in captivity. The wild ancestors of pigs (*Sus scrofa domesticus*) lived in small groups, but commercial farms often maintain much larger aggregations (Rault 2012). Individuals in these unnaturally large groups cannot discriminate all their conspecifics to develop a stable dominance hierarchy, causing persistent aggressive behaviours like tail-biting (d'Eath *et al.* 2010, Turner *et al.* 2020). Human environments also limit animals' agency and ability to make decisions about their lives (Špinka 2019). In preference tests, captive animals often choose options unavailable in many commercial settings (Fraser &

Nicol 2018, Jensen & Pedersen 2008, Kirkden & Pajor 2006, Rasmussen *et al.* 2020). Dairy cattle given the choice between pasture and indoor housing, for instance, usually spend longer at pasture, particularly at night (Charlton *et al.* 2011a, 2013, Falk *et al.* 2012, Legrand *et al.* 2009, Shepley *et al.* 2017). Motivation tests, where options require energetic investment, have also been developed to measure drive (Fraser & Nicol 2018, Jensen & Pedersen 2008, Kirkden & Pajor 2006, Rasmussen *et al.* 2020). When pasture access requires walking long distances (Charlton *et al.* 2013, Motupalli *et al.* 2014) or pushing weighted doors (von Keyserlingk *et al.* 2017), dairy cows appear to value pasture as highly as fresh food.

1.2.2 Cognition and Biodiversity Loss

Conservation biologists and fundamental ethologists typically treat cognition as a "black box" and focus on behavioural outputs (cf. Barrett *et al.* 2019, Greggor *et al.* 2014, 2020, Proppe *et al.* 2017). However, cognition may underpin numerous cases of maladaptive animal behaviour in anthropogenic environments (see Ehrlich & Blumstein 2018, Greggor *et al.* 2019, Robertson *et al.* 2013, Schlaepfer *et al.* 2002).

First, information-gathering. Inability to detect HIREC can lead to biodiversity loss, such as billions of birds hitting glass buildings every year (Sabo *et al.* 2016). Another example is animals unable to detect invasive predators (the naïve prey hypothesis; Cox & Lima 2006). For example, New Zealand freshwater crayfish (*Paranephrops zealandicus*) can detect chemical cues from native eels (*Anguilla dieffenbachii*), but not introduced brown trout (*Salmo trutta*; Shave *et al.* 1994). Tadpoles can detect chemical cues from native turtles (European pond turtle, *Emys orbicularis*; Spanish terrapin, *Mauremys leprosa*), but not introduced red-eared sliders (*Trachemys scripta*; Polo-Cavia *et al.* 2010). Moreover, human activity may disrupt animals' ability to perceive and attend fitness-relevant features of their environment. Anthropogenic noise, for example, can distract animals from ecologically important stimuli (Chan *et al.* 2010, Nowacek *et al.* 2007, Shannon *et al.* 2016), whilst eutrophication reduces visual and chemical signal transmission, increasing hybridisation in freshwater fish (Rosenthal & Stuart-Fox 2012).

Second, acting on information. For instance, some species cannot discriminate conspecific mates from closely related – but historically allopatric – heterospecifics. If both species become sympatric under HIREC (e.g. due to human introductions or range shifts), hybridisation can ensue (Rosenthal 2013). Sika deer (*Cervus nippon*), for example, do not distinguish conspecific vocalisations from the calls of red deer (*C. elaphus*; Wyman *et al.* 2014), causing extensive hybridisation where sika deer have been introduced into red deer habitat (McDevitt *et al.* 2009, Senn & Pemberton 2009). Some species even prefer heterospecific mates to conspecifics (Pfennig 2007). Female plains spadefoot toads (*Spea bombifrons*) choose Mexican spadefoot (*Spea multiplicata*) males as mates under certain environmental conditions (Chen & Pfennig 2020). In such cases, animals make accurate judgements but potentially maladaptive decisions.

By underlying behavioural flexibility, cognitive flexibility also facilitates rapid responses to HIREC. Around Kibale Forest, for example, chimpanzees (*Pan troglodytes*) raid maize at night, when the farms are unguarded (Krief *et al.* 2014). Chimpanzees at Bulindi eat crops when wild fruit ability is low (McLennan 2013). In both cases, the chimpanzees recognise the risks and rewards of crop-raiding, and have learnt to respond appropriately (Hockings *et al.* 2015). Indeed, cognitive capacity and flexibility predict phylogenetic success in the Anthropocene. Comparative analyses reveal that invasive mammals and birds are big-brained and behaviourally flexible (Sol *et al.* 2005, 2008), although correlation does not demonstrate causation.

1.2.3 Summary

HIREC has left many species with cognitive abilities not adapted to their current environment. This can be detrimental to both animal welfare and population survival. Nevertheless, some species' cognitive flexibility allows them to modify their behaviour and respond rapidly to new anthropogenic selection pressures.

1.3 | Emotion

Until recently, it was psychological and ethological taboo to discuss animals' emotions and moods ("affective states"; see Anderson & Adolphs 2014, Boissy *et al.* 2007, Crump *et al.* 2020a, Désiré *et al.* 2002, Gygax 2017, Kremer *et al.* 2020, Ledoux 2012, Mendl *et al.* 2010, Mendl & Paul 2020, Panksepp 2011, Paul & Mendl 2018, Paul *et al.* 2020, Webb *et al.* 2018). "Behaviourists" believed that studying affective states was unscientific, because mental phenomena could not be directly accessed (Fraser 2009, Skinner 1953). Especially in the last 30 years, however, animal emotions and moods have become legitimate objects of scientific inquiry (Kremer *et al.* 2020, Mendl *et al.* 2010). Many researchers operationalise emotions as short-term states elicited by stimuli (or their predictors) that animals will work to acquire (rewards; e.g. prey) or avoid (punishments; e.g. predators; Carver 2001, Ledoux 2012, Rolls 2005). Moods are longer-term states, which represent the cumulative average of emotions over time (Nettle & Bateson 2012, Trimmer *et al.* 2013). These functional definitions apply to any organism with a central nervous system (Anderson & Adolphs 2014). Animal welfare scientists, neuroscientists, and psychopharmacologists now recognise that affective states play a key role in cognition and behaviour (Mendl *et al.* 2010, Mendl & Paul 2020).

Two main dimensions characterise affective states: valence and arousal (Mendl *et al.* 2010, Posner *et al.* 2005, Russell 1980, 2003; Figure 2). Valence ranges from positive to negative, encapsulating the fitness benefits and costs associated with a stimulus (either anticipated or actual; Mendl & Paul 2020). Arousal (emotional intensity) indicates stimulus importance or urgency. High-arousal affective states divert attentional resources to the stimulus (Storbeck & Clore 2008) and predispose vigorous action (Bach & Dayan 2017). As well as emotions and moods, valence and arousal define sensations (e.g. pain) and interoception (e.g. hunger; Paul *et al.* 2020). Burgdorf and Panksepp (2006) hypothesised that positive-valence, high-arousal states represent the activation of a reward acquisition system, whereas negative-valence, high-arousal states represent the activation of a punishment avoidance system. By conceptualising affective states in terms of reward and punishment, this dimensional approach captures their evolutionary function and avoids categorical labels that can lead to anthropomorphism (e.g. Panksepp 2011).

Emotions are elicited by appraisals: evaluations of stimuli, their context, and their personal significance (Moors *et al.* 2013). Scherer (2001) proposed that humans sequentially appraise stimulus novelty, intrinsic valence, congruence with personal goals, outcome probability, discrepancy from expectations, situation controllability, other individuals’ responsibility, and whether potential responses are socially acceptable. Appraisal outcomes determine and differentiate emotions (Moors 2013), with continuously-updated re-appraisals regulating the response (Uusberg 2019). Other mammals, birds, and fish also appear to appraise stimuli (Désiré *et al.* 2002, Faustino *et al.* 2015). In lambs (*Ovis aries*), for example, stimulus novelty, discrepancy from expectations, controllability, and social context impact physiology and behaviour (Désiré *et al.* 2004, 2006, Greiveldinger *et al.* 2007, 2009, 2011, Veissier *et al.* 2009). These inferred appraisals elicit flexible emotional responses, which account for current conditions and personal circumstances, as well as intrinsic stimulus characteristics.

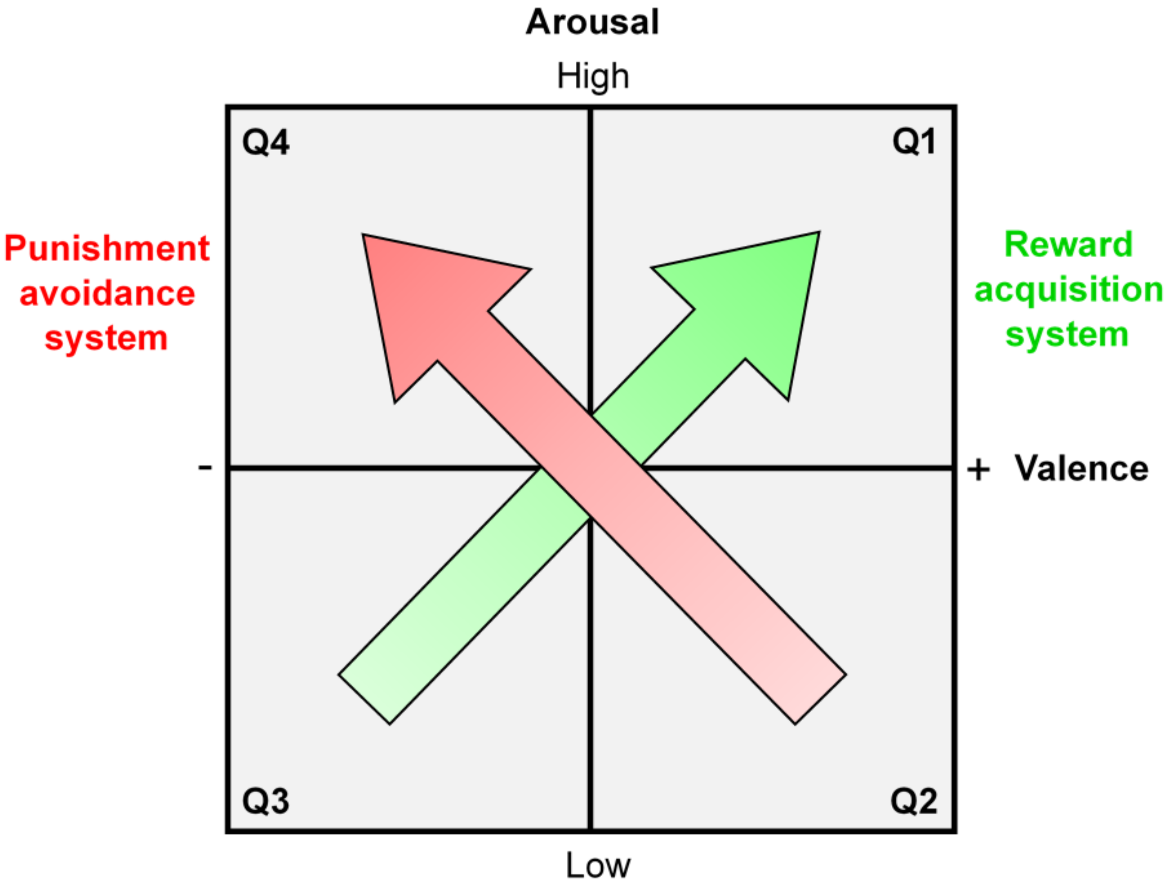


Figure 2. Valence and arousal define affective states (grey box), which encompasses emotions and moods (Crump *et al.* 2020a, Mendl *et al.* 2010). Moving from Q3-Q1 is increasingly appetitive; Q2-Q4 is increasingly aversive.

Emotions have multiple components that can be empirically measured (Lerner *et al.* 2015, Paul *et al.* 2020; Figure 3). These include changes in (1) cognition: information-gathering and processing; (2) drive (motivation): manifested as the work animals will invest to access reward or avoid punishment; and (3) neurophysiology: central and peripheral nervous system activity, and neuroendocrine function. Such changes facilitate the performance of (4) behaviour, producing an organism-level response to rewards and punishments (Damasio &

Carvalho 2013, LeDoux 2012, Nesse & Ellsworth 2009). Threatening stimuli, for instance, impact (1) cognition: increasing attention to the threat; (2) drive: maximising the work animals will invest in performing freeze, fight, or flight responses; and (3) neurophysiology: activating both the sympathetic nervous system and hypothalamic-pituitary-adrenal axis. These changes prepare the individual for (4) behaviour: avoiding, attacking or escaping the threat.

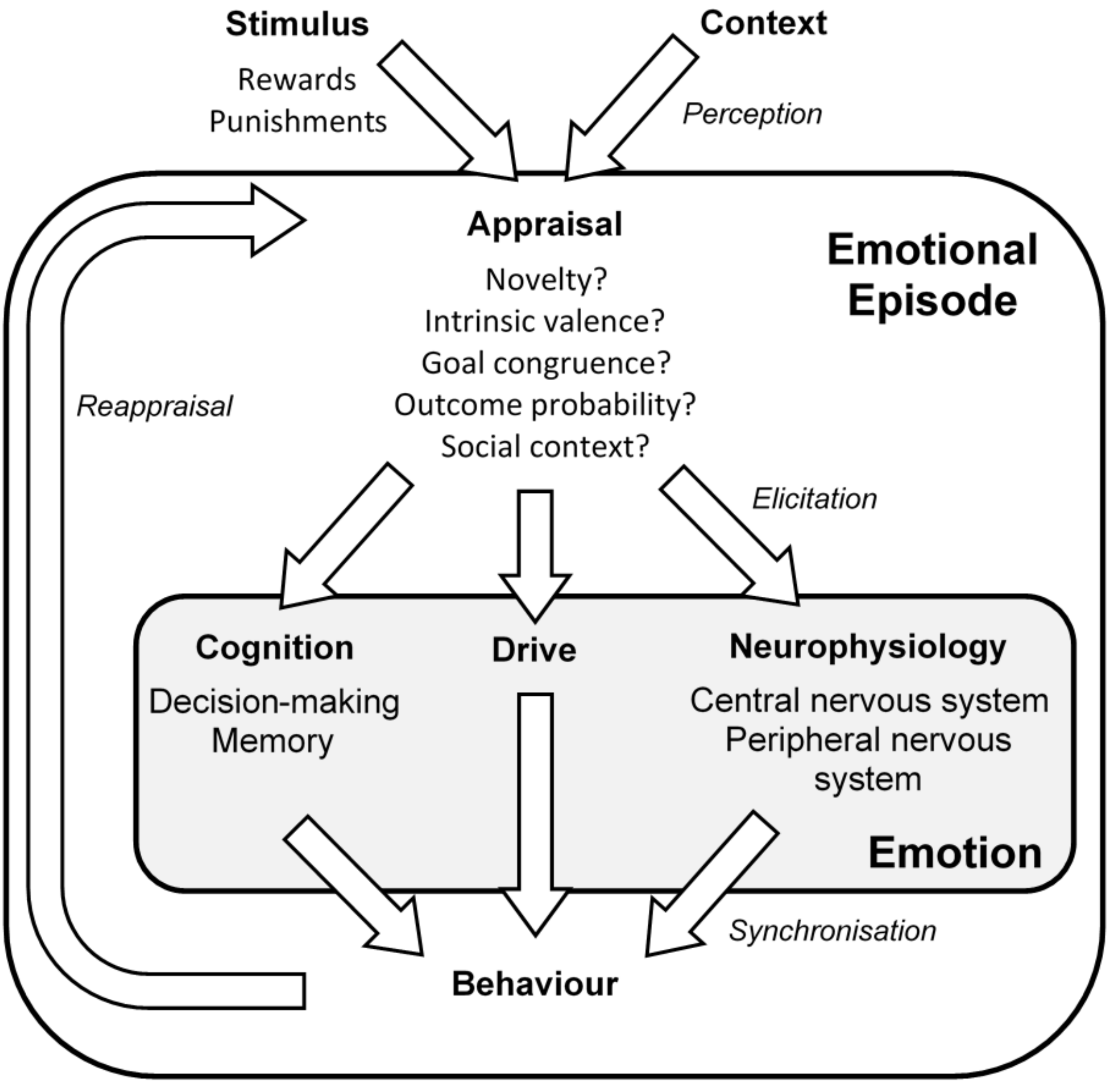


Figure 3. An emotional episode (white box; Crump et al. 2020a). Appraisals of stimuli, their context, and their personal significance elicit the emotion (grey box), whose components include cognition, drive, and neurophysiology. These components govern the expression of behaviour. Conscious "feelings" are another potential component, but not essential.

Conscious feelings, another potential emotion component, cannot be directly measured. Humans describe feelings through language, which is not possible for animals. As a result, animal researchers usually study other emotion components and remain agnostic about feelings (Kremer *et al.* 2020, Paul & Mendl 2018, Paul *et al.* 2020; for a pro-feelings approach, see Fraser 2009, Panksepp 2011, Wemelsfelder 1997). Indeed, many human psychologists recognise unconscious emotion, where the measurable components occur without corresponding feelings (Winkielman & Berridge 2004). For example, Winkielman *et al.* (2005) showed people positive or negative facial expressions. The images appeared too briefly for conscious awareness. When subsequently offered a novel drink, subjects shown the positive expression poured more, drank more, and paid more than subjects shown the negative expression. Self-reported affective states did not differ between treatments, indicating a dissociation between emotion and feeling. In animals, the relationship between feeling and non-feeling emotion components is an important area for future research (Birch 2020, Birch *et al.* 2020b, Boly *et al.* 2013, Paul *et al.* 2020). However, for present purposes, I view emotions as functional states elicited by rewards and punishments. They may or may not be accompanied by feelings.

1.3.1 Emotion and Animal Welfare

Valence underpins the psychological wellbeing conception of animal welfare (Mendl *et al.* 2010). From this perspective, welfare reflects the balance of positive and negative valence (Boissy *et al.* 2007, Robbins *et al.* 2018, Webb *et al.* 2018). As such, quantifying the psychological component of affective states is a core challenge of animal welfare science.

Affective states can be investigated through both experimental manipulations and observational studies. Researchers use rewards to induce positive emotions, such as food, enrichment, and social contact (Boissy *et al.* 2007). Negative-valence interventions are also possible with punishments like food deprivation, electric shocks, and social isolation (Deakin 1997). However, in both positive and negative emotion induction experiments, the resulting affective state can be unclear (Deakin 1997). In addition to physical manipulations, pharmacological treatment can induce positive- and negative-valence states (Neville *et al.* 2020). For relatively minor treatments, individual rewards or punishments typically induce emotions, whereas multiple stimuli over longer periods induce moods (Mendl *et al.* 2010. Nettle & Bateson 2012, Trimmer *et al.* 2013).

If the goal of a study is to infer (observe) animals' emotions, rather than induce them, the measurable components of an emotional episode can indicate valence (Kremer *et al.* 2020). This includes changes in (1) cognition: attention, judgement, and memory biases (Paul *et al.* 2005); (2) drive: the work animals will invest to access reward or avoid punishment (Fraser & Nicol 2018, Jensen & Pedersen 2008, Kirkden & Pajor 2006); (3) neurophysiology: brain, neuroendocrine, and peripheral nervous system activity (LeDoux 2012, Panksepp 2011); and (4) behaviour: approach, exploration, and play are often positively valenced, whereas avoidance, hiding, and self-directed behaviours are often negatively valenced (Boissy *et al.* 2007). Simultaneously measuring multiple components usually gives the most robust results (Kremer *et al.* 2020).

Behaviour and physiology are the most popular indicators of animals' psychological wellbeing (Appleby *et al.* 2011, Veerasamy *et al.* 2011). These present problems, though, because behaviour is often species-specific, difficult to interpret, and varies between individuals (personality; Sih *et al.* 2004). It may only highlight extremes of welfare and can become dissociated from affective state, as in stereotypies (e.g. Higham *et al.* 2009). Physiology, meanwhile, fluctuates with activity level and circadian rhythms, often signalling arousal rather than valence (see Mendl *et al.* 2010). Moreover, behavioural and physiological welfare indicators have traditionally focused on negative affective states, but good welfare also requires recognizing and promoting positive states (Boissy *et al.* 2007). Additional measures are, therefore, needed.

A promising avenue of research for measuring affective states in animals comes from cognitive psychology. In humans, theory and methods to investigate the relationship between affective state, cognition, and subjectively experienced feelings are well established. For example, people in negative-valence states interpret ambiguous information more pessimistically, allocate more attention to potential threats, and recall more negative memories than happy people (Paul *et al.* 2005). In animal welfare science, affect-modulated cognition is termed cognitive bias. Affect-linked biases in judgement, attention, and memory have all been demonstrated in animals (for reviews and meta-analyses, see Baciadonna & McElligott 2015, Bethell 2015, Crump *et al.* 2018, Lagisz *et al.* 2020, Mendl *et al.* 2009, Mendl & Paul 2020, Neville *et al.* 2020, Paul *et al.* 2005, Roelofs *et al.* 2016).

1.3.2 Emotion and Biodiversity Loss

Conservationists rarely consider animal emotions. Unlike welfare scientists, they prioritise populations and ecosystems over individuals (Soulé 1985). A controversial example is culling invasive and surplus animals, using methods widely considered inhumane (Littin 2010, Littin *et al.* 2004). As well as ensuring that remaining individuals survive (Sih *et al.* 2010), this practice tends to be cheaper and less time-consuming than humane methods, maximising available resources (Lynch & Blumstein 2020). However, conservationists' neglect of individuals has recently been challenged.

Compassionate conservation aims to achieve conservation goals, whilst eliminating or minimising negative outcomes for individual animals (Bekoff 2013, Wallach *et al.* 2018). Practitioners differ in their approaches; many justify their stance through virtue ethics (i.e. prioritising the actor's intentions; e.g. Wallach *et al.* 2018), but often implicitly rely on deontological ethics (i.e. animals have intrinsic rights; Driscoll & Watson 2019). However, many compassionate conservationists adopt the outcome-based psychological wellbeing approach to animal welfare (Johnson *et al.* 2019; see also "conservation welfare": Beausoleil 2020, Beausoleil *et al.* 2018). These practitioners' twin goals are conserving populations and maximising impacted individuals' psychological wellbeing. Affective states, thus, underpin this approach to compassionate conservation. However, it remains rarely practised and contested by traditional conservationists (e.g. Oommen *et al.* 2019).

1.3.3 Summary

Emotions are states elicited by rewards and punishments. This functional definition does not allow us to infer conscious experience but facilitates measuring affective states in animals. As components of an emotional episode, neurophysiology, cognition, and behaviour can indicate animals' affective state. These components are, therefore, widely studied as welfare indicators. Conversely, conservation biologists rarely consider animals' affective states. This is an ethically important and potentially fruitful avenue of research.

1.4 | Thesis Outline

In this thesis, I explore how anthropogenic change impacts animal cognition and emotion. I discuss one context relevant to captive animal welfare, and another context relevant to biodiversity loss.

The first experiment explores how full-time indoor housing impacts a cognitive measure of psychological wellbeing – judgement bias – in dairy cows (Crump *et al.* 2019a, b, 2021). Cattle in Europe and the United States are increasingly housed indoors year-round (USDA 2016, Van den Pol *et al.* 2015). Even cows with pasture access are usually kept inside during the winter and around calving. However, welfare scientists and dairy consumers are concerned that full-time housing impacts welfare (Arnott *et al.* 2017, Charlton & Rutter 2017). For Chapters Two and Three, I investigated how pasture influences cattle cognition and behaviour. I recorded 29 cows' judgement bias, lying behaviour, and step counts during three weeks of overnight pasture access and three weeks of full-time indoor housing. These data indicate whether pasture access matters for psychological wellbeing.

I then move on from judgement to consider attention. In Chapter Four, I review studies investigating whether attention biases indicate affective state in animals (Crump *et al.* 2018). Although research is limited, evidence has been found in several species, especially primates and livestock. These studies are discussed in relation to tasks developed for measuring attention in humans. I also identify findings from human psychology that could be applied to animals, particularly species not studied before, and recommend incorporating additional measures into attention bias paradigms (e.g. ear movements). I conclude that attention bias is a promising welfare indicator. However, whilst judgement bias indicates general valence, attention may reveal more specific emotions and motivations.

Chapter Five describes an experiment investigating the effects of HIREC on animal cognition (Crump *et al.* 2020b). The anthropogenic change is oceanic microplastic pollution, and the cognitive process is hermit crab shell selection. This is a crucial survival behaviour, because good shells increase growth, reproduction, and survival. To investigate the impact of microplastic exposure, I kept common European hermit crabs (*Pagurus bernhardus*) in tanks containing either polyethylene spheres (a common microplastic pollutant) or no plastic (control) for five days. I then moved the hermit crabs into low-quality shells and offered them alternative high-quality shells. As information-gathering and resource assessment underpin shell selection, this is the first study investigating whether microplastics disrupt animal cognition. The findings have implications for whether HIREC contributes to biodiversity loss.

Whilst cognition is well-studied in wild animals, behavioural ecologists and conservation biologists rarely consider animal emotion. In Chapter Six, I review the evidence that emotions underpin animals' resource assessments, decision-making, and behaviour, explaining existing results and generating new predictions (Crump *et al.* 2020a). Contest behaviour illustrates this insight. Rivals weigh the benefits of winning resources against the probability of incurring costs. I liken these assessments to emotional appraisals and suggest that a central affective state determines contest decisions and behaviour. More generally, I consider how emotions carry over across behavioural contexts to influence unrelated assessments and decisions. I argue that animal behaviour researchers should consider these cross-context effects.

2 | Does full-time housing compromise emotional wellbeing in dairy cattle?

Published as:

Crump, A., Jenkins, K., Bethell, E. J., Ferris, C. P., Kabboush, H., Weller, J., & Arnott, G. (2021). Optimism and pasture access in dairy cows. *Scientific Reports, 11*(1), 1-11.

Crump, A., Jenkins, K., Bethell, E. J., Ferris, C. P., Kabboush, H., O'Connell, N. E., Weller, J., & Arnott, G. (2019). Is the grass half-full? Investigating optimism as a welfare indicator for dairy cows with and without pasture access. *Pharmacological Reports, 71*(6), 1308.

Abstract. Allowing dairy cattle to access pasture can promote natural behaviour and improve their health. However, the psychological benefits are poorly understood. I compared a cognitive indicator of emotion in cattle either with or without pasture access. In a repeated-measures crossover experiment, I gave 29 Holstein-Friesian dairy cows 18 days of overnight pasture access and 18 days of full-time indoor housing. To assess emotional wellbeing, I tested cows on a spatial judgement bias task. Subjects learnt that buckets at one location were rewarded, whereas buckets at another location were not. I then presented cows with "probe" buckets intermediate between the trained locations. Approaching the probes reflected an expectation of reward under ambiguity – an "optimistic" judgement bias, suggesting positive emotional states. I analysed the data using linear mixed effects models. There were no treatment differences in latency to approach the probe buckets, but cows approached the known rewarded bucket slower when they had pasture access than when they were indoors full-time. My results indicate that cattle with pasture access value known rewards less than cattle housed indoors full-time, suggesting that their environments are comparatively

rewarding. Pasture may, therefore, induce more positive emotional states than cubicle housing.

2.1 | Introduction

As global consumer demand grows, dairy farming will continue to intensify (Barkema *et al.* 2015). Housing cattle indoors year-round reduces labour inputs, facilitates the provision of high-energy diets, and increases milk yield without increasing farm size (Burow *et al.* 2013a, Robbins *et al.* 2016). Indoors, cows are also better protected against gastrointestinal parasites (Charlier *et al.* 2005) and inclement weather (Van Iaer *et al.* 2014). As a result, the percentage of European and North American dairy cattle with pasture access is decreasing (USDA 2016, van den Pol *et al.* 2015). Across Europe, there is substantial variation in management. An estimated 98% of Irish and 92% of British dairy farms operate pasture-based systems, compared to only 20% in Czechia, less than 10% in Greece, and virtually none in Bulgaria (van den Pol *et al.* 2015). In the United States, just 34% of dry cows and 20% of lactating cows are let out to pasture (USDA 2016). Even herds with pasture access are usually housed indoors over the winter and around calving.

However, full-time housing raises animal welfare concerns (reviewed by Arnott *et al.* 2017, Charlton & Rutter 2017, Mee & Boyle 2020, Phillips *et al.* 2013, Smid *et al.* 2020). Compared to pasture, surfaces tend to be more abrasive for lying and locomotion (Crump *et al.* 2019a). Indoor housing is a risk factor for hock lesions (Burow *et al.* 2013b), lameness (Haskell *et al.* 2006, Olmos *et al.* 2009, Wagner *et al.* 2018), and mastitis (Goldberg *et al.* 1992, Washburn *et al.* 2002), as well as injuries from slipping on slurry-covered concrete (van der Tol *et al.* 2005). These health issues are putatively painful for cattle (Broom &

Fraser 2015, Polsky & von Keyserlingk 2017) and contribute to higher mortality in herds without pasture access (Alvåsen *et al.* 2012, 2014, Burow *et al.* 2011, Thomsen *et al.* 2006). In terms of behaviour, indoor housing restricts movement and limits cows' behavioural repertoire (Ventura & Croney 2018), potentially preventing the expression of highly motivated behaviours. Preference testing indicates that cattle given the choice spend longer at pasture, especially at night (Charlton *et al.* 2011a, Falk *et al.* 2012, Kismul *et al.* 2018, Legrand *et al.* 2009, Shepley *et al.* 2017), although this effect may be reversed for animals reared indoors (Charlton *et al.* 2011b). In motivation tests, cows are prepared to incur a cost for pasture access, such as walking long distances (Charlton *et al.* 2013, Motupalli *et al.* 2014) or pushing weighted doors (von Keyserlingk *et al.* 2017). Consumers also value the perceived welfare benefits of pasture-based systems (Cardoso *et al.* 2014, Ellis *et al.* 2009, Schuppli *et al.* 2014).

Whilst the health, behavioural, and motivational costs of full-time housing are well-documented, the emotional impact is poorly understood (Ede *et al.* 2020, Mee & Boyle 2020). In humans, positive emotions cause more optimistic judgements about ambiguous stimuli ("judgement bias"; Blanchette & Richards 2010, Everaert *et al.* 2017, Hirsch *et al.* 2016, Schoth & Liossi 2017, Stuijfzand *et al.* 2018). Optimism also indicates emotional wellbeing in animals (Harding *et al.* 2004), from primates to insects (reviews and meta-analyses: Bethell 2015, Lagisz *et al.* 2020, Mendl *et al.* 2009, Neville *et al.* 2020, Roelofs *et al.* 2016). When presented with ambiguous stimuli, animals in positive-valence states expect more positive outcomes than animals in negative-valence states. To measure this judgement bias, researchers train subjects to respond differently to two unidimensional stimuli (e.g. spatial locations; Burman *et al.* 2008). One stimulus (P) signals a relatively positive outcome, whereas the other stimulus (N) signals a relatively negative outcome. After training, subjects are exposed to ambiguous intermediate stimuli (probes). P responses to the probes indicate that the animal expects a positive outcome (i.e. optimism), whereas N responses indicate that the animal expects a negative outcome (i.e. pessimism). In a meta-analysis of 71 studies on 22 species, Lagisz *et al.* (2020) linked better housing and husbandry to more optimistic judgements of ambiguous stimuli.

Judgement biases are a popular indicator of livestock emotions and welfare (Baciadonna & McElligott 2015). For example, Neave *et al.* (2013) trained dairy calves to respond differently to red and white screens. "Go" responses (nose-touching) to one colour (P; counterbalanced) yielded a milk reward, whilst "No-go" responses to the other colour (N) avoided a one-min time-out. When subsequently tested on ambiguous probe colours (pink screens), calves made significantly more Go (i.e. optimistic) responses before hot-iron disbudding than after (see also Lecorps *et al.* 2019). In other calf studies, maternal separation induced pessimism (Daros *et al.* 2014), and pair-housing induced optimism (Bučková *et al.* 2019). Moreover, pasture access led to optimistic judgement biases in horses (*Equus ferus caballus*; Henry *et al.* 2017, Löckener *et al.* 2016). Previous researchers have not investigated judgement bias in adult cattle, but this method could reveal whether pasture access influences cows' psychological wellbeing (Arnott *et al.* 2017).

The present repeated-measures crossover study measured emotional wellbeing in cows, which were given both 18 days of overnight pasture access (PAS treatment) and 18 days of full-time housing (PEN treatment). This is the first judgement bias study on adult cattle (Crump *et al.* 2019b, 2021). I trained subjects on a spatial Go/No-go task, where a bucket at one location (P) contained food and a bucket at another location (N) was empty. Go responses and short response latencies to three intermediate probe locations indicated optimistic judgement biases. I hypothesised that cows in the PAS treatment would make more Go responses and have shorter response latencies to the probes than cows in the PEN treatment, indicating greater emotional wellbeing. I also predicted that likelihood to respond to the probe buckets would decrease – and latency would increase – with day number, as subjects learnt that the probes were unreinforced (Doyle *et al.* 2010b).

2.2 | Methods

2.2.1 Ethics

This research was approved by Queen's University Belfast's Animal Research Ethics Committee, School of Biological Sciences (approval number: QUB-BS-AREC-18-005). In accordance with the Animals (Scientific Procedures) Act 1986, experimental procedures were described to a Home Office inspector beforehand and deemed not to require a license. I prioritised animal welfare throughout.

2.2.2 Subjects and Housing

I carried out this study during summer 2018 at the Agri-Food and Biosciences Institute, Hillsborough, County Down, Northern Ireland (54°5' N; 6°1' W). The experiment involved 29 autumn-calving, lactating, Holstein-Friesian dairy cows (mean of 4.34 years, range 2.69-8.72 years; mean of 241 days calved, range 209-273 days). All subjects were kept at pasture prior to the study, but they were housed inside for eight weeks pre-testing to standardise conditions (see below). The indoor housing consisted of two adjoining pens (each 13.3 × 8.5 m). Both pens had 16 cubicles (fitted with rubber mats) and concrete standing and walking areas (cleaned by an automatic scraper system six times per day). The building was naturally ventilated, with no additional ventilators servicing the pens. Cows had *ad libitum* access to grass silage offered daily at approximately 09.00 via an open feed barrier along the front of each pen, and *ad libitum* access to fresh water. They were milked in a rotary parlour twice daily (06.30 and 15.00).

As well as the study animals, the herd included three non-study cows (total herd size: 32). These three additional animals allowed me to maintain a consistent 1:1 cow/cubicle ratio. Four days before testing, a veterinary graduate scored each subject's mobility, following the Agriculture and Horticulture Development Board's four-point system (AHDB 2019; Table 1). Cattle were individually observed from the front and side, whilst walking and standing on a flat surface. Scores of 0 or 1 were classified as non-lame; scores of 3 or 4 were classified as lame (results in Table 1).

Table 1. Description of Mobility Scoring System, with baseline results for the present study (adapted from AHDB 2019).

Score	Description of Cow Behavior	Mobility	*N*
0	Walks with even weight bearing and rhythm on all four feet, with a flat back; long, fluid strides possible	Non-lame	4
1	Steps uneven or strides shortened; affected limb or limbs not immediately identifiable	Non-lame	15
2	Uneven weight bearing on an immediately identifiable limb or obviously shortened strides (usually with an arched back)	Lame	8
3	Unable to walk as fast as a brisk human pace; lame leg easy to identify – limping; may barely stand on lame leg(s); back arched when standing and walking	Lame	2

2.2.3 Procedure and Treatments

Before the study, all 32 cows were housed in the indoor pens without pasture access for eight weeks. The pens were connected, and the animals managed as one group. When the experiment began, cows were pseudorandomly divided into two groups of 16 (balanced for lameness), and the pens were visually isolated from each other using plywood sheeting. I carried out a two-period crossover experiment with two concurrent treatments: 18 days of overnight pasture access (PAS) and 18 days of full-time housing (PEN; first period: 25/06/2018-13/07/2018; second period: 16/07/2018-03/08/2018). Throughout the study, both groups were kept in the indoor pens with the same silage type from 10.00 to 16.00. Cows in the PEN treatment were also housed overnight with *ad libitum* silage. Cows in the PAS treatment had 18 h of daily pasture access, from approximately 16.00 (post-afternoon milking) until 10.00 the next morning. This covered the main grazing times (dawn and dusk; Gregorini 2012, Ruckebusch & Bueno 1978, Shabi *et al.* 2005) and is when cattle choose to access pasture (Charlton *et al.* 2011a, 2013, Falk *et al.* 2012, Kismul *et al.* 2018, Legrand *et al.* 2009, Motupalli *et al.* 2014).

PAS cows were managed in a rotational grazing system, so the treatment groups were kept on different pastures. Area grazed ranged from 1370-3950 m^2, and distance to parlour ranged from 190-295 m. I analysed grass samples three times during each period (six times in total). Herbage was generally high quality, although lower quality in the second period. Across the study, mean oven dry matter (DM) content was 226.8 (SD 27.8) g/kg, mean crude protein content was 216.5 (SD 24.2) g/kg DM, and mean metabolizable energy content was 11.4 MJ/kg DM (first period: 238.5, SD 8.6, g/kg; 226.0, SD 11.5, g/kg DM; and 12.0 MJ/kg DM, respectively; second period: 215.0, SD 8.6, g/kg; 207.0, SD 11.5, g/kg DM, 10.9 MJ/kg DM, respectively). When the first period ended, the cows swapped treatments and I repeated the procedure. The group at pasture first (PAS-first) had 14 study animals (mean of 4.47 years, range 2.69-8.72 years; mean of 240 days calved, range 219-260 days) and the group at pasture second (PAS-second) had 15 study animals (mean of 4.22 years, range 2.74-7.76 years; mean of 242 days calved, range 209-273 days).

2.2.4 Judgement Bias Task

Judgement bias testing involved two pens adjacent to the home pens: the holding area, where subjects were kept before sessions and during inter-trial intervals, and the testing area (13.3 × 3.1 m), where the task was carried out. Subjects in the holding area could not see the testing area. Once per weekday, I individually moved each cow into the holding area (subject order randomised each day). I used a spatial Go/No-go judgement bias task, with a bucket at one of five locations (Burman *et al.* 2008, Hintze *et al.* 2018, Lecorps *et al.* 2018; Figure 4). The P and N stimuli were buckets at the right and left locations (location counterbalanced between subjects). Rewarded P buckets contained 130 g of grain-based concentrate feed, which cattle find very desirable (Webb *et al.* 2014). N buckets were unreinforced. The ambiguous probe stimuli were buckets at three intermediate locations; these were also unreinforced. I ended trials if subjects did not make a Go response within 20 s. If the subject made a Go response and the bucket was rewarded, I allowed them an additional 30 s to feed. I pseudorandomised trial order – subjects never had more than two consecutive buckets at the same location. Between trials, I moved the cow back into the holding area and re-set the bucket. Sessions were filmed on a tripod-mounted Sony HDR-CX450 1080p Camcorder.

Before the experiment began, I had 18 training days divided into six blocks of three days (Table 2). By the final three-day training block, each cow was receiving two rewarded P trials (P-Rew), one unrewarded P trial (P-Unr), and three unrewarded N trials (N-Unr) per day across a six-trial session. P-Unr trials introduced a one-third variable reinforcement ratio. Variable reinforcement reduces extinction learning towards unrewarded probes, which can look like increased pessimism without any change in emotional state (Doyle *et al.* 2010b). To maintain task motivation, subjects never received more than two consecutive unreinforced trials (either P-Unr or N-Unr), and the last P trial was always P-Rew.

Table 2. Training timeline, with the number of rewarded P trials (P-Rew), unrewarded P trials (P-Unr), and unrewarded N trials (N-Unr) per cow in each consecutive three-day block.

Days	**P-Rew Trials**	**P-Unr Trials**	**N-Unr Trials**	**Total Trials**
1-3	1	0	0	1
4-6	2	0	0	2
7-9	2	0	1	3
10-12	2	0	2	4
13-15	2	0	3	5
16-18	2	1	3	6

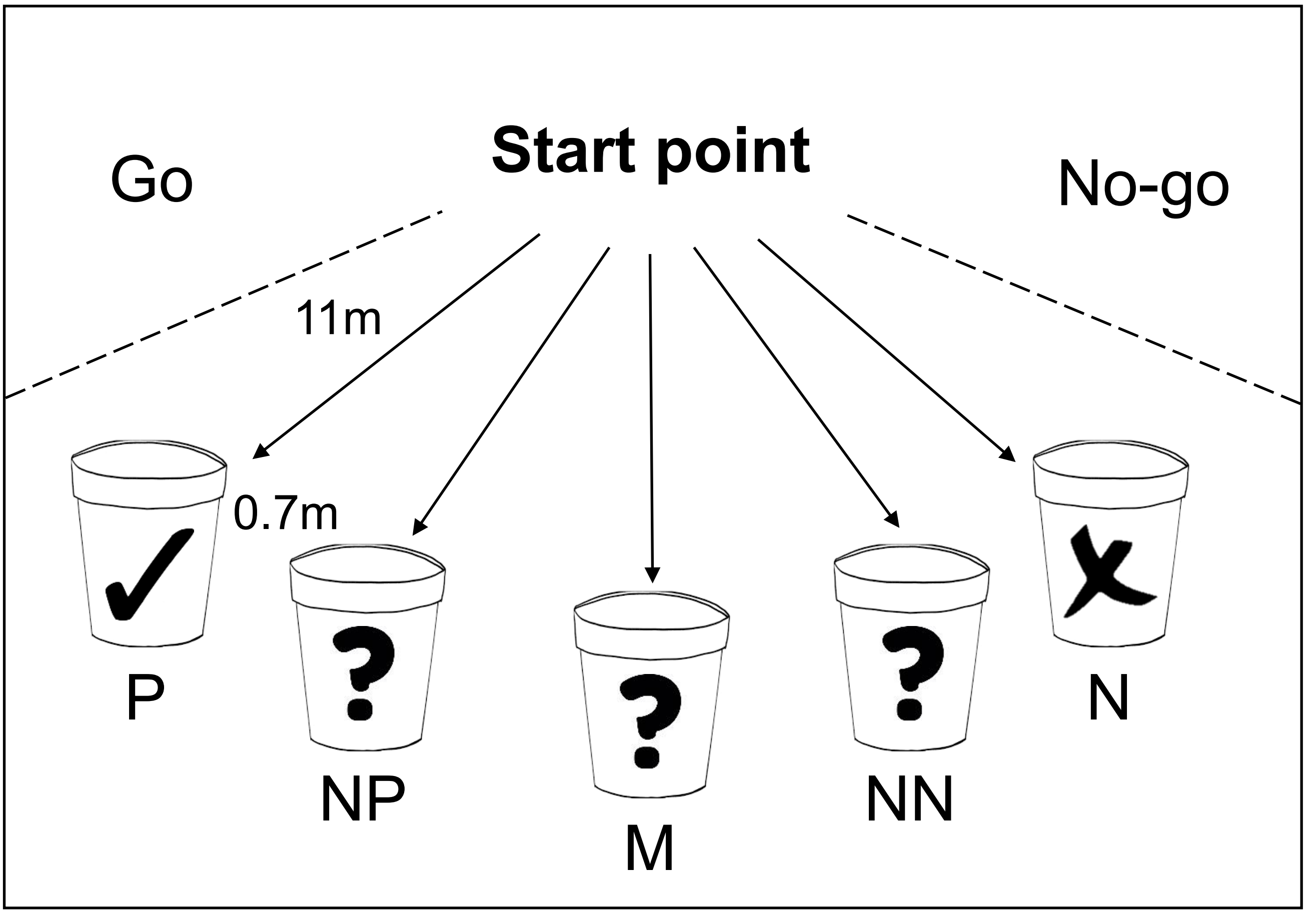


Figure 4. Diagram of the experimental setup, illustrating the five bucket locations (positive, P; near-positive, NP; middle, M; near-negative, NN; negative, N) and trained responses (Go, No-go).

After the training phase, I carried out three days of inclusion testing to confirm that subjects had learnt the spatial discrimination task. I recorded responses in six inclusion trials per day (18 trials total). Three trials per day involved the P location (2 × P-Rew; 1 × P-Unr), and three trials per day involved the N location (3 × N-Unr). For each subject, I extracted the latency for all 18 trials, with No-go responses given a ceiling latency of 20 s. My inclusion criteria are outlined in the "Statistical Analyses" section.

During both experimental phases, I carried out judgement bias testing every Monday, Wednesday, and Friday (8 × testing sessions per individual per phase; 16 × testing sessions per individual total). Half of testing sessions included three P trials (2 × Rew; 1 × Unr) and two N trials, whilst the other half included two P trials (2 × Rew) and three N trials. The remaining trial was a probe bucket at one of three equidistant intermediate locations: near-positive (NP; 0.7 m from P), middle (M; 1.4 m from both P and N), and near-negative (NN; 0.7 m from N). The probe trial randomly replaced either a P-Unr or N trial. I extracted data for the P, N, and probe buckets from video footage. If the subject's muzzle touched or entered the bucket, a Go response was recorded. Otherwise, a No-go response was recorded. Latency was also recorded, from one hoof crossing a standardised start line to the Go response (distance: 11 m). Data were extracted from video recordings blind to treatment. Throughout the experiment, I continued training sessions on Tuesdays and Thursdays. This increased the P/N:probe ratio, further reducing extinction learning towards the probes (Bethell 2015).

2.2.5 Statistical Analysis

I analysed the data in R (R Core Team, Cran-r-project, Vienna, Austria, version 3.6.2). I checked data and model assumptions using histograms and qqplots, applying transformations where appropriate. I used the package "lme4" to run mixed-effects models and dropped interactions when this reduced the model's Akaike Information Criterion (AIC) value by > 5. I then extracted *p*-values using type III Wald's tests. Where factors had multiple levels or interactions involved multiple comparisons, I performed a Tukey's post-hoc test ("lsmeans" package) to identify significant differences between levels or comparisons. I consider $p < .05$ significant, and present data as means ± standard error (unless otherwise stated).

For the training data, I used a statistical inclusion criterion. I ran a Wilcoxon test on the latency data from each cow's inclusion trials ($n = 18$; 9 × P, 9 × N; Kis *et al.* 2015). To proceed, subjects needed significantly shorter response latencies to the P location than the N location. I also ran a general liner mixed effects model (GLM) on the inclusion data to establish that subjects learnt the left/right association, rather than using olfactory cues to approach the rewarded locations. Latency was included in the model as the response variable; location/reward category (P-Rew, P-Unr, N-Unr) was included as a fixed effect; and cow ID was included as a random effect. I identified significant differences between categories with a Tukey's post-hoc test. Subjects not using olfactory cues would show no difference between P-Rew and P-Unr, but a difference between P and N; subjects using olfactory cues would show no difference between P-Unr and N-Unr, but a difference between Rew and Unr.

For the judgement bias testing data, I ran separate models with the binary Go/No-go responses and response latency as the dependent variable (Lagisz *et al.* 2020). I fitted a generalised linear mixed effects model (GLIM) for the Go/No-go data (binomial distribution, logit link). I ran a GLM for the latency data, which I transformed by taking the natural logarithm of the value +1 (hereafter, "log-transformed"). I excluded No-go responses from this model. In both models, the fixed effects were housing treatment (PAS, PEN), treatment order (PAS-first, PAS-second), bucket location (P, NP, M, NN, N), and day number (1-16). I included treatment × treatment order, treatment × bucket location, and bucket location × day number interactions. Cow ID was again included as a random effect. I also ran a separate model on latency (log-transformed) to the P location only. Fixed and random effects were the same as for the previous model, except I removed bucket location. To account for food motivation, I also included body condition score and time of day as fixed effects, as well as body condition score × treatment and time of day × treatment interactions.

2.3 | Results

2.3.1 Judgement Bias Training

During inclusion testing, all 29 cows approached the P location faster than the N location (every subject: $p < .001$) and advanced to the experimental phase. Investigating the effect of bucket location and food reward presence/absence, I found a significant difference in latency between P-Rew trials (median latency ± SD: 5.75 ± 0.92 s), P-Unr trials (5.75 ± 0.93 s), and N-Unr trials (20 ± 4.36 s; $\chi^2_2 = 2248$, $p < .001$). Post-hoc tests revealed no significant difference between P-Rew and P-Unr ($z = -0.14$, $p < 1.00$). However, subjects were significantly faster to both P-Rew ($z = -42.34$, $p < .001$) and P-Unr ($z = -33.62$, $p < .001$), than the N-Unr. By demonstrating that bucket location (rather than reward presence) influenced latency, these results demonstrate that subjects learnt the spatial discrimination task – they were not using olfactory cues to locate the reward.

2.3.2 Judgement Bias Testing

I collected data from 2,741 judgement bias trials. Excluding the 1,342 No-go trials, latency data were available from 1,399 Go trials. Latency from start line to bucket ranged from 2.75 s to 18.91 s (mean: 7.03 s).

Cows in the PAS treatment were significantly less likely to approach the buckets (PAS: 47.75 % trials; PEN: 53.24 % trials; $\chi^2_1 = 9.90$, $p < .001$) and took longer to do so (PAS: 7.12 ± 0.07 s; PEN: 6.42 ± 0.05 s; $\chi^2_1 = 26.91$, $p < .001$). Treatment order did not affect approach likelihood ($\chi^2_1 = 2.35$, $p = .13$) or latency ($\chi^2_1 = 0.38$, $p = .54$). There was a significant treatment × treatment order interaction for both likelihood to approach ($\chi^2_1 = 14.99$, $p < .001$) and latency to approach ($\chi^2_1 = 6.08$, $p = .01$; Figure 5). During the PEN treatment, the PAS-first group had a smaller increase in approach likelihood and reduction in approach latency than the PAS-second group.

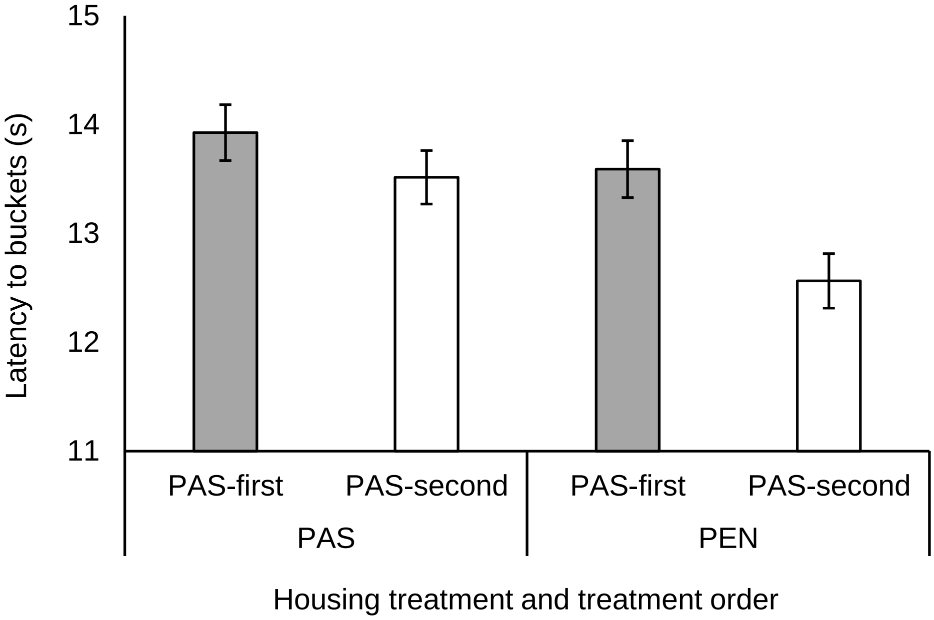


Figure 5. Interaction between housing treatment (pasture access: PAS; cubicle housing: PEN) and treatment order (PAS-first, PAS-second) in response latency to all five bucket locations. Error bars represent the standard error of the mean.

There was a significant effect of bucket location on both the number of Go responses (χ^2_4 = 816.31, $p < .001$) and approach latency (χ^2_4 = 1089.89, $p < .001$; Figure 6). Post-hoc tests revealed that all five bucket locations were significantly different from one another in terms of both approach likelihood and latency (Table 3). There was no treatment × bucket location interaction for approach likelihood (χ^2_4 = 2.11, p = .72), but the interaction was significant for approach latency (χ^2_4 = 15.87, $p < .005$). This showed that the main effect of treatment on latency was localised to the P location: cows were slower to approach P when they were in the PAS treatment than the PEN treatment (PAS: 6.38 ± 0.04 s; PEN: 6.28 ± 0.05 s; $t_{1,386}$ = 6.39, $p < .001$; Figure 7). There was no treatment difference in latency to any other location (NP: $t_{1,385}$ = 0.42, $p < 1.00$; M: $t_{1,386}$ = −0.66, $p < 1.00$; NN: $t_{1,387}$ = −1.60, p = .85; N: $t_{1,387}$ = 0.45, $p < 1.00$).

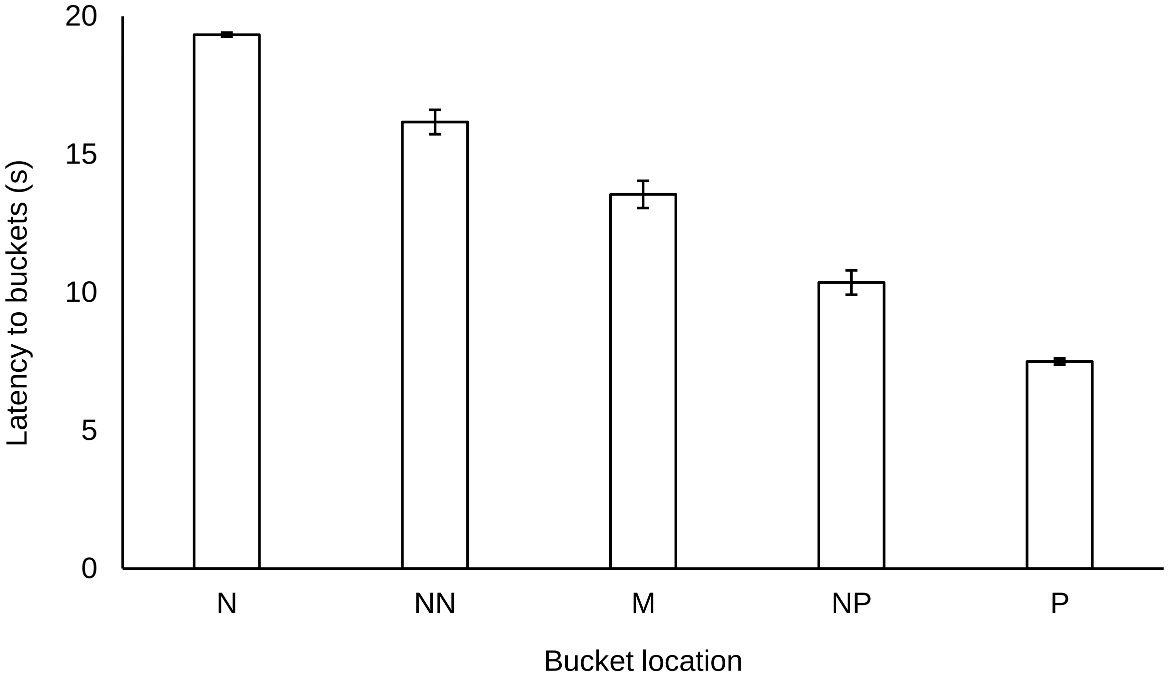


Figure 6. Response latency to the five bucket locations throughout the experiment (negative: N; near-negative: NN; middle: M; near-positive: NP; positive: P). Error bars represent the standard error of the mean.

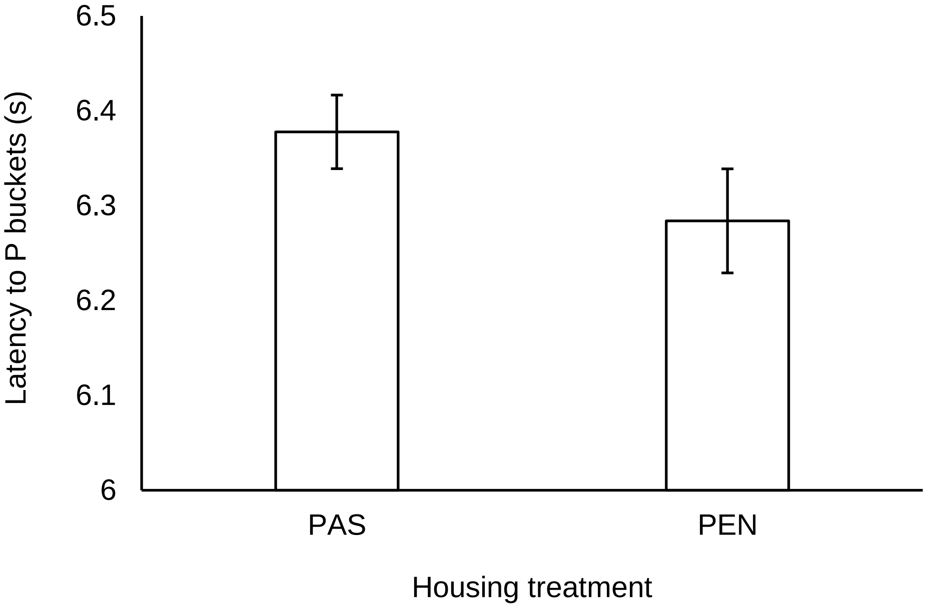


Figure 7. Response latency to the positive (P) bucket location in each housing treatment (pasture access: PAS; cubicle housing: PEN). Error bars represent the standard error of the mean.

Table 3. Pairwise comparisons of the likelihood and latency to approach each bucket location, and for the bucket location × day number interaction. Bold *p*-values are significant.

Comparison	Bucket location approach				Bucket location × day number			
	Likelihood		Latency		Likelihood		Latency	
	z	*p*	*t*	*p*	*z*	*p*	*t*	*p*
P – NP	−5.98	**<0.001**	9.40	**<0.001**	−2.86	**0.03**	3.88	**<0.005**
P – M	−11.00	**<0.001**	13.14	**<0.001**	−4.11	**<0.001**	2.91	**0.03**
P – NN	−15.52	**<0.001**	14.70	**<0.001**	−2.59	0.07	−0.22	<1.00
P – N	−28.23	**<0.001**	26.29	**<0.001**	−2.39	0.12	−1.34	0.67
NP – M	−3.84	**<0.005**	4.48	**<0.001**	−0.93	0.88	−0.20	<1.00
NP – NN	−7.73	**<0.001**	7.26	**<0.001**	0.42	0.99	−2.46	0.10
NP – N	−16.78	**<0.001**	15.52	**<0.001**	1.21	0.75	−3.81	**<0.005**
M – NN	−4.17	**<0.001**	3.09	**0.02**	1.42	0.61	−2.11	0.22
M – N	−13.80	**<0.001**	10.06	**<0.001**	2.42	0.11	−3.20	**0.01**
NN – N	−9.53	**<0.001**	6.01	**<0.001**	0.79	0.93	−0.64	0.97

As the study progressed (i.e. day number increased), likelihood to approach the buckets decreased (χ^2_1 = 27.62, p < .001; Figure 8a) and approach latency increased (χ^2_1 = 19.28, p < .001; Figure 8b). There was also a bucket location × day number interaction for approach likelihood (χ^2_4 = 21.72, p < .001) and latency (χ^2_4 = 25.83, p < .001; Table 3).

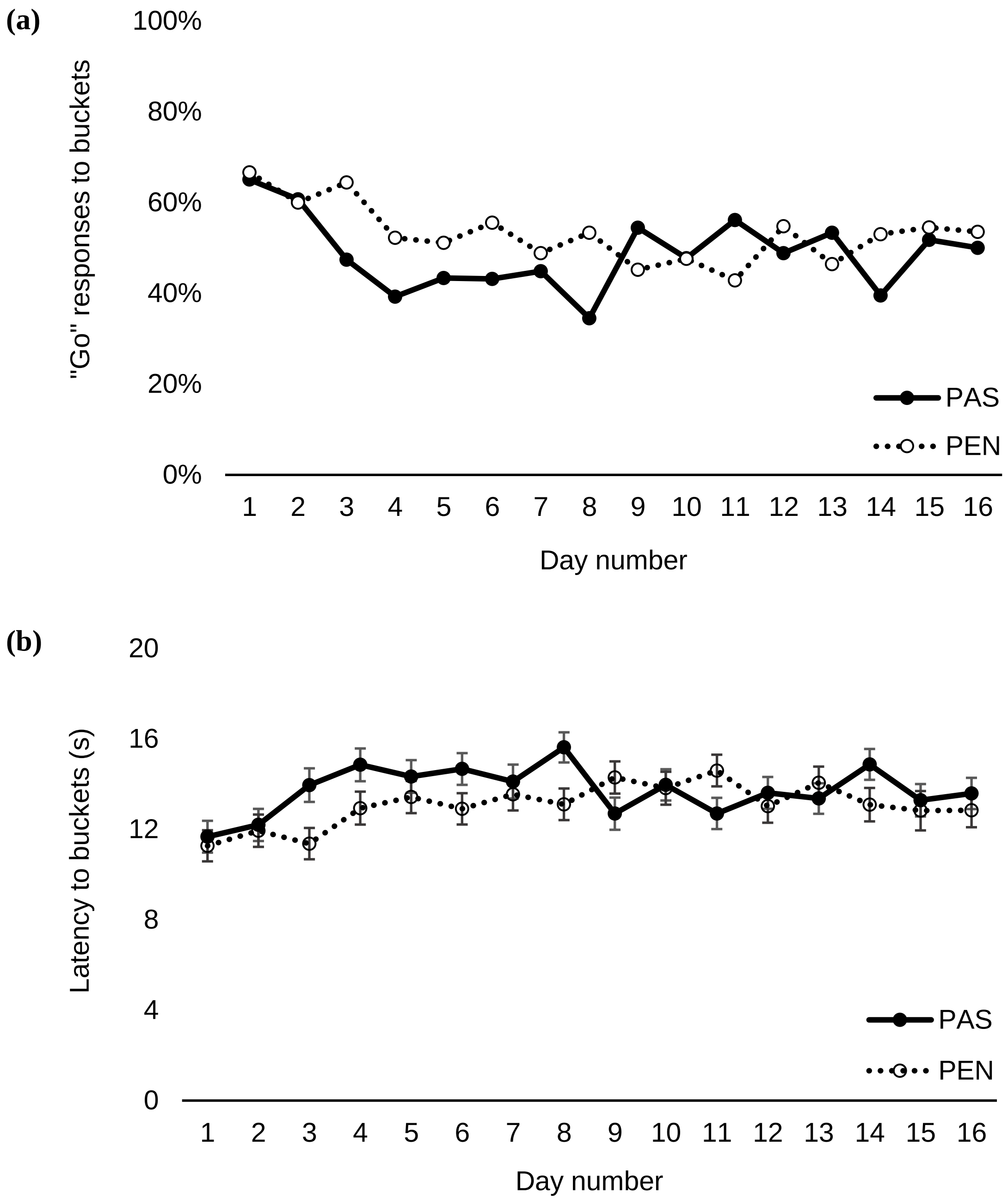


Figure 8. (a) Percentage of “Go” responses and **(b)** response latency to all buckets in each treatment (pasture access: PAS; cubicle housing: PEN) throughout the experiment (days 1-16). Error bars represent the standard error of the mean.

When I modelled latency to the P location, there was no significant effect of either time of day ($\chi^2_1 = 0.66$, $p = .42$) or body condition score ($\chi^2_1 = 0.00$, $p = .96$). There was no treatment × time of day ($\chi^2_1 = 0.53$, $p = .47$) or treatment × body condition score interactions ($\chi^2_1 = 0.20$, $p = .66$).

2.4 | Discussion

This study investigated whether pasture access enhances emotional wellbeing in dairy cows. There was no treatment difference in judgement bias. Subjects in the PAS treatment were neither more likely nor faster to approach buckets when the reward contingency was ambiguous. However, cows with pasture access approached known rewarded buckets slower than cows housed indoors full-time.

I did not predict that the PAS treatment would be slower to the P location than the PEN treatment. A core assumption of judgement bias tasks is that affective states bias decision-making when outcomes are uncertain (Gygax *et al.* 2014, Mendl *et al.* 2010, Trimmer *et al.* 2013). As a result, treatment effects in judgement bias are expected towards the probes – not the trained P and N stimuli (Gygax *et al.* 2014, Mendl *et al.* 2010). Most studies meet this assumption (Lagisz *et al.* 2020; for exceptions, see Anderson *et al.* 2013, Harding *et al.* 2004, Horváth *et al.* 2016, exp. 4, Seehuus *et al.* 2013). Moreover, I expected pasture access to reduce latency, representing a higher expectation of reward and an optimistic judgement bias. An obvious explanation for this surprising P result is that cows were less food motivated in the PAS treatment than the PEN treatment (e.g. see Burman *et al.* 2011, Freymond *et al.* 2014, Verbeek *et al.* 2014). However, treatments only differed at night. Every subject was kept indoors with *ad libitum* feed during the daytime. If food motivation were responsible, the effect would be strongest earliest in the day and decrease as all subjects spent longer with equivalent rations. Time of day did not affect latency to the P location. Additionally, I scored every cows’ body condition during both experimental phases. Higher scores reflect better nutrition (AHDB 2020), so body condition score is inversely correlated with food motivation. I did not find any relationship between P latency and body condition score. These converging lines of evidence suggest that food motivation was not responsible.

It is possible that reduced reward anticipation, linked to positive emotional states, explains why the PAS treatment were slower to the P location than the PEN treatment. Spruijt *et al.* (2001) hypothesised that animals exposed to fewer, lower-quality rewards value each reward more (Figure 9; reviewed by an der Harst & Spruijt 2007, Watters & Krebs 2019; for a critique, see Anderson *et al.* 2020). As an example, rats in poor conditions responded to a sucrose-predicting cue with more activity and behavioural transitions than rats in enriched housing (van der Harst *et al.* 2003). This effect means that, in a judgement bias task, we predict opposite welfare-based differences in response patterns towards the P stimulus and the probes. If animals have received more, higher-quality rewards, the P stimulus will elicit less anticipatory behaviour, whereas the probes will elicit more (Watters & Krebs 2019). Latency to a rewarded bucket meets Spruijt *et al.'s* definition of anticipatory behaviour: "responses elicited by rewarding stimuli that lead to and facilitate consummatory behavior" (p. 160). It is, therefore, plausible that the PAS treatment's longer P latencies reflected lower reward anticipation, indicating that they had more rewarding lives and better welfare, rather than pessimistic judgement biases, which would indicate less rewarding lives and worse welfare. This inverse relationship between reward frequency and reward anticipation does not apply to chronically stressed animals, which display reduced reward valuation (anhedonia; Treadway & Zald 2011). My results may suggest that PEN cows were not anhedonic but had less rewarding lives than PAS cows. It should be noted, however, that reward anticipation is an *a posteriori* explanation for unexpected results. I did not hypothesise or conclusively demonstrate this effect in the present study.

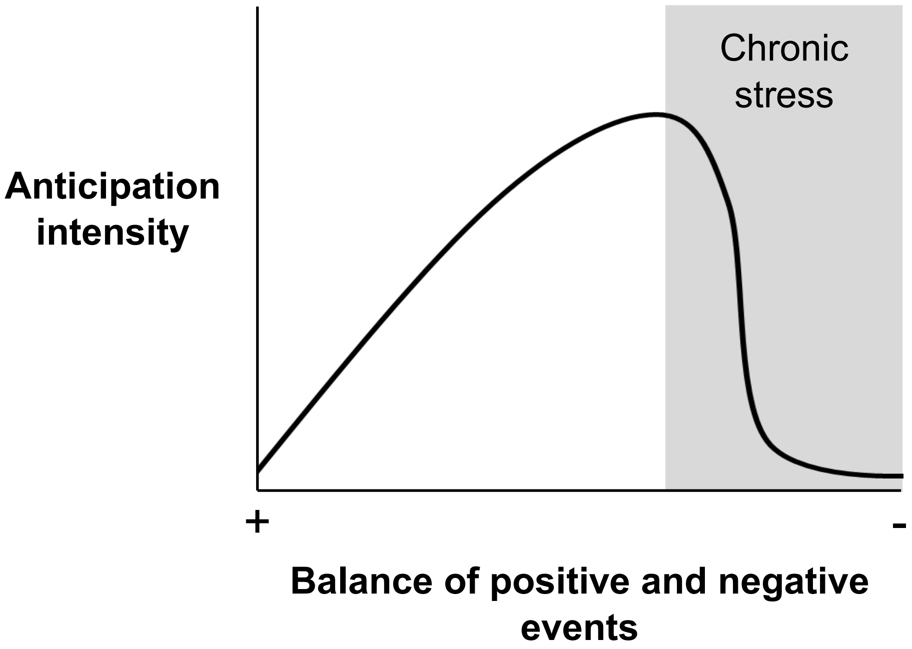


Figure 9. Relationship between the balance of positive and negative events in an animal's life and anticipation intensity towards individual rewards (adapted from Watters 2014).

My reward anticipation explanation highlights how judgement bias tasks may quantify effects besides judgement bias (Bethell 2015, Mendl *et al.* 2009). However, few studies have compared judgement bias and reward anticipation. Optimistic judgement biases were linked to reduced anticipatory behaviour in dolphins (*Tursiops truncatus*; Clegg & Delfour 2018), whereas enrichment did not influence chickens' (*Gallus gallus domesticus*) responses to either a judgement bias or reward anticipation task (Wichman *et al.* 2012). Other studies suggest that treatment differences in anticipatory behaviour may influence responses to a judgement bias task. For example, disrupting reward-related behaviours in chicks reduced latencies towards the P stimulus (Seehuus *et al.* 2013). The antidepressant reboxetine likewise reduced P responses in rats (Anderson *et al.* 2013), and deep-litter enrichment reduced P responses in quail (*Coturnix japonica*; Horváth *et al.* 2016, exp. 4), although neither finding was consistent across experiments. Like my results, these P response patterns might be attributed to increased reward anticipation among subjects in more negative affective states. Moreover, because judgement bias and reward anticipation predict opposite responses, it is possible that they cancel each other out. In a meta-analysis of judgement bias studies using pharmacological manipulations, effect sizes were smaller for the P stimulus than either the probes or N stimulus (Neville *et al.* 2020). To differentiate the effects of judgement bias and reward anticipation, I suggest that judgement biases are more plausible when treatment differences only occur towards the probes, whereas treatment differences localised around the P stimulus imply reward anticipation.

Despite P responses suggesting that the PAS treatment induced more positive emotional states, pasture access did not influence judgement bias. This is surprising, as aversive events lead to pessimism in dairy calves (Bučková *et al.* 2019, Daros *et al.* 2014, Lecorps *et al.* 2019, Neave *et al.* 2013), and pasture access leads to optimism in horses (Henry *et al.* 2017, Löckener *et al.* 2016). However, studies on pigs (Carreras *et al.* 2016), chickens (Wichman *et al.* 2012), and quail (Horváth *et al.* 2016) have found no difference in judgement bias between housing conditions. There are two possible reasons for my null results. First, pasture access may not influence affective state in dairy cows. This explanation might seem implausible, given pasture's behavioural and potential health benefits, and cows' preference and motivation for pasture (Arnott *et al.* 2017, Charlton & Rutter 2017). However, I tested judgement bias during the daytime, when both treatments were indoors. Pasture may only improve emotional wellbeing whilst cows are at pasture, without persisting after they go indoors. Ruet *et al.* (2020) found that, when confined indoors again, horses given pasture access rapidly return to previous poor welfare states. Conversely, Anderson and Adolphs (2014) identified persistence as a defining feature of emotions. Their characterisation is consistent with my reward anticipation findings, which indicate that positive affective states from overnight pasture access carried over into daytime indoor housing.

The second potential explanation for my null judgement bias results is that treatment differences in affective state existed, but my task did not detect them. In their meta-analysis, Lagisz *et al.* (2020) identified four methodological factors that may be responsible for my findings. (1) Sex: males exhibit larger effects than females, and my population was female. (2) Stimuli: sound and tactile stimuli lead to larger effects than spatial stimuli, which I used. (3) Responses: Go/Go tasks (where both P and N require active responses) produce larger effects than Go/No-go tasks; I tested the latter. (4) Reinforcement: methods with rewarded/punished stimuli or differentially rewarded stimuli generate larger effects than the rewarded/unreinforced stimuli that I used. Another potential methodological flaw is that cognitive tasks can be inherently rewarding (Hagen & Broom 2004, Manteuffel *et al.* 2009, Meagher *et al.* 2020). Thus, performing the judgement bias task may have itself influenced cows' affective state, especially in the unstimulating PEN treatment. Collectively, these factors could have overridden treatment differences in judgement bias.

2.5 | Conclusions

Based on dairy cows' responses to a judgement bias task, it is unclear whether pasture access induces more positive emotional states than cubicle housing. I found no difference in judgement bias between cows with and without pasture access. However, cows in the pasture treatment were slower to approach a known reward. This finding implies reduced reward anticipation, possibly suggesting that cows in the pasture-based system had more rewarding lives.

3 | Pasture access impacts behavioural indicators of dairy cow welfare

Published as:

Crump, A., Jenkins, K., Bethell, E. J., Ferris, C. P., & Arnott, G. (2019). Pasture access affects behavioral indicators of wellbeing in dairy cows. *Animals*, *9*(11), 902.

Abstract. Cattle are highly motivated to lie and walk, and herds synchronise lying behaviour when they have comfortable surfaces and little competition for space. Indoor housing can disrupt these behaviours. I measured lying and locomotory behaviours to assess cow welfare either with or without access to pasture. During the crossover experiment described in Chapter Two, I recorded lying and walking with accelerometers and analysed the data using linear mixed models. When they had overnight pasture access, cows displayed longer lying durations, fewer lying bouts, longer lying bouts, fewer transitions between lying and standing, and more synchronous herd lying behaviour. In addition, step counts were higher at pasture than indoors. I did not observe any differences in daytime behaviour, when both treatments were housed inside. These results suggest that pasture access improves dairy cow welfare by increasing comfort, reducing competition, and facilitating highly motivated behaviours.

3.1 | Introduction

Chapter Two had twin objectives: validate a judgement bias task for dairy cows and use it to indicate husbandry-induced differences in affective state. Without additional data, however, these objectives were incompatible. The judgement bias task could not be validated unless I knew it was measuring different affective states, and the judgement bias task could not indicate different affective states unless it had been validated. Although previous studies suggest that welfare is generally better at pasture (Arnott *et al.* 2017, Charlton & Rutter 2017, Mee & Boyle 2020, Phillips *et al.* 2013, Smid *et al.* 2020), diverse factors modulate the benefits, such as weather conditions and previous experience (e.g. Charlton *et al.* 2011b). My null judgement bias results could, therefore, indicate either that spatial Go/No-go judgement bias tasks cannot discriminate valence states in dairy cows or that valence did not differ between treatment groups. To resolve this paradox, I measured the cows' behaviour as an independent measure of affective state.

Lying behaviour is a key indicator of cow welfare (Haley *et al.* 2000, Tucker *et al.* 2020, Vasseur *et al.* 2012). In dairy cattle, lying is highly motivated (Jensen *et al.* 2005, Metz 1985, Munksgaard *et al.* 2005, Tucker *et al.* 2018), and lying deprivation activates the hypothalamic-pituitary-adrenal axis (Fisher *et al.* 2002, Munksgaard *et al.* 1999, Munksgaard & Simonsen 1996). Furthermore, rumination occurs whilst lying, so shorter lying durations jeopardise metabolic processes (Chaplin *et al.* 2000). Disrupted lying behaviour is also associated with lameness (Ito *et al.* 2010), mastitis (Cyples *et al.* 2012), and enteritis (Charlton *et al.* 2019). Pasture is usually more comfortable than cubicles, with several studies finding longer lying durations at pasture than in indoor housing (O'Connell *et al.* 1989, Olmos *et al.* 2009, Singh *et al.* 1993). However, some researchers report longer lying times indoors (Hernandez-Mendo *et al.* 2007, Kismul *et al.* 2019, Roca-Fernández *et al.* 2013). This may reflect different activity budgets in indoor housing compared to pasture (e.g. reduced feeding durations), greater cow comfort in cubicles (e.g. by providing soft lying surfaces) or reduced cow comfort (e.g. due to difficulty standing; Charlton & Rutter 2017). More consistently, dominant cows displace subordinates from cubicles (Miller & Wood-Gush 1991, O'Connell *et al.* 1989). Indoor housing, thus, typically reduces both total lying duration and mean lying bout duration, but increases the number of lying bouts (Olmos *et al.* 2009). This disrupted lying behaviour indicates discomfort and competition for lying space.

As well as impacting lying activity, indoor housing desynchronises herd behaviour in dairy cows (Flury & Gygax 2016, Krohn *et al.* 1992, Miller & Wood-Gush 1991, Roca-Fernández *et al.* 2013) and bulls (Tuomisto *et al.* 2019). Synchrony describes the proportion of individuals performing the same behaviour at the same time. It occurs through two mechanisms: allelomimetic (when animals directly mimic conspecifics) and concurrent (when different individuals respond to the same cues in the same way; Stoye *et al.* 2012). As cows are herd animals, allelomimetic synchrony is internally motivated regardless of concurrent motivations, such as group milking and feeding (Flury & Gygax 2016). Herd synchrony is, therefore, a characteristic of semi-natural environments, including pasture (Flury & Gygax 2016, Kilgour 2012). Desynchronisation is linked to reduced lying time, more cubicle displacements, and more daytime lying in subordinate individuals (Fregonesi *et al.* 2007, Krawczel *et al.* 2008, Winckler *et al.* 2015). Consequently, many authors suggest that synchrony signals good welfare (Asher & Collins 2012, Fregonesi & Leaver 2001, Miller & Wood-Gush 1991, Napolitano *et al.* 2009, O'Driscoll *et al.* 2008, Phillips *et al.* 2013).

By providing more space and a comfortable surface, pasture access also facilitates locomotion (Black & Krawczel 2016, Charlton *et al.* 2011a, b, Hernandez-Mendo *et al.* 2007, Krohn *et al.* 1992). During grazing, cows spend more time walking than when they are feeding indoors, and grazing areas are normally farther from the milking parlour than the feeding area of indoor housing. Walking is a "behavioural need" (Hughes & Duncan 1988, Jensen & Toates 1993): cows are motivated to walk even without external motivations. Krohn *et al.* (1992) gave dairy cattle free access to indoor and outdoor areas. Despite having food, water, and shelter inside, subjects walked outside for 2.5 km per day in summer and 0.8 km per day in winter. Moreover, cattle that spend longer indoors are more active after being let outside (Jensen 1999, 2001, Loberg *et al.* 2004). These findings indicate that exercise is a positive welfare outcome in itself. Walking also has physical benefits, especially for cows' legs, feet, and hooves (Bielfeldt *et al.* 2005, Hernandez-Mendo *et al.* 2007, Loberg *et al.* 2004, Somers *et al.* 2003). Gustafson and Lund-Magnussen (1995) suggested that exercise improves the condition of dairy cows' joints, tendons, and ligaments, easing transitions up and down. Regular walking on a treadmill reduced gestating cows' working heartrate and plasma lactate concentrations, indicating reduced metabolic stress (Davidson & Beede 2009). Therefore, higher step counts improve health, as well as reflecting increased grazing at pasture.

During the repeated-measures crossover experiment described in Chapter Two, I recorded dairy cows' lying and walking activity. This covered 18 days of overnight pasture access and 18 days of full-time housing. I predicted that cows at pasture would have longer total lying durations, fewer and longer lying bouts, more synchronous lying behaviour, and higher step counts. These results would indicate that pasture access improves cattle welfare.

3.2 | Methods

3.2.1 Ethics

See subsection 2.2.1. Queen’s University Belfast’s Animal Research Ethics Committee and a Home Office inspector approved the behavioural data collection within the context of the larger study (approval number: QUB-BS-AREC-18-005).

3.2.2 Subjects and Housing

See subsection 2.2.2. In addition to the information therein, I fitted all 29 subjects with an IceQube (IceRobotics Ltd., Edinburgh, United Kingdom) before the experiment. IceQubes are commercially available hind-leg activity monitor sensors that distinguish lying from standing and record step counts using a tri-axial accelerometer (sampling rate: 16 Hz; time resolution: 1 s; dimensions: 95.0 × 82.3 × 31.5 mm; weight: 130 g).

3.2.3 Procedure and Treatments

See subsection 2.2.3.

3.2.4 Data Preparation

Using the IceQubes, I measured seven variables: overnight lying duration (h/night), daytime lying duration (h/daytime), number of lying bouts (bouts/24 h), lying bout duration (total duration/bouts), overnight transitions up or down (transitions/night), daytime transitions (transitions/daytime), and overnight step count (steps/night). Overnight data were analysed from 16.30 to 09.30 and daytime data from 10.00 to 15.00, so effects of walking to and from pasture were eliminated. Lying duration was the total time the IceQube was horizontal; lying bouts were the duration from vertical to horizontal and back again; and steps were counted whenever cows lifted their tagged leg. Lying duration, transitions, and step counts were recorded in 15-min intervals; bout length data were only available per day. To measure synchrony, I classified cows as lying if they spent over half the 15-min interval lying (> 449 s). I compared the binary lying data (either lying or not) between herd members within each interval. To my knowledge, this automated method is a novel way to assess behavioural synchrony (further detailed below).

3.2.5 Statistical Analyses

I analysed the data in R (R Core Team, CRAN-r-project, Vienna, Austria, version 3.4.4). Data were checked for normality by plotting histograms; transformations were applied where these improved the distribution. I fitted GLMs using maximum likelihood (ML), including all interactions. To improve the models' fit to the data, I removed interactions in a stepwise fashion and selected models with the lowest AIC values. I re-ran these models using the restricted maximum likelihood (REML) approach. P-values were extracted using a Wald's test, with $p < .05$ considered statistically significant. Data are presented as means ± standard error.

I fitted separate models for the following response variables: overnight and daytime lying duration, number of lying bouts, lying bout duration, overnight and daytime transitions, and overnight step count. The fixed effects were treatment and treatment order (either PAS first or second); cow ID and day number were random effects. Lying bout data included substantial outliers: the longest was 14.25 h, but the second longest was 7.77 h. As both values were from the same individual on consecutive days, I ran the bout models on both the original dataset and data within two SD of the mean. This did not change the significance level of any results, so only the original dataset model is reported. Because overnight step counts were positively skewed, I applied a square-root transformation to these data. Step counts are provided alongside walking distance, based on a stride length of 1.5 m (Alsaaod *et al.* 2017).

I measured lying synchrony using Fleiss' Kappa coefficient of agreement (K_F), a test of inter-observer reliability for > 2 raters (Fleiss 1971). Treating each cow as a rater, I measured synchrony as intra-herd "agreement" in lying behaviour during each 15-min interval (Asher & Collins 2012). $K_F > 0$ indicates agreement greater than chance, $K_F = 0$ indicates chance levels, and $K_F < 0$ indicates disagreement greater than chance. Fleiss' Kappa assumes independent data (Engel & Lamprecht 1997), which I determined with the IceQubes' recordings of maximum bout lengths. However, given the outliers in the lying bout data, I defined maximum bout length as two SD above the mean (3.75 h). This provided five intervals per night (17.00-17.15, 21.00-21.15, 01.00-01.15, 05.00-05.15, 09.00-09.15). Using the "IRR" package in R (Various Coefficients of Interrater Reliability and Agreement), I calculated daily K_F values for each treatment group and analysed them as the response variable in a GLM (fixed effects: treatment and treatment order; random effect: day number).

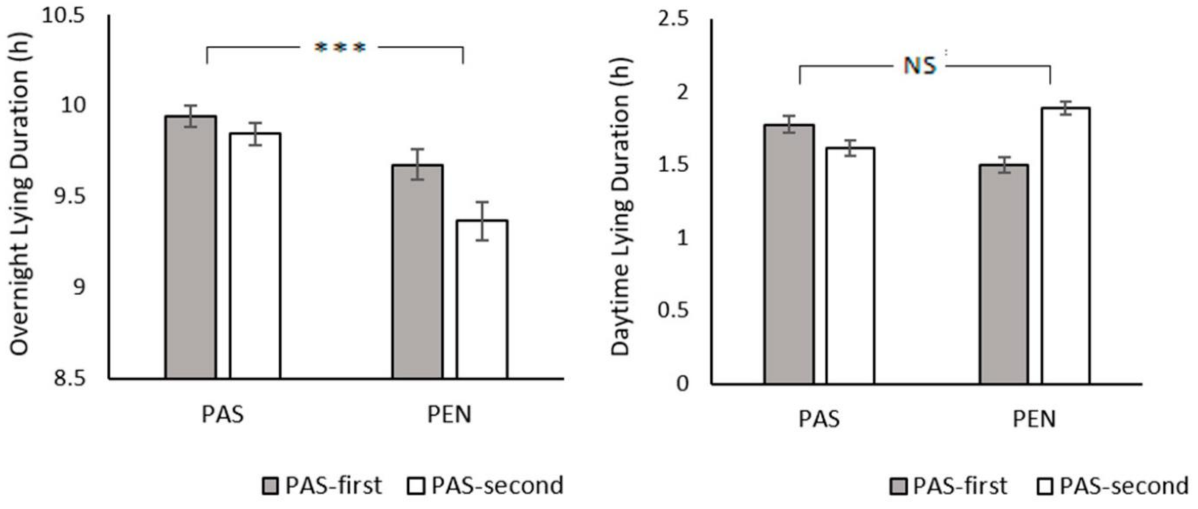
3.3 | Results

I collected data from 29 cows across 36 days. However, the IceQubes did not record every study day or 15-min interval for every subject, reducing the number of measurement days (number of cows × number of study days) and measurement intervals (number of cows × number of study intervals) available for analysis. For both overnight and daytime lying duration, I collected data from all individuals for every day (1,044 measurement days). Overnight lying durations were compiled from 70,429 measurement intervals (563 measurement intervals unrecorded) and daytime lying durations were compiled from 20,759 measurement intervals (121 measurement intervals unrecorded). I gathered data on lying bout frequency and duration from 1,034 measurement days (106 measurement days unrecorded). To measure transitions, I collected data for all subjects from every study day (1,044 measurement days). Overnight transition data came from 70,429 measurement intervals (563 measurement intervals unrecorded) and daytime transition data came from 20,759 measurement intervals (121 measurement intervals unrecorded). For lying synchrony, I calculated 36 herd K_F values for both groups, with 18 per herd per treatment. These scores were based on 5,140 measurement intervals from individual cows (80 measurement intervals unrecorded). Finally, I extracted step counts from 70,429 measurement intervals (563 measurement intervals unrecorded).

Cows with pasture access had significantly longer overnight lying durations than cows indoors (PAS: 9.89 ± 0.04 h; PEN: 9.52 ± 0.07 h; $\chi^2_1 = 27.51$, $p < .001$; Figure 10a). Neither treatment order ($\chi^2_1 = 0.90$, $p = .342$), nor the treatment × treatment order interaction were significant ($\chi^2_1 = 2.21$, $p = .137$). For daytime lying durations, treatment had no significant effect (PAS: 1.70 ± 0.04 h; PEN: 1.71 ± 0.04 h; $\chi^2_1 = 0.06$, $p = .814$) and neither did treatment order ($\chi^2_1 = 0.40$, $p = .530$; Figure 10b). There was a treatment × treatment order interaction ($\chi^2_1 = 43.78$, $p < .001$). The PAS-first group had longer daytime lying durations in the PAS treatment than the PEN treatment, but the PAS-second group had shorter daytime lying durations in the PAS treatment.

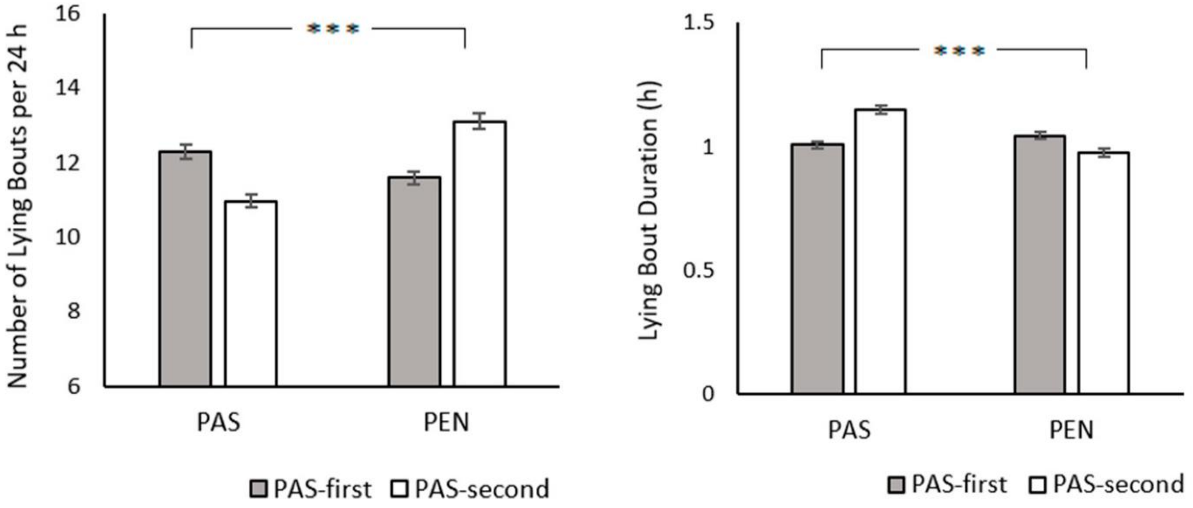
PAS cows had fewer lying bouts than PEN cows (PAS: 11.65 ± 0.13; PEN: 12.31 ± 0.13; $\chi^2_1 = 22.53$, $p < .001$; Figure 11a) and their lying bouts were significantly longer (PAS: 1.08 ± 0.01 h; PEN: 1.01 ± 0.01 h; $\chi^2_1 = 25.23$, $p < .001$; Figure 11b). Treatment order did not influence either the number ($\chi^2_1 = 0.02$, $p = .902$) or duration of lying bouts ($\chi^2_1 = 0.37$, $p = .543$). However, there were significant treatment × treatment order interactions for number

($\chi^2_1 = 97.02$, $p < .001$) and duration of lying bouts ($\chi^2_1 = 79.27$, $p < .001$). Both groups had more and shorter lying bouts in their first treatment.



(a) **(b)**

Figure 10. Effect of treatment and treatment order on **(a)** overnight lying duration and **(b)** daytime lying duration (overnight pasture access: PAS; indoor housing: PEN). Between-treatment significance levels: non-significant: NS; $p < .05$: *; $p < .01$: **; $p < .001$: ***. Error bars represent the standard error of the mean.



(a) **(b)**

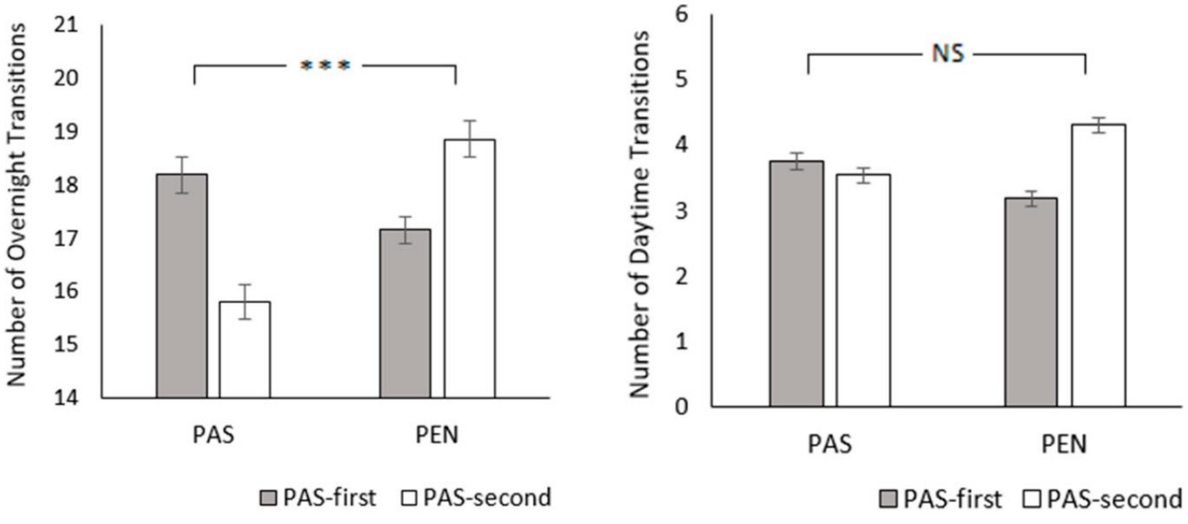
Figure 11. Effect of treatment and treatment order on **(a)** number of lying bouts per 24 h and **(b)** lying bout duration (overnight pasture access: PAS; indoor housing: PEN). Between-

treatment significance levels: non-significant: NS; $p < .05$: *; $p < .01$: **; $p < .001$: ***. Error bars represent the standard error of the mean.

There were significantly fewer overnight transitions in the PAS treatment than the PEN treatment (PAS: 16.96 ± 0.23; PEN: 18.04 ± 0.22; $\chi^2_1 = 16.63$, $p < .001$; Figure 12a). Treatment order did not affect transition frequency ($\chi^2_1 = 0.11$, $p = .743$), but there was a treatment × treatment order interaction ($\chi^2_1 = 58.91$, $p < .001$). In the PAS-first group, subjects transitioned more at pasture than inside, whereas PAS-second cows had fewer transitions at pasture. For daytime transitions, treatment (PAS: 3.65 ± 0.08; PEN: 3.76 ± 0.09; $\chi^2_1 = 1.37$, $p = .242$) and treatment order were not significant ($\chi^2_1 = 1.28$, $p = .258$), but the interaction persisted ($\chi^2_1 = 47.15$, $p < .001$; Figure 12b).

In terms of lying synchrony, K_F values were significantly greater in the PAS treatment than the PEN treatment (PAS: 0.60 ± 0.02; PEN: 0.18 ± 0.02; $\chi^2_1 = 230.254$, $p < .001$; Figure 13). Treatment order also had a marginally significant effect, with lower K_F values in the PAS-first group (PAS-first: 0.36 ± 0.04; PAS-second: 0.41 ± 0.04; $\chi^2_1 = 4.007$, $p = .045$). I did not find a treatment × treatment order interaction ($\chi^2_1 = 0.1628$, $p = .687$).

Compared to the PEN treatment, overnight step counts were higher in the PAS treatment (PAS: 1548.45 ± 22.22; PEN: 571.43 ± 9.76; $\chi^2_1 = 2805.77$, $p < .001$; Figure 14). Treatment order also had a significant effect, with lower step counts in the PAS-first group (PAS-first: 955.30 ± 24.65; PAS-second: 1159.42 ± 29.01; $\chi^2_1 = 9.34$, $p < .005$). Furthermore, the treatment × treatment order interaction was highly significant ($\chi^2_1 = 15.45$, $p < .001$). PAS-first cows had a smaller increase in step count at pasture than PAS-second cows.



(a) (b)

Figure 12. Effect of treatment and treatment order on **(a)** number of overnight transitions and **(b)** number of daytime transitions (overnight pasture access: PAS; indoor housing: PEN). Between-treatment significance levels: non-significant: NS; *p* < .05: *; *p* < .01: **; *p* < .001: ***. Error bars represent the standard error of the mean.

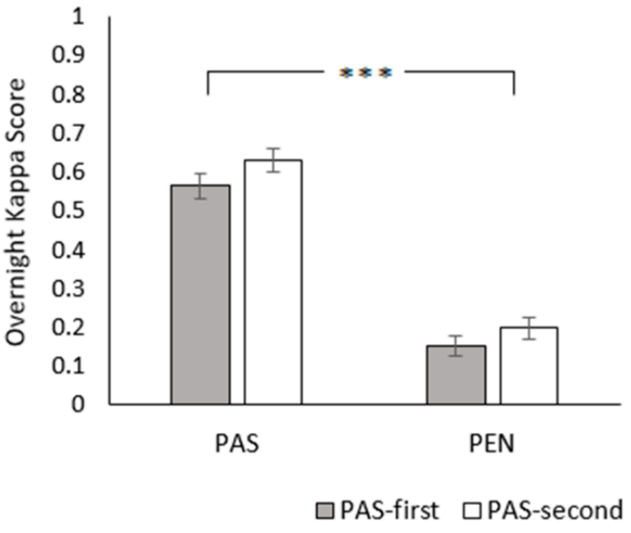


Figure 13. Effect of treatment and treatment order on overnight KF (a measure of group synchrony; overnight pasture access: PAS; indoor housing: PEN). Between-treatment significance levels: non-significant: NS; *p* < .05: *; *p* < .01: **; *p* < .001: ***. Error bars represent the standard error of the mean.

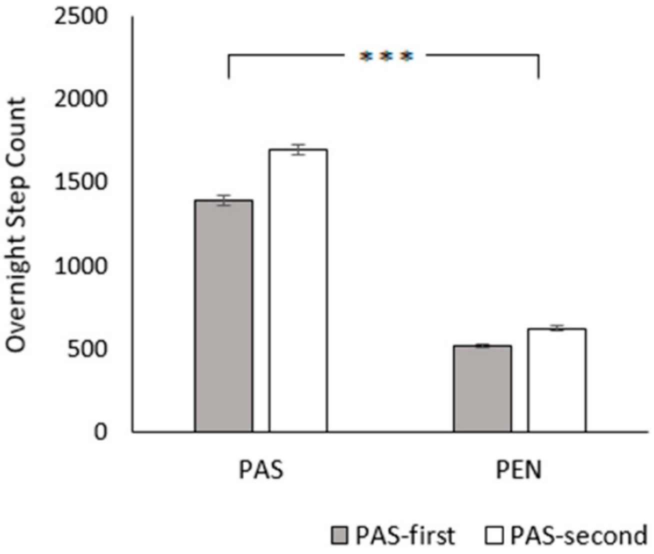


Figure 14. Effect of treatment and treatment order on overnight step count (overnight pasture access: PAS; indoor housing: PEN). Between-treatment significance levels: non-significant: NS; *p* < .05: *; *p* < .01: **; *p* < .001: ***. Error bars represent the standard error of the mean.

3.4 | Discussion

I investigated how overnight pasture access and full-time indoor housing impact dairy cows' lying and walking behaviour, as indicators of their welfare. Pasture access increased behaviours associated with wellbeing in cattle and reduced signs of discomfort, displacements, and poor health. Overnight lying durations were longer at pasture, whilst there was no difference in daytime lying durations when both groups were in indoor housing. Lying is a highly motivated behaviour important for cow welfare, so my results support previous work that cattle are more comfortable at pasture (Fisher *et al.* 2002, Jensen *et al.* 2005, Metz 1985, Munksgaard *et al.* 2005, Munksgaard & Simonsen 1996). At pasture, cows also rested in fewer and longer lying bouts with fewer transitions and greater herd synchrony. This suggests that pasture access reduces restlessness and competition for lying space (Miller & Wood-Gush 1991, O'Connell *et al.* 1989). Finally, cows had higher overnight step counts at pasture, probably because they spent more time grazing.

The lying data indicate that pasture provided a more comfortable surface than cubicles, and more lying space than fully-stocked indoor housing. Cows in the PAS treatment were less restless, with fewer but longer lying bouts, and fewer overnight transitions. Longer lying bouts reflect increased cow comfort (Drissler *et al.* 2005). Moreover, low-ranking individuals often cannot access cubicles at preferred times (Fregonesi *et al.* 2007, O'Connell *et al.* 1989, Olmos *et al.* 2009, Singh *et al.* 1993). The treatment difference in overnight lying duration suggests additional lying bouts did not compensate for this disruption. In addition, I found no difference in lying duration or transitions during the daytime, when both treatments were housed indoors, implying that pasture access was responsible.

My study also supports previous findings that pasture access increases herd synchrony in lying behaviour (Krohn *et al.* 1992, Roca-Fernández *et al.* 2013, Tuomisto *et al.* 2019). Cattle synchronise under semi-natural conditions, indicating that this is their preferred behaviour pattern (Flury & Gygax 2016, Kilgour 2012). Whether animals have what they want is integral to welfare (Dawkins 2003, Franks 2019, Franks & Higgins 2012, Gygax 2017). My results suggest that low-ranking cows in the PEN treatment could not lie when they wanted. Although cubicles were available for every animal, cattle exhibit longer lying durations, less daytime lying, fewer displacements, and greater lying synchrony when cubicle housing is understocked than fully-stocked (Winckler *et al.* 2015). This could be because limited cubicles prevent subordinates from lying where they want. Pasture, by contrast, provides ample lying space. As a result, I suggest that pasture access promotes the animals' agency, an important aspect of welfare (Špinka 2019).

Moreover, these results flag boredom as a potential welfare issue for cattle housed indoors full-time. In animals, boredom is an aversive state that arises from general under-stimulation, rather than the frustration of any specific need or motivation (Mason & Burn 2018). Subjects in the PAS treatment spent a greater proportion of the night lying and walking, and cattle in the PEN treatment were standing inactive for longer. “Idle standing” may indicate poor welfare in cattle, and is associated with hard lying surfaces (Haley *et al.* 2000, Leonard *et al.* 1994, Rushen *et al.* 2007). From a health perspective, excessive standing can cause lameness, especially when the animal is partially in a cubicle (Dippel *et al.* 2011, Galindo *et al.* 2000, Proudfoot *et al.* 2010), as well as being a symptom of disease (e.g. mastitis: Fogsgaard *et al.* 2012; metritis: Patbandha *et al.* 2012). Cows at pasture also spend a greater proportion of the day feeding (Phillips 2002), although the IceQubes did not record these data. As such, cattle housed indoors full-time have little to do for long timespans. Burn (2017) linked under-stimulation with restlessness and disrupted sleep patterns in mammals (e.g. humans: Nanda *et al.* 2012; rats: Abou-Ismail *et al.* 2010). Boredom could, therefore, explain the PEN treatment’s disrupted lying behaviour, compounded by abrasive surfaces and competition for cubicles. However, standing inactive has been attributed to depression-like states, as well as under-stimulation (Fureix *et al.* 2012, Harvey *et al.* 2019, Meagher *et al.* 2017). Isolating boredom requires specific behavioural indicators that I did not record, such as measures of time perception and responses to novel stimuli (Burn 2017, Meagher 2018).

Contrary to the overall lying results, both groups displayed signs of discomfort during the first testing period. The PAS-first group had longer daytime lying durations, more and shorter lying bouts, and more overnight transitions at pasture compared to indoor housing – results that were opposite to the PAS-second group. I attribute this to heat stress (reviewed by Kadzere *et al.* 2002, Polsky & von Keyserlingk 2017). Despite similar mean daily temperatures in both periods, the maximum temperature was substantially higher in the first period (Table 4). Thermal stress reduces walking (Polsky & von Keyserlingk 2017), which may be why the PAS-first group exhibited a smaller increase in step count at pasture than the PAS-second group. Moreover, daily sunlight hours were longer in the first period. The PAS treatment had no shade, further explaining the cows' discomfort (Kendall *et al.* 2006, Van Iaer *et al.* 2014, Vizzotto *et al.* 2015, West 2003). On the other hand, the first period had fewer hours per day with relative humidity ≥ 90%. Increasing relative humidity worsens heat stress (Kadzere *et al.* 2002). During hot weather, some preference studies have recorded cattle spending more time in their indoor housing (Falk *et al.* 2012, Legrand *et al.* 2009). However, Charlton *et al.* (2011a) observed high temperatures increasing durations at pasture, possibly reflecting their setup's temperate climate. This finding illustrates the importance of context in dairy cow management. During extreme weather, pasture access may compromise welfare if animals must remain outside with no shelter.

Table 4. Meteorological data for both periods of the experiment (recorded 24 km from study site). Crown copyright (2018). Information provided by the National Meteorological Library and Archive–Met Office, United Kingdom.

Testing Period	Mean Temperature (°C)	Maximum Temperature (°C)	Sunshine Suration (h/d)	Relative Humidity ≥ 90% (h/d)	Rainfall (mm/d)
1	15.7	30.0	8.8	4.9	0.0
2	15.8	25.8	2.9	8.9	5.5

The PAS treatment's higher overnight step counts indicate that cows at pasture were healthier and satisfying a behavioural need, which indoor housing constrained. Pasture access increases walking because gait improves (Hernandez-Mendo *et al.* 2007), feeding durations are longer (Kennedy *et al.* 2009, Roca-Fernández *et al.* 2013), and cattle must continually walk whilst grazing (Broom & Fraser 2015). Furthermore, treatment order had an effect, with less walking in the group that went out to pasture first. The increase in step counts in the PAS treatment was also smaller for the PAS-first group than the PAS-second group. This may reflect the higher quality herbage in the first period, which potentially reduced walking distances whilst grazing. Alternatively, PAS-first cows were indoors for 18 fewer days than PAS-second cows before going out to pasture. Longer indoor housing could have increased the PAS-second group's motivation to move (Jensen 1999, 2001, Loberg *et al.* 2004). In addition to improving physical health, motor activity may enhance cows' psychological wellbeing, as exercise can have antidepressant effects in humans (Bailey *et al.* 2018, Byrne & Byrne 1993, Cheval *et al.* 2018, Ernst *et al.* 2006, Penedo & Dahn 2005) and rodents (Aujnarain *et al.* 2018, Cevik *et al.* 2018, Liu *et al.* 2013). To my knowledge, animal welfare scientists have not directly tested whether physical activity influences psychological indicators of wellbeing.

3.5 | Conclusions

I explored how overnight pasture access influences behavioural indicators of dairy cow welfare. Lying durations were longer at pasture than in indoor housing. Herd lying behaviour was also more synchronous outside, and partitioned into fewer but longer lying bouts, with fewer transitions. This suggests that pasture was a more comfortable lying surface, reduced competition for lying space, and allowed cows to lie when and where they wanted. However, I found several unexpected treatment × treatment order interactions. Cows that went outside first were more restless at pasture than in indoor housing. I attribute this to heat stress and recommend providing shelter at pasture (depending on the local climate). Additionally, overnight step counts were higher in the pasture treatment, which may benefit cattle physically and psychologically. Reduced lying and walking durations also suggest boredom is an issue in indoor housing, as cows have nothing to do for much of the day. These findings indicate that overnight pasture access improves dairy cattle welfare, and that the judgement bias task failed to detect differences in affective state. As judgement bias apparently did not indicate emotions in dairy cows, alternative cognitive bias tasks may complement judgement bias tasks as welfare indicators. I now review attention bias as a potential welfare indicator.

4 | Affect-driven attention biases as animal welfare indicators: A methodological review

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Abstract. Attention bias describes the differential allocation of attention towards one stimulus compared to others. In humans, observer affective state can mediate this bias, which is implicated in the onset and maintenance of mood disorders. Affect-driven attention bias (ADAB) has also been identified in other species. Here, I review ADABs in animals and discuss their use as welfare indicators. Negative affective states modulate attention to negative (i.e. threatening) stimuli. Positive-valence states may also influence animals' ADAB. I discuss attention bias tasks and conclude that looking time, dot-probe, and emotional spatial cueing paradigms are especially promising. However, research is needed to test more species, investigate attentional scope as an affective state indicator, and explore the causative role of attention biases in animal wellbeing. Finally, I argue that ADAB may not indicate general valence, but instead reveal specific emotions, motivations, aversions, and preferences. Paying attention to the human literature could facilitate these advances.

4.1 | Introduction

In Chapter Two, a judgement bias task failed to detect treatment differences in affective state, despite data on reward anticipation, lying behaviour, and step counts indicating that pasture access improved psychological wellbeing. This finding illustrates the limitations of judgement bias as a welfare indicator. Long training periods are time-consuming for researchers, impractical in applied settings, and lead to attrition of subjects. The effects of stress on learning (Conrad 2010, Sandi 2013, Vogel & Schwabe 2016) may also cause a selection bias, with animals in negative-valence states less likely to meet inclusion criteria (Mendl *et al.* 2009). Furthermore, subjects tested repeatedly can learn that the probes are unreinforced, making them less likely to respond (Brilot *et al.* 2010, Doyle *et al.* 2010b). This gives the appearance of increased pessimism without any change in affective state. Additionally, judgement bias tasks require well-designed controls for non-valence variables, such as arousal, motivation, distraction, and general activity (Bethell 2015, Mendl *et al.* 2009). These methodological issues may explain the sizable minority of judgement bias studies reporting null results (Anderson *et al.* 2013, Brilot *et al.* 2009, Carreras *et al.* 2016, Crump *et al.* 2019b, Gott *et al.* 2019, Müller *et al.* 2012, Parker *et al.* 2014, Scollo *et al.* 2014, Wichman *et al.* 2012) or findings opposite to predictions (Briefer & McElligott 2013, Burman *et al.* 2011, Doyle *et al.* 2010a, Freymond *et al.* 2014, Sanger *et al.* 2011). Cognitive bias paradigms that require less training and fewer controls may obviate such issues, thereby enabling researchers to detect the impact of HIREC on animals’ emotional wellbeing.

Another class of cognitive bias, attention bias, describes the differential allocation of attentional resources towards one stimulus compared to others (for earlier discussion, see Bethell 2015, Clegg 2018, Mendl *et al.* 2009, Paul *et al.* 2005). Unlike judgement bias, attention bias can be measured with little or no training and without interpreting optimistic or pessimistic responses. Moreover, attention is the interface between external stimuli and downstream cognitive processes that determine internal valence. In humans, attention biases towards negative information are thus implicated in the onset and maintenance of mood disorders, such as anxiety, social phobia, and post-traumatic stress disorder (McNally 2019, Sipos *et al.* 2014). The stimuli that animals attend likewise underpin their affective experience and, ultimately, their psychological wellbeing. Attention biases, therefore, warrant investigation (Bethell *et al.* 2012, Brilot *et al.* 2009, Crump *et al.* 2018).

Cognitive psychologists distinguish between different aspects of attention: initial engagement (attentional capture or orienting, which is enhanced for threat-relevant stimuli; Öhman *et al.* 2001), maintenance of attention towards a stimulus (enabling detailed processing), and disengagement (which facilitates shifting to other stimuli; Posner & Petersen 1990). Affective state influences each stage, from faster engagement to enhanced maintenance and facilitated (Amir *et al.* 2003, Fox *et al.* 2001) or impaired disengagement (Rudaizky *et al.* 2014). As an example, clinically anxious populations look towards threatening information faster and for longer than non-anxious populations (Bar-Haim *et al.* 2007, Cisler & Koster 2010, MacLeod *et al.* 2019). Some studies also associate depression with an attention bias to threat (Mathews *et al.* 1996, Mogg *et al.* 1995) and away from positive-valence stimuli (Armstrong & Olatunji 2012). These attention biases are measured using attention bias tasks (ABTs), which experimentally measure attention allocation to stimuli (reviewed by Yiend 2010). Gaze might be tracked directly or response latencies recorded to specific cues.

In animal welfare science, attention modulated by the observer’s affective state is usually called “attention bias”. However, the human literature also recognises attention biases unrelated to affective state. For example, people locate inverted letters amongst upright letters faster than upright letters amongst inverted letters (Reicher *et al.* 1976). Neither stimulus valence nor the observer's affective state induced this attention bias to novelty. To maintain clarity and facilitate inter-disciplinary knowledge-transfer, I suggest that welfare scientists adopt the term affect-driven attention bias (ADAB). ADABs are attention biases towards or away from emotional information, which are influenced by the observer's affective state. Emotional stimuli may be either innately valenced (primary reinforcers, e.g. facial expressions; Bradley *et al.* 2000) or conditionally valenced, with emotional content acquired through association with primary reinforcement (secondary reinforcers, e.g. shock-paired images; Lim *et al.* 2009).

In this review, I evaluate ADAB as a welfare indicator and outline existing animal studies. Research on visual attention is prioritised, although attentional resources can be allocated to information from other sensory modalities. I discuss animal studies in the context of the most common ABTs, focusing on their potential as welfare indicators. Finally, I suggest future directions for ADAB research.

4.2 | Literature Search and Study Selection

I reviewed the literature on attention bias as an indicator of affective states in animals. In March 2018, I searched the Web of Science database with the term "attention bias animal welfare" (26 results). This was updated in July 2018 and August 2020. References to "attention" or "attention bias" were also identified in previous reviews of cognitive bias (Baciadonna & McElligott 2015, Bethell 2015, Mendl *et al.* 2009, Paul *et al.* 2005, Roelofs *et al.* 2016) and ABTs for animals (van Rooijen *et al.* 2017, Winters *et al.* 2015). In addition, the references in papers identified through these methods and the papers citing them were systematically searched, as well as papers citing the reviews. I read the titles and abstracts to ascertain relevance. Subjects must have been tested in different valence conditions, and their attention measured towards an emotional stimulus or stimuli. I also included animal welfare research where the authors described their findings as an attention bias. Table 5 summarises studies that met these criteria.

Table 5. Affect-driven attention bias studies on animals.

Species	Reference	*N*	Stimuli	Measure/Manipulation of Affective State/Trait	Measure of Attention	Findings
			Single-Presentation Looking Time Task			
Starling	Brilot *et al.* (2009)	32	Eyespots, ambiguous eyespots, CTRLs	NV: predator call, alarm call, white noise	Orienting towards stimuli	No treatment difference
Sheep	Verbeek *et al.* (2014)	41	Empty food bucket	NV: food-deprivation	Detection/approach latency, object interaction	No effect for detection/approach latency; NV sheep interacted longer
	Vögeli *et al.* (2015)	29	Aggressive, affiliative, & non-social behaviours (video)	NV: unpredictable, unenriched housing; PV: predictable, enriched housing	Orienting towards stimuli	Time oriented towards stimuli (all subjects): aggressive > neutral > affiliative. NV: oriented towards stimuli longer overall
			Dual-Presentation Looking Time Task			
Tufted capuchin	Boggiani *et al.* (2018)	15	Image of neutral (student) or NV human (vet)	PV: Subordinate bystander; NV: Dominant bystander	Choosing reward under image	NV subjects: faster to take reward under NV human image, indicating attention to threat

Cattle	Lee *et al.* (2018)	36	Dog / food	NV: anxiogenic; PV: anxiolytic	Looking time, head up duration, latency to eat	NV looking duration / head up / latency to feed > CTRL; no effect for PV
Pig	Luo *et al.* (2019)	128	Flashing light + moving door / food	NV: barren housing; PV: enriched housing	Looking time, vigilance	Early-life conditions: no effect; current conditions: PV = ADAB to threat
Rhesus macaque	Bethell *et al.* (2012)	7	Aggressive / neutral faces	NV: post-vet health-check; PV: 1 wk enrichment	Eye gaze	No effect for orienting; NV monkeys disengaged faster from aggressive faces
Starling	Brilot *et al.* (2012)	14	Alarm call / food	NV: no water bath	Head up/down duration	NV birds longer head-up bout & shorter head-down bout duration
Sheep	Lee *et al.* (2016)	60	Dog / food	NV: anxiogenic; PV: anxiolytic	Looking time, head up duration, latency to eat	Looking time to dog / head up / latency to eat: NV > CTRL > PV
	Monk *et al.* (2018a)	50	Dog / conspecific photo	NV: anxiogenic	Looking time	Looking time to photo: NV > CTRL

Monk *et al.* (2018b)	60	Dog / food	NV: anxiogenic; PV: anxiolytic	Looking time, head up duration, latency to eat	Looking time to dog / head up / latency to eat: NV > CTRL > PV
Monk *et al.* (2019a)	32	Dog / conspecific photo	NV: anxiogenic	Looking time	No treatment difference
Monk *et al.* (2019b)	80	Dog / conspecific photo	NV: anxiogenic	Looking time	No treatment difference
Monk *et al.* (2020)	80	Dog / conspecific photo	NV: anxiogenic	Looking time	No treatment difference
Raoult & Gygax (2019)	32	Dog vocalisation / conspecific vocalisation	NV: 2 wk aversive events; PV: 2 wk positive events	Looking time	Looking time to dog vocalisation: NV > PV
Verbeek *et al.* (2019)	60	Dog / conspecific photo	NV: Sleep deprivation and individual housing	Looking time	Looking time to photo: NV > CTRL
Emotional Stroop Task					

Chimpanzee	Allritz *et al.* (2016)	7	Vet (NV) & other humans	NV: post-vet health-check	Colour discrimination task RTs	All subjects: RTs slower to touch correct colour when it contained vet image than non-threatening humans. NV subjects: slower than CTRLs to touch correct colour when it contained vet image
Laboratory mouse	Trevarthen *et al.* (2019)	62	Flashing light (NV) & food (PV)	NV: tail-handling Relatively PV: tunnel-handling	Runway latency	All subjects: faster to approach food than light. No difference in runway latency between NV and relatively PV treatments
Orange-winged amazon	Cussen & Mench (2014)	20	Human	Subjective personality assessment	Spatial memory task RTs	Negative correlation between neuroticisim ratings & task performance (suggests greater distraction from human present)
			Visual Search Task			
Guinea baboon	Marzouki *et al.* (2014)	6	T-/L-shapes (conditioned valence)	NV & PV behaviours (observational)	RT to the target	RT: NV > CTRL > PV

Dual-Presentation Judgement Bias Task						
Laboratory rat	Parker *et al.* (2014)	16	Tones (conditioned valence)	NV: unpredictable housing	Lever pressed (binary) & RT to lever press	NV rats pressed positive lever (optimistic responses) more than CTRLs, suggesting ADAB towards negative-valence stimulus

Abbreviations: negative valence (NV), positive valence (PV), response latency (RT), control (CTRL), affect-driven attention bias (ADAB).

4.3 | Results and Discussion

I identified 21 ADAB studies, which investigated 11 species and used five ABT methodologies. Sixteen studies identified significant treatment differences potentially attributable to ADAB. I now discuss this body of research in the context of ABTs from cognitive psychology and other attention studies on animals. In particular, I focus on state ADAB, rather than trait affect, and experiments where ADABs were not confounded with judgement biases, which have been reviewed elsewhere (Baciadonna & McElligott 2015, Bethell 2015, Mendl *et al.* 2009, Neville *et al.* 2020, Paul *et al.* 2005, Roelofs *et al.* 2016).

4.3.1 Looking Time Tasks

The simplest ABTs are looking time tasks (reviewed by Winters *et al.* 2015). Originally developed for human infants (Fantz 1958), looking time tasks directly measure gaze patterns towards visual stimuli, presented either singly or simultaneously. Single-presentation tasks compare looking time between successive trials and reveal which aspects of a stimulus are attended or avoided in the absence of distractions. By contrast, dual-presentation tasks (the preferential looking paradigm or visual paired comparison) introduce competition between stimuli for processing (Desimone & Duncan 1995).

Although the preferential looking paradigm had been used to investigate social attention (e.g. Waitt *et al.* 2006), Bethell *et al.* (2012) conducted the first ADAB study with rhesus macaques (*Macaca mulatta*). Subjects were shown two images of conspecific faces simultaneously (one aggressive, the other neutral) and ADAB was quantified as more time spent looking at one image than the other. Monkeys were tested after a negative-valence manipulation (veterinary health-check) and during a positive-valence manipulation (enhanced enrichment). The macaques showed an attention bias towards the aggressive face: they looked towards it faster than the neutral face. However, the affective state manipulation mediated maintenance of attention towards the aggressive face. Monkeys continued looking at the aggressive face during enrichment but looked away faster following the veterinary check (and continued to avoid the face for the rest of the trial).

In a subsequent primate study, Boggiani *et al.* (2018) exposed tufted capuchins (*Sapajus apella*) to either a submissive subordinate conspecific or an aggressive dominant conspecific. These treatments were designed to induce a relatively positive and negative state, respectively. In the conspecific's presence, capuchins were shown two images: a neutral human (a student in the lab) and an aversive human (the veterinarian). A food reward was placed under each of these competing stimuli, and the measure of attention was latency to the reward. The authors hypothesised that shorter response latencies to the veterinarian-linked reward indicated a stronger ADAB to threat. As predicted, capuchins exposed to the aggressive conspecific were faster to the veterinarian-linked reward than capuchins exposed to the subordinate. This was interpreted as aggression inducing a negative-valence state, which induced an ADAB to threat.

Another ADAB looking time paradigm has been developed for sheep (Lee *et al.* 2016) and cattle (Lee *et al.* 2018; see also Welp *et al.* 2004). After subjects entered a test arena with food available, a hatch opened for 10 s to reveal a dog (a threatening predator stimulus). The response variables were looking time towards the dog and towards the closed hatch after the dog's removal, as well as latency to feed. Early studies found that, in both sheep and cattle, looking time towards the hatch increased with the administration of anxiogenic drugs and decreased with anxiolytics (Lee *et al.* 2016, 2018, Monk *et al.* 2018b). However, using food as the positive stimulus introduced food-motivation as a confound. The authors subsequently used a conspecific photograph for the positive stimulus, but this produced equivocal results.

Sheep treated with anxiogenics either directed more attention towards the conspecific image than the dog (Monk *et al.* 2018a) or there were no treatment differences in looking behaviour (Monk *et al.* 2019a, b, 2020). Sheep chronically stressed through sleep disruption and individual housing also displayed an ADAB towards the positive stimulus, as well as a relatively optimistic judgement bias (Verbeek *et al.* 2019). These findings may be because the conspecific photo was perceived as novel, rather than a conspecific. Future research could introduce a live sheep as the positive stimulus.

Three further studies have investigated ADAB in sheep (Raoult & Gygax 2019, Verbeek *et al.* 2014, Vögeli *et al.* 2015; see also McBride & Morton 2018). Verbeek *et al.* (2014) demonstrated that food-deprived sheep interacted with an empty food bucket longer than satiated sheep, which the authors interpreted as enhanced attention. In a longer-term study, Vögeli *et al.* (2015) kept flocks in two housing conditions, either enriched and predictable to cause positive-valence moods or unenriched and unpredictable to induce negative-valence moods. Subjects were then shown videos of other sheep engaged in aggressive, affiliative or non-social behaviours. Both treatments spent the most time oriented towards the aggressive behaviours and the least towards the affiliative behaviours. Negative-valence sheep spent longer oriented towards the stimuli overall, however, which may have been an ADAB to social information. A video-based preferential looking paradigm has also been tested on sheep (Raoult & Gygax 2018), although this study did not include an affective state manipulation. Unlike in Vögeli *et al.'s* study, the authors found no significant differences between the positive- (conspecifics) and negative-valence stimuli (dogs). Finally, Raoult & Gygax (2019) exposed sheep to either two weeks of unpredictable, negative events or two weeks or predictable, positive events. Sheep were then played two competing sound stimuli: a negative-valence dog bark and a positive-valence sheep bleat. Subjects in the negative-valence treatment allocated more attention to the dog bark – a potential ADAB to threat.

Contrary to previous livestock studies, Luo *et al.* (2019) found no effect of long-term environmental conditions on ADAB to threat in pigs. Subjects were housed from birth in either barren or enriched housing. At seven weeks old, pigs either swapped or did not swap housing conditions. At 11 weeks old, they were simultaneously exposed to a threatening stimulus (flashing light and moving door) and a positive stimulus (food; following Lee *et al.* 2016). All pigs displayed an attention bias to threat: they spent longer looking towards the threat than the positive stimulus. However, housing from one to seven weeks did not influence looking behaviour. This finding indicates that early-life conditions do not have long-term impacts on affective state in pigs. On the other hand, current housing (seven to 11 weeks) did mediate responses. Compared to pigs in barren housing, enriched pigs were more vigilant and looked towards the threat more frequently. These results correspond with previous studies suggesting that the link between valence and ADAB to threat is more complex than a linear negative correlation (e.g. humans: Bar-Haim *et al.* 2007; macaques: Bethell *et al.* 2012; sheep: Verbeek *et al.* 2019).

Brilot *et al.* (2009) reported null results in an ADAB to threat study on starlings (*Sturnus vulgaris*). The experimenters switched off cage lights, added food, and exposed birds to either a negative-valence treatment (alarm calls, predator calls, and white noise) or a control treatment (conspecific calls). When the lights came on again, predator eyespots appeared and competed with the food for attention. However, there were no treatment differences in time oriented towards the stimuli. Brilot *et al.* attributed this to eyespots not being inherently aversive.

Looking time tasks are a practical way to measure ADAB. Quantifying gaze directly avoids potentially confounding proxies and allows different aspects of attention to be distinguished. Moreover, gaze patterns across stimuli can be observed. For instance, Somppi *et al.* (2016)

demonstrated that dogs fixated on certain facial features, especially the eyes, and the face's valence influenced this effect. Measuring untrained looking behaviour is also useful when conditioning would be impractical or impossible, such as with wild animals and marine species. By suspending objects from a ship, for example, Siniscalchi *et al.* (2012) measured the looking time of striped dolphins (*Stenella coeruleoalba*) in the Mediterranean Sea. Other paradigms have been successful with free-ranging macaques (Dubuc *et al.* 2016, Mandalaywala *et al.* 2014, 2017, Schell *et al.* 2011). Future research might also investigate underrepresented groups (e.g. reptiles; see Matsubara *et al.* 2017, Wilkinson & Huber 2012). Indeed, studies on lizards have already measured looking behaviour towards conspecific (Frohnwieser *et al.* 2017) and predator stimuli (Bonati *et al.* 2013).

However, the relationship between looking time and valence is difficult to interpret. In Bethell *et al.'s* (2012) macaque study, the authors predicted that negative-valence subjects would allocate more attention towards the threatening faces, but their looking times were shorter. Human studies have also associated negative-valence states with both attention to threat (Reicher *et al.* 1976) and threat-avoidance (Bar-Haim *et al.* 2007, Cisler & Koster 2010, MacLeod *et al.* 2019, Mathews *et al.* 1996, Mogg *et al.* 1995). This directionality issue may be overcome by varying stimulus intensity. Human research has identified avoidance of low-level threat and attention to high-level threat in nonclinical populations (Mogg *et al.* 2000, Wilson & MacLeod 2003). Demonstrating this effect in macaques may require more objective methods for classifying stimuli, such as the Macaque Facial Action Coding System (MaqFACS; Parr *et al.* 2010).

Another potential flaw is that some ADAB studies measure looking time imprecisely (e.g. whether the subject's head is up; Brilot *et al.* 2009). Alternatives include manually coding gaze from video footage (e.g. Bethell *et al.* 2012) and automated eye-tracking (see Hopper *et* *al.* 2020, Machado & Nelson 2011, Winters *et al.* 2015; human studies reviewed by Armstrong & Olatunji 2012, Beesley *et al.* 2019, Lisk *et al.* 2020, Hansen & Ji 2009, Mele & Federici 2012). The latter is fast, objective, and accurate, but also expensive and needs modifying for new species (e.g. marmosets, *Callithrix jacchus*: Kotani *et al.* 2017; peafowl, *Pavo cristatus*: Yorzinski *et al.* 2013; archerfish, *Toxotes chatareus*: Ben-Simon *et al.* 2009). Although impractical outside controlled conditions, eye-trackers have been mounted on freely-moving ring-tailed lemurs (*Lemur catta*; Shepherd & Platt 2006, 2008). Head-trackers provide similar information for birds, which move their heads in coordination with their eyes (Land 1999). Kano *et al.* (2018) measured homing pigeons' (*Columba livia*) head movements as a gaze proxy during long-range flights. Whilst existing tasks typically measure attention to static images, responses to photographs are often quantitatively weaker or qualitatively different than responses to moving images or the objects themselves (Bovet & Vauclair 2000, Mustafar *et al.* 2015). Researchers could experiment with videos (D'Eath 1998, Nelson & Fijn 2013, Oliveira *et al.* 2000, Waitt & Buchanan-Smith 2006), computer animations (Chouinard-Thuly *et al.* 2017, Woo & Rieucau 2011), and real animals or objects.

These studies demonstrate the potential of looking time tasks to investigate ADAB, with evidence that gaze is affect-modulated in macaques, capuchins, sheep, cattle, and pigs. Similar paradigms would be suitable for any animal with measurable gaze, including birds and reptiles, and the simplest methods do not require training. Looking time tasks could, therefore, be adapted to diverse species and situations.

4.3.2 Emotional Stroop Tasks

The emotional Stroop task measures how much emotional information distracts an individual as they perform an otherwise neutral cognitive task (Stroop 1935; reviewed by MacLeod *et* *al.* 1991). Typically, participants are instructed to name the colour in which words appear on a screen. Anxious populations are slower to name the colour of negative-valence words (e.g. pain) than neutral words (e.g. gain), an effect absent in non-anxious people (Williams *et al.* 1996). Variants of the task using facial expressions (neutral, aggressive, and happy) instead of words produce similar results (Mauer & Borkenau 2007). Emotional Stroop effects are interpreted as negative-valence states enhancing attentional capture by negative-valence distractor content (Mathews & Macleod 1985, Mogg *et al.* 1989, Reynolds & Langerak 2015). However, the task does not distinguish between attentional capture, maintenance, and disengagement, nor rule out alternative explanations such as freeze response (Algom *et al.* 2004).

Allritz *et al.* (2016) developed an emotional Stroop task for chimpanzees. Subjects were trained to press a blue-framed square on a touchscreen, but not a yellow-framed square. Response latencies were then recorded to blue-framed squares containing images of either the veterinarian or non-threatening humans. The chimpanzees were slower to touch the blue frame when it contained a picture of the veterinarian, a slowing effect that was stronger when they had recently undergone a veterinary procedure. This was attributed to ADAB; specifically, stimuli associated with negative-valence states capturing attention (see also Bethell *et al.* 2016).

However, Allritz *et al.'s* (2016) paradigm required extensive training. Of 16 chimpanzees conditioned on the blue/yellow discrimination task, only seven met the inclusion criteria. Even those needed 900-6,700 trials. This extended training period and attrition of subjects suggests the paradigm may be impractical for welfare assessment. More fundamentally, reaction latencies in the emotional Stroop paradigm can reflect motor action biases rather than ADAB, so changes in response are difficult to interpret in terms of attention. This is less of an issue in other ABTs, which measure reaction latencies to neutral targets after the emotional stimuli have disappeared.

Other studies have quantified emotional Stroop effects by observing how emotional stimuli distract from a task. Trevarthen *et al.* (2019) trained mice (*Mus musculus*) to traverse a runway. Subjects then underwent either a relatively positive (tunnel-handling; Gouveia & Hurst 2013) or negative manipulation (tail-handling), before being tested on a runway containing either a positive (food) or negative stimulus (flashing light). Mice approached the food faster than the light. However, there was no significant difference in runway latency between the positive- and negative-valence treatments. Such latency-based tasks may also measure startle responses, rather than attention. In another study, human presence impaired amazon parrots' (*Amazona amazonica*) performance in a foraging task, and this effect correlated with subjective ratings of the birds' neuroticism (Cussen & Mench 2014). Landman *et al.* (2014) found that threatening facial expressions distracted macaques from a visual task, whereas Bellegarde *et al.* (2017) reported that sheep learnt a discrimination task faster when it involved negative-valence facial stimuli than neutral images.

Emotional Stroop effects have also been identified in learned helplessness. A classic model of depression, learned helplessness describes the unresponsiveness of animals that cannot escape repeated uncontrollable stressors (Maier & Seligman 2016). It is linked to an attention bias towards goal-irrelevant external stimuli (Lee & Maier 1988). In studies on rats, subjects with learned helplessness performed equivalently to controls on a cognitive task, but they were slower and more error-prone when the experimenter was present as a distraction (Jackson *et al.* 1980, Minor *et al.* 1984). Rodd *et al.* (1997) eliminated training completely by investigating innate behaviour in chickens. When eyespots were present, helpless birds froze for longer than controls, but recovered faster in the presence of unaffected conspecific distractors. Despite indicating a putatively negative-valence state, I do not consider these examples of ADAB, because they are attention biases towards external stimuli rather than emotional stimuli *per se* (Lee & Maier 1988). Learned helplessness research nonetheless demonstrates that depression-like states induce attentional shifts, as well as anxiety. Similar experiments could investigate ADAB.

The conventional emotional Stroop task has only been tested on chimpanzees, although emotional Stroop effects are observed in various species. Given training requirements and interpretation issues, the human paradigm is unlikely to translate to applied settings. However, neutral task performance or behavioural shifts in the presence of a threatening stimulus are a simple, adaptable way to measure ADAB in animals.

4.3.3 Dot-Probe Tasks

The dot-probe paradigm presents participants with two stimuli on a screen (MacLeod *et al.* 1986; reviews and meta-analyses by Peckham *et al.* 2010, van Rooijen *et al.* 2017, Winer & Salem 2016). These stimuli may be words (e.g. threatening/neutral pairs; MacLeod *et al.* 1986, Mogg *et al.* 1992) or images (e.g. different facial expressions; Bradley *et al.* 2000, Matthews *et al.* 2003). After a fixed duration, both stimuli disappear and one is replaced by the “dot-probe” – a neutral target that subjects must respond to. Shorter response latencies indicate that the participant’s attention was already fixed on that location, whereas longer response latencies suggest that their attention shifted from the other location. In humans, dot-probe studies pairing negative and neutral stimuli demonstrate that attention to threat is stronger in anxious (Bradley *et al.* 1998, Reicher *et al.* 1976) and depressed people (Peckham *et al.* 2010), and during high-stress situations (Bar-Haim *et al.* 2010, Sipos *et al.* 2014).

To my knowledge, no dot-probe studies have tested for ADAB in animals. However, Kret *et al.* (2016) identified attention biases to positive-valence social cues in bonobos (*Pan paniscus*). When presented with image pairs of conspecifics performing emotion-regulatory and neutral behaviours, subjects responded faster when targets replaced the emotional stimuli, but only for certain behaviour classes. Effects were significant for grooming and sex, but not play or distress. This attention bias towards affiliative interactions might facilitate bonobos' characteristic conflict-resolution and emotion-regulation strategies (Clay & de Waal 2013).

Other researchers have trained macaques to perform dot-probe tasks (e.g. Lacreuse *et al.* 2013, Masataka *et al.* 2018, Parr *et al.* 2013). King *et al.* (2012) observed a baseline attention bias towards threatening stimuli (open-mouth conspecifics), which testosterone administration did not affect. In a study on Japanese macaques (*Macaca fuscata*), Koda *et al.* (2013) used stimulus pairs of newborns and adults, but response latencies were not significantly different. These tasks offer a snapshot of attention allocation; adjusting stimulus duration can explore engagement and maintenance of attention. Testing with multiple durations offers a better understanding of the aspects of attention involved, with shorter durations measuring engagement (e.g. Koda *et al.* 2013) and longer durations measuring disengagement (e.g. Lacreuse *et al.* 2013).

Future dot-probe studies could investigate whether affective state manipulations influence response latencies and explore the aspects of attention underpinning ADAB. Although the task requires relatively little training, touchscreens are best suited to controlled settings and dexterous subjects, especially primates.

4.3.4 Emotional Spatial Cueing Tasks

Spatial cueing tasks also quantify attention biases through response latencies to a neutral target (Posner 1980). Subjects first fixate on the centre of a screen. The objective is to respond as quickly as possible to a target, which can appear on either side. Before the target's appearance, a cue signals its position. This cue is usually located where the target will be, but is on the other side of the screen in a minority of trials. Response latencies when the cue correctly predicts the target's location indicate attentional engagement towards the cue, whereas response latencies when the target and cue appear in different locations indicate cue disengagement (Stormark *et al.* 1995, Yiend & Matthews 2001). Hence, spatial cueing distinguishes between different aspects of attention.

The emotional spatial cueing paradigm manipulates the cue's affective content. As an example, Fox *et al.* (2001) tested anxious and non-anxious people on a task with threatening words and faces as cues. There was no treatment difference in engagement, but a significant difference in disengagement. Anxious individuals were slower to shift their attention from the threatening cue to the neutral target.

No studies have adapted the emotional spatial cueing task for animals. However, non-valenced predictive cue paradigms have been successful with macaques (Cook & Maunsell 2002), rats (Marote & Xavier 2011), chickens (Sridharan *et al.* 2014), honeybees (*Apis mellifera*; Eckstein *et al.* 2013), and archerfish (Saban *et al.* 2017). In the latter study, a touchscreen was suspended above the tank, and a cue predicted the location of a food-delivering target. Fish were trained to hit the target using mouth-propelled water jets – a natural behaviour for archerfish. Response latencies were faster when the target appeared in the same location as the cue.

To create an emotional spatial cueing task, researchers could introduce affective stimuli into the predictive cue paradigm and test subjects in different valence states. This might be effective with diverse taxa, albeit under controlled conditions.

4.3.5 Visual Search Tasks

In visual search tasks, participants are instructed to locate a target stimulus in an array of distractor stimuli (e.g. Öhman *et al.* 2001, Wieser *et al.* 2018). Faster target detection reveals an attention bias for the stimulus, whereas slower detection suggests either that the target does not capture attention or does so less than the distractor images.

Marzouki *et al.* (2014) used abstract shapes with conditioned valence in a visual search task for Guinea baboons (*Papio papio*). Subjects were trained to locate a T-shaped target among seven L-shape distractors. To investigate affective state, the authors analysed trials preceded by ostensibly valenced behaviours. Response latencies in trials following negative-valence behaviours were slower than those following positive-valence behaviours. However, behavioural inferences about affective valence can be equivocal. Whilst Marzouki *et al.* categorised self-grooming as positive, this displacement activity is linked to stress (Castles & Whiten 1998, Troisi 2002). Resting, analysed as negative, is a biological necessity. It is also a low-arousal activity, suggesting that the observed effect could be attributed to arousal rather than valence. Well-designed affective state-induction experiments avoid these confounds and demonstrate causality.

Primate response latencies have also been recorded towards non-symbolic emotional images, although without comparing affective states. Chimpanzees located conspecific faces faster than neutral objects (Tomonaga & Imura 2015), and human faces faster when their gaze was forward rather than averted (Tomonaga & Imura 2010). In Japanese macaques, median response latencies were faster towards target aggressive faces amongst neutral face distractors than vice versa (Kawai *et al.* 2016; see Nakata *et al.* 2018). Macaques also detected snakes faster than fear-irrelevant stimuli (Kawai & Koda 2016, Shibasaki & Kawai 2009). Instead of response latencies, Simpson *et al.* (2017) tracked infant macaques' gaze across visual search arrays. This eliminated training and potential motor response biases.

Diverse taxa have been trained to perform visual search tasks, including barn owls (*Tyto alba*; Lev-Ari & Gutfreund 2018, Orlowski *et al.* 2018), zebrafish (*Danio rerio*; Proulx *et al.* 2014), and bumblebees (*Bombus terrestris*; Nityananda & Pattrick 2013). The latter study conditioned bees to associate specific colours with rewards, which they could detect in arrays of distractor colours. This research did not investigated whether affective state impacts visual search performance, but judgement bias studies have validated affective state manipulations for bees (Bateson *et al.* 2011, Perry *et al.* 2016).

Visual search tasks are criticised in cognitive psychology, because stimulus arousal influences searching, rather than stimulus valence (Lee *et al.* 2014, Lundqvist *et al.* 2015, Mather & Sutherland 2011). In a systematic reanalysis of human studies, Lundqvist *et al.* (2014) concluded that happy faces captured attention faster than angry faces when they were rated higher on arousal indices, but this effect reversed when the angry faces were higher arousal. Another study exposed subjects to either an arousing negative-valence sound, an arousing positive-valence sound or a neutral sound (Sutherland & Mather 2018). Both high-arousal sounds had similar effects on visual search performance, regardless of valence. To avoid these issues, visual search experiments should control for arousal (see Zsido *et al.* 2020).

The complexity and arousal-dependence of visual search tasks suggests that they are not an immediate priority for ADAB research. However, studies could investigate how different affective state manipulations influence searching.

4.3.6 Related Paradigms

As well as standard ABTs, other tests and metrics might measure ADAB. Based on human paradigms (Wilkinson 1963), the five-choice serial reaction time task (5-CSRTT) presents subjects with five holes and requires them to approach the one just illuminated (Carli *et al.* 1983; reviewed by Fizet *et al.* 2016). It is framed in terms of attention. In a 5-CSRTT study on pain in rats, Boyette-Davis *et al.* (2008) tested subjects injected with formalin. Formalin-treated rats made fewer approaches, interpreted as a failure to attend the task when in pain (see also Freitas *et al.* 2015, Pais-Vieira *et al.* 2009; pain-induced cognitive impairment reviewed by Moriarty *et al.* 2011). Behavioural data confirmed that subjects which did not receive morphine showed the highest rates of locomotion in open field tests, suggesting that reduced activity did not explain their failure to respond. Data from trials when rats did approach further indicated that responses were no slower in the pain group. Like emotional Stroop tasks, the 5-CSRTT measures affective state-induced attentional impairments.

As well as judgement biases, judgement bias tasks may quantify attention (Mendl *et al.* 2009). Conventional intermediate-probe judgement bias tasks only show one stimulus type at a time, so there is no competition for attention. In dual-presentation judgement bias tasks, however, the probe trials are simultaneous displays of the P and N stimuli. Responses may, therefore, measure ADABs to either positive or negative information. After associating two sound tones with different valence outcomes, Parker *et al.* (2014) tested rats on intermediate probes, as well as dual presentations of both trained tones. Contrary to predictions, the control rats made more pessimistic responses in each judgement bias task than rats in unpredictable housing. I recommend avoiding judgement bias tasks as secondary measures of ADAB, as this approach leads to uncertainty about the mechanism involved. In the dual-presentation task, for instance, responses relied on the rats hearing one or both tones (attention), categorising the presentation as either positive or negative (judgement), remembering the lever associated with each outcome (memory), and choosing which to press (decision-making). More research is needed to identify which cognitive faculties contribute to observed biases, bearing in mind that they may act synergistically (Everaert *et al.* 2013, Kress & Aue 2017, 2019, Kress *et al.* 2018, Segerstrom 2001, Singh *et al.* 2020; see Mendl *et al.* 2009 for further discussion).

Paul *et al.* (2005) also suggested using standard personality tests to measure ADAB. Novel object and human reactivity tests often record looking time, latency to touch, and subsequent interactions (Forkman *et al.* 2007), which could quantify attention. Startle tests also measure looking behaviour towards the source (Grillon & Baas 2003, Lanier *et al.* 2000). Stress potentiates the startle reflex in humans (Schmitz *et al.* 2011), and startle is associated with clinical anxiety (Bakker *et al.* 2009) and chronic pain (Alfvén *et al.* 2017). Moreover, negative-valence states increase the startle response in macaques (Davis *et al.* 2008) and rodents (Brown *et al.* 1951), whereas enrichment attenuates startle in chickens (Ross *et al.* 2019). In a study on lambs, Destrez *et al.* (2013a) exposed both chronically stressed and control subjects to a battery of personality tests. Stressed lambs touched a novel human fewer times and looked towards a novel object for shorter bouts, although a startle test revealed no treatment differences. These paradigms have been refined for various applied settings, although researchers should account for trait differences in responsiveness.

Finally, fear and anxiety impact vigilance (scanning the environment for threats; Beauchamp 2017). Following an alarm call, starlings with a water bath were less vigilant than birds without (Brilot *et al.* 2012). Bathing maintains feather condition, so removing the water bath reduced flight ability and increased vulnerability. In livestock, anxiolytic treatment reduced vigilance during isolation tests (Destrez *et al.* 2012) and following predator exposure (Lee *et al.* 2016, 2018, Monk *et al.* 2018b). Cows were also less vigilant around gentle, compared to aversive, stock people (Welp *et al.* 2004). Furthermore, dangerous or stressful conditions heighten vigilance in wild animals (Elgar 1989). In playback experiments, coots (*Fulica atra*) scanned their surroundings for longer after dog barks than control sounds (Randler 2006). Observational studies have further linked vigilance with predation risk in African ungulates (Creel *et al.* 2014), human disturbance in Japanese cranes (*Grus japonensis*; Wang *et al.* 2011), and proximity to neighbouring territories in spider monkeys (*Ateles geoffroyi*; Busia *et al.* 2016). Despite not meeting my stimulus-directed definition of ADAB, these studies demonstrate how attention biases might be measured in the field and indicate their adaptive function (see Chapters Five & Six).

4.4 | Future Directions

4.4.1 Different Senses

Although I have focussed on visual attention, other sensory modalities warrant investigation (Paul *et al.* 2005; see Nielsen 2018). Judgement bias studies, for example, have used auditory (Harding *et al.* 2004), olfactory (Bateson *et al.* 2011), and tactile cues (Brydges *et al.* 2011). Some ABTs have incorporated sound stimuli, such as starling alarm calls (Brilot *et al.* 2009) and threatening dog barks (Albuquerque *et al.* 2016), but most measured looking time towards the source. In some species, though, other response variables might be more appropriate. Ruminants have a wide field of vision, rendering head orientation a potentially unreliable proxy for gaze. Instead, ear posture signals direction of attention (Edwards-Callaway 2019) and affective state (e.g. cattle: Proctor & Carder 2014, Lambert & Carder 2019; goats: Baciadonna *et al.* 2020, Briefer *et al.* 2015; sheep: Boissy *et al.* 2011, Reefman *et al.* 2009; pigs: Camerlink *et al.* 2018, Reimert *et al.* 2013). A preferential hearing paradigm might replace competing images with a positive-valence conspecific vocalisation and a negative-valence predator vocalisation (see Briefer 2012, Raoult & Gygax 2019). Eye gaze or ear position would indicate ADAB. Like eye-trackers, an automated ear tracking system has even been developed for sheep (Vögeli *et al.* 2014). However, ear postures can be purely communicative and indicate arousal as well as valence (Proctor & Carder 2014).

Animal welfare scientists also overlook olfaction (Nielsen *et al.* 2015), despite it being a dominant sense for widely-used species (e.g. chickens: Jones & Roper 1997; dogs: Gazit & Terkel 2003; pigs: Brunjes *et al.* 2016; rats: Kroon & Carobrez 2009). Moreover, olfaction is integral for communication and information-gathering in arthropods (Hansson 1999), which are likewise underrepresented in welfare research (Horvath *et al.* 2013). Oberhauser *et al.* (2019) conditioned ants (*Lasius niger*) to associate a high-value and a low-value food reward with different arms of a Y-maze and different chemical odours. When the odours were swapped between arms, ants overwhelmingly followed the chemical rather than spatial cues. In another study, Cárdenas *et al.* (2012) presented predatory spiders (*Zodarion rubidum*) with a control chamber and an experimental chamber, which they channelled different prey odours into. Approaches into the experimental chamber indicated attractive kairomones. Whilst olfactory stimuli are difficult to work with (Nielsen *et al.* 2015), ADAB researchers might use similar methods to investigate whether affective state influences responses to food, conspecific, and predator odours. Such non-visual ABTs may facilitate research on commercially important and poorly studied taxa.

4.4.2 Effect Specificity

In humans, ADABs are often stimulus- or motivation-specific (Pool *et al.* 2016). Veterans with post-traumatic stress disorder exhibit facilitated engagement and impaired disengagement towards war-related stimuli, but not disgusting, neutral or positive-valence stimuli (Olatunji *et al.* 2013). In emotional Stroop tasks, anxiety sufferers concerned about physical threats are slower to name the colour of words like “attack” and “illness”, whereas words like “incompetent” and “stupid” distract those with social anxiety (Mogg *et al.* 2000, Wilson & McLeod 2003). Insomniacs struggle to disengage from sleep-related stimuli (Akram *et al.* 2018); addicts are biased towards opiates (Lubman *et al.* 2000), cigarettes (Ehrman *et al.* 2002), and alcohol (Townshend & Duka 2001); and, in healthy populations, food cues are more salient to hungry people (Castellanos *et al.* 2009, Davidson *et al.* 2018, Tapper *et al.* 2010). These findings suggest that blanket valence-based interpretations of ADAB may be inappropriate in animal welfare science. Whilst judgement bias can be understood as a correlation between optimism and valence, ABTs defy simple, overarching explanations.

Nonetheless, the studies reviewed herein demonstrate that attention biases can reveal specific emotions, motivations, aversions, and preferences. In the aforementioned sheep and cattle ABT, for example, anxiogenic and anxiolytic drugs modulated attention allocation towards a dog (Lee *et al.* 2016, 2018, Monk *et al.* 2018b). This threat-based task measured fear and anxiety specifically – not negative valence generally. Verbeek *et al.* (2014) found that food-motivated sheep attended a food-delivering bucket, whilst the chimpanzee Stroop task used a contextual aversive stimulus (images of the veterinarian) that induced ADABs after subjects had undergone a procedure (Allritz *et al.* 2016).

Dawkins (2003) defined animal welfare without recourse to affective states, arguing that it could be distilled into two questions: is the animal physically healthy and does the animal have what it wants? Whilst other variables can increase attention towards a stimulus (Lee *et al.* 2016), ABTs might be a “quick and dirty” method to identify promising avenues for labour-intensive preference, motivation or aversion tests (reviewed by Fraser & Nicol 2018, Jensen & Pedersen 2008, Kirkden & Pajor 2006). For developmentally and physically disabled people, longer gaze durations indicate preferred stimuli (Fleming *et al.* 2010). The same may be true for animals. Hence, ADAB could answer Dawkins’ second question: do animals have what they want?

4.4.3 Attentional Scope

ADAB towards specific stimuli might not indicate general valence, but attentional scope may do so. The broaden-and-build theory of positive emotions proposes that, since positive-valence states often reflect overall wellbeing, contented individuals can devote resources to exploration, learning, and building up resources (Fredrickson 2001, 2003; reviewed by Vanlessen *et al.* 2016; for a critique, see Harmon-Jones *et al.* 2013). Positive affective states are, therefore, associated with a broad attentional scope and more attention allocated to the visual field’s periphery (i.e. seeing the forest rather than the trees). On the other hand, negative states are typically directed towards specific threats, so they narrow attentional scope and maximise attention to the visual field’s centre (i.e. seeing the trees rather than the forest; Easterbrook 1959). In the Kimchi test, for instance, a target shape is presented, followed by two comparison shapes (Kimchi & Palmer 1982). Subjects must select the comparison most like the target. To test broaden-and-build theory, Gasper and Clore (2002) showed participants either a triangle consisting of three squares or a square consisting of four triangles. After a positive affective state manipulation, subjects chose the larger shape as a closer match than the component shape more than subjects in a negative condition, suggesting a broader attentional scope. Similar experiments might also indicate positive emotions and general wellbeing in animals (e.g. chimpanzees: Fagot & Tomonaga 1999; Guinea baboons: Deruelle & Fagot 1998; tufted capuchins: Spinozzi *et al.* 2003; pigeons: Kelly & Cook 2003; honeybees: Dyer *et al.* 2016).

4.4.4 Attention Bias Modification

Animal welfare scientists study attention biases as a symptom of negative affective states, but some cognitive models of affective disorders identify them as a cause (e.g. Beck & Clark 1997, Eysenck *et al.* 2007, Mogg & Bradley 1998; reviewed by Van Bockstaele *et al.* 2014). For anxious populations, exaggerated attention to threat may generate a feedback loop that reinforces existing biases (Mathews 1990). Attention bias modification aims to disrupt this harmful relationship (reviews and meta-analyses by Beard *et al.* 2012, Grafton *et al.* 2017, Jones & Sharpe 2017, Krebs *et al.* 2018, Kruijt *et al.* 2019, Price *et al.* 2016, Salemink *et al.* 2019). Using computer-based tasks, subjects are repeatedly presented with valence/neutral stimulus pairs, such as angry and neutral facial expressions. In this example, correct responses would always require focusing on the neutral stimulus, training participants to divert attention away from threats through operant conditioning. In a modified dot-probe task, for instance, probes only ever appear behind neutral stimuli (e.g. Amir *et al.* 2009). Although several studies have reported null effects (Carlbring *et al.* 2012, Enock *et al.* 2014, Julian *et al.* 2012), the more promising tasks could be adapted for animals (e.g. the positive search paradigm; De Voogd *et al.* 2014, Waters *et al.* 2016). For anxious individuals or contexts where chronic stress is unavoidable, attention bias modification might cost-effectively enhance mood states. However, this is no substitute for good housing and husbandry.

4.5 | Conclusions

I reviewed affect-driven attention bias as a welfare indicator and identified 21 studies. Initial results are promising. In chimpanzees, macaques, capuchins, sheep, cattle, and pigs, affective state manipulations have modulated attention towards or away from emotional stimuli, as well as the speed and duration of fixation. Both positive and negative states have been studied, with most research on fear, anxiety, and threat biases. However, whilst welfare scientists were quick to recognise the potential of judgement bias, affect-driven attention biases have been comparatively overlooked. Methods might be developed diverse taxa, including birds, reptiles, fish, and insects, and tested in both captive and free-range settings. Different attentional tasks measure different aspects of attention, but the looking time, dot-probe, and spatial cueing paradigms are especially promising. Future studies could use them to distinguish engagement and disengagement of attention, investigate effect specificity, and explore attentional scope as a welfare indicator. Attention bias modification might also ameliorate negative-valence moods in chronically stressed animals. By describing potential methodologies and evaluating the existing literature, I hope this review stimulates attention bias research into the effects of HIREC on animals' emotional wellbeing.

5 | Microplastics disrupt hermit crab shell selection

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Abstract. Microplastics (plastics < 5 mm) threaten marine biodiversity. However, the effects of microplastic pollution on animal behaviour and cognition are poorly understood. I used shell selection in common European hermit crabs as a model to test whether microplastic exposure impacts the essential survival behaviours of contacting, investigating, and entering an optimal shell. I kept 64 female hermit crabs in tanks containing either polyethylene spheres (n = 29) or no plastic (n = 35) for five days. I then transferred subjects into suboptimal shells and placed them in an observation tank with an optimal alternative shell. Plastic-exposed hermit crabs showed impaired shell selection: they were less likely than controls to contact optimal shells or enter them. They also took longer to contact and enter the optimal shell. Plastic exposure did not affect time spent investigating the optimal shell. These results indicate that microplastics may impair cognition, thereby disrupting an essential behaviour in hermit crabs.

5.1 | Introduction

Having considered animal welfare, I now explore how HIREC impacts wild populations. Microplastics (plastics < 5 mm in length; Thompson *et al.* 2004) are polluting oceans worldwide, causing substantial scientific and societal concern (Barnes *et al.* 2009, Lam *et al.* 2018, Nelson *et al.* 2019). Waste microplastics enter marine environments either directly, as industry-made particles (primary microplastics; Napper *et al.* 2015), or indirectly, as plastics greater than 5 mm degrade (secondary microplastics; Cole *et al.* 2011). In total, up to 10% of global plastic production ends up in the ocean (Barnes *et al.* 2009). Microplastic exposure can reduce growth, reproduction, and survival in diverse taxa, from corals to mammals (Anbumani & Kakkar 2018, Auta *et al.* 2017, Lassen *et al.* 2015, Wright *et al.* 2013). However, the ecological validity and scientific rigour of existing research is questionable, with recent meta-analyses (Bucci *et al.* 2019, Cunningham & Sigwart 2019, Foley *et al.* 2018) and reviews (Burns & Boxall 2018, Connors *et al.* 2017, Phuong *et al.* 2016) finding impacts equivocal and context-dependent. As microplastic concentrations are highest along coastlines, littoral species face the greatest potential risks (Cole *et al.* 2011).

To date, research into how microplastic pollution impacts marine organisms has focused on fitness and physiology (Franzellitti *et al.* 2019). Recent studies have also investigated behavioural impacts, finding that microplastics disrupt locomotion (zebrafish: Chen *et al.* 2020; oysters, *Crassostrea gigas*: Bringer *et al.* 2020a, b; amphipods, *Platorchestia smithi*: Tosetto *et al.* 2016; copepods, *Temora turbinata*: Suwaki *et al.* 2020), feeding (amphipods, *Orchestoidea tuberculata*: Carrasco *et al.* 2019; copepods, *Calanus helgolandicus*: Cole *et al.* 2015), and social behaviours (Crucian carp: *Carassius carassius*: Mattsson *et al.* 2016). Importantly, behaviour depends on cognition (see Introduction). Crooks *et al.* (2019) identified ingested microplastics in the brains of velvet swimming crabs (*Necora puber*) and suggested that this could impact crucial survival behaviours. Microplastics also transfer from blood to brain in carp, which may disrupt feeding and swimming (Mattsson *et al.* 2017). However, the effects of microplastic exposure on animal cognition have not been explicitly tested.

Shell selection in common European hermit crabs is an essential survival behaviour. Hermit crabs inhabit empty gastropod shells to protect their soft abdomens from predators (Elwood & Neil 1992), with body weight determining optimal shell weight (Elwood *et al.* 1979). The location and sensory perception of new shells represent aspects of cognition. Hermit crabs then cognitively evaluate shell quality by investigating the interior and exterior with their chelipeds (Elwood 2018). They decide to swap shells if the new one is assessed as an improvement over the current shell. Accurate assessments are highly adaptive, as lower quality shells reduce growth, fecundity, and survival (Lancaster 1990). Because hermit crabs gather information about the new shell, assess its quality compared to their current shell, and make a decision manifested in behaviour, shell selection offers a tractable model of cognitive assessments in marine environments (Elwood 2018).

In this experiment, I investigated whether microplastics influence hermit crab shell selection under controlled conditions. After keeping hermit crabs in tanks either without microplastics (CTRL) or with microplastics (PLAS), I transferred them into a suboptimal shell and offered an optimal alternative. I hypothesised that, if plastic pollution impedes cognition, the PLAS treatment would be less likely to find the optimal shell, accurately assess its quality, and decide to swap shells. Specifically, I predicted that CTRL hermit crabs would be more likely and faster to contact, investigate, and enter the optimal shell than PLAS hermit crabs.

5.2 | Methods

Crustacean research is not regulated under United Kingdom law (Birch *et al.* 2020a), but I followed the Association for the Study of Animal Behaviour's *Guidelines for the Use of Animals in Research*. After the experiment, all hermit crabs were returned to the shore unharmed. I prioritised animal welfare throughout the study.

Hermit crabs were collected from Ballywalter Beach, Northern Ireland, and maintained in Queen's University Belfast's animal behaviour laboratory at 11 °C with a 12:12 h light:dark cycle. I randomly allocated subjects to either CTRL or PLAS treatments. For five days, I kept both groups in 0.03 m^3 glass tanks (45 cm × 25 cm × 25 cm). All tanks contained 10 L of aerated seawater and 80 g of bladder wrack seaweed (*Fucus vesiculosus*). The PLAS treatment also included 50 g of polyethylene spheres (Materialix Ltd., London, United Kingdom; size: 4 mm, 0.02 g; concentration: 25 particles l^{-1}, 5 g l^{-1}). Lower than most exposure studies, this concentration represented natural conditions more realistically (Cunningham & Sigwart 2019). Polyethylene is the most abundant microplastic found in marine organisms (De Sá *et al.* 2018).

After five days, hermit crabs were removed from their current shell using a small bench-vice to crack the shell (Walsh *et al.* 2017). Each subject was then sexed and weighed (Elwood 2018). I only selected non-gravid females for the study (*n* = 35 CTRL, 29 PLAS) to control for sex differences in behaviour (Elwood & Neil 1992). Based on their body weight, each hermit crab was given a suboptimal *Littorina obtusata* shell 50% of their preferred shell weight (Elwood *et al.* 1979). After 2 h acclimating to the suboptimal shell, subjects were individually placed in a 15 cm-diameter crystallising dish 10 cm from an optimum-weight *L. obtusata* shell (i.e. 100% the preferred weight for the weight of the hermit crab). The dish contained aerated seawater to a depth of 7.5 cm. I recorded latency to contact the optimal shell, time spent investigating the optimal shell, and latency to enter the optimal shell. If the hermit crab did not approach and enter the optimal shell within 30 min, the session ended.

Statistical analyses were performed in R (R Core Team, Cran-r-project, Vienna, Austria, version 3.4.4). Data were categorical (1/0) and continuous (latency). Kolmogorov-Smirnov tests revealed that my data were not normally distributed, so I used nonparametric tests throughout. I analysed categorical data using Pearson's chi-squared tests and latency data using Mann-Whitney *U* tests. If subjects did not contact or enter the optimal shell, I assigned a ceiling latency of 30 min. I present data as medians ± inter-quartile range and consider $p < .05$ statistically significant.

5.3 | Results

Fewer PLAS hermit crabs contacted the optimal shell than CTRL hermit crabs ($\chi^2_1 = 8.736$, $p < .005$; Table 6). The proportion entering the optimal shell was also lower following microplastic exposure ($\chi^2_1 = 5.343$, $p = .021$; Table 6). Moreover, the PLAS treatment had longer latencies to contact ($W = 290$, $p < .005$; CTRL median = 948 s, IQR = 184-1800 s; PLAS median = 1800 s, IQR = 1356-1800 s; Figure 15) and enter the optimal shell ($W = 349$, $p = .021$; CTRL median = 1379 s, IQR = 511-1800; PLAS median = 1800 s, IQR = 1559-1800 s; Figure 16). Investigation time did not differ between treatments ($W = 142.5$, $p = .406$; CTRL median = 129.5 s, IQR = 74.75-195.5 s; PLAS median = 80.5 s, IQR = 70.75-183.5 s).

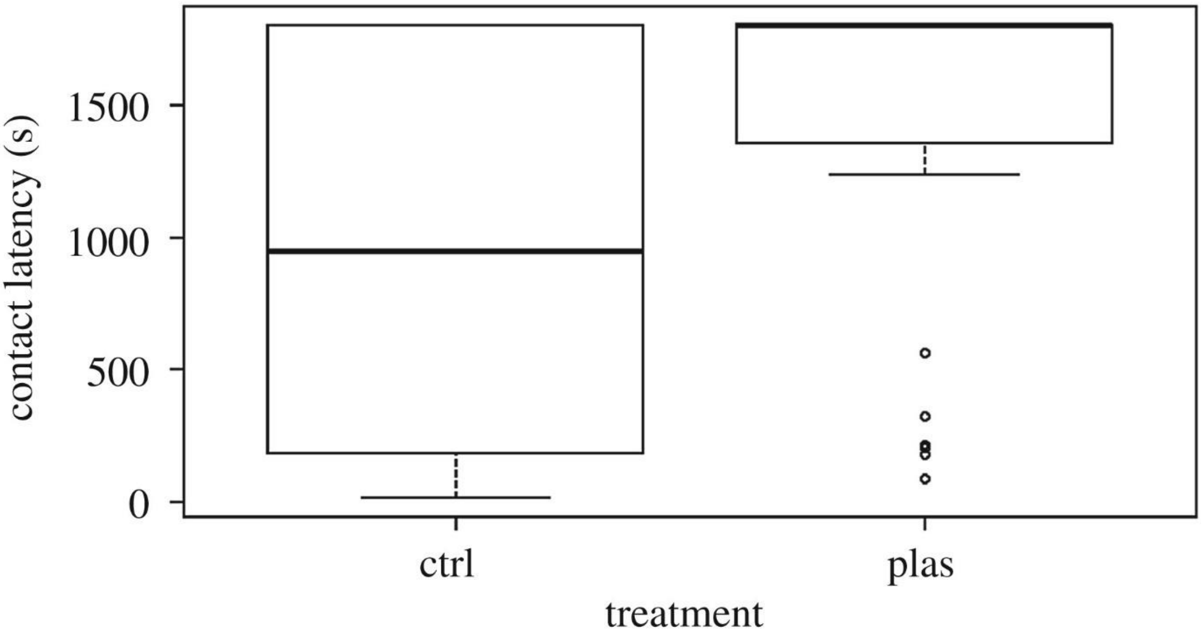

Figure 15. Latency (s; median, IQR) to contact the optimal shell for control (ctrl) and microplastic (plas) treatments.

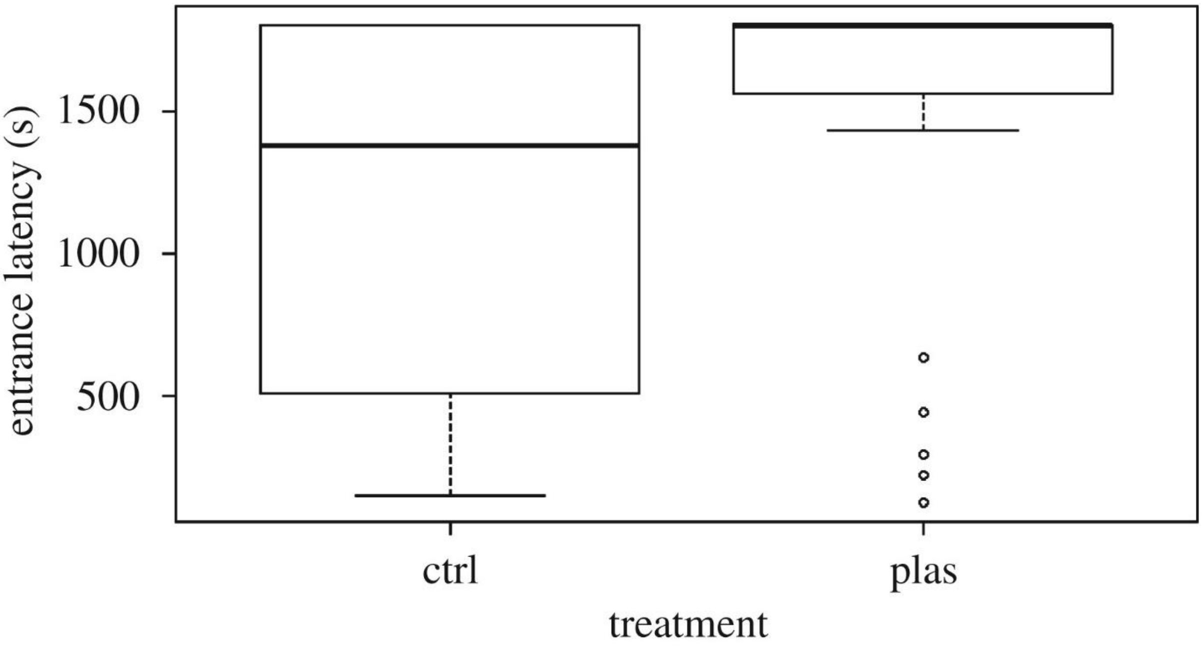

Figure 16. Latency (s; median, IQR) to enter the optimal shell for control (ctrl) and microplastic (plas) treatments.

Table 6. Number and percentage of hermit crabs that contacted and entered the optimal shell from CTRL and PLAS treatments.

Treatment	**Contact optimal shell (% contacting)**	**Enter optimal shell (% entering)**
CTRL (*n* = 35)	25 (71%)	21 (60%)
PLAS (n = 29)	10 (34%)	9 (31%)

5.4 | Discussion

Microplastic exposure impaired shell selection behaviour in hermit crabs. Shell selection requires gathering and processing information about shell quality, so my findings suggest that microplastics inhibited aspects of cognition. To my knowledge, this is the first study explicitly testing the cognitive effects of microplastic exposure, and the first microplastic study on common European hermit crabs.

Despite microplastic exposure disrupting shell selection, the mechanism is unclear. Ingested microplastics enter the brain in crabs (Crooks *et al.* 2019) and carp (Mattson *et al.* 2017), potentially impeding information-gathering, resource assessments, decision-making, and behavioural responses. However, both gut-brain studies used much smaller microparticles than my study (0.5 µm, Crooks *et al.* 2019, and 53 nm, Mattson *et al.* 2017). Smaller microparticles translocate more easily from the gut into other tissues (Ding *et al.* 2020, Von Moos *et al.* 2012). To establish whether microplastics passed through the gut membrane, researchers could extract subjects' haemolymph after testing (e.g. Farrell & Nelson 2013). More general mechanisms may also be responsible for my results. Ingesting microplastics can induce false satiation in crustaceans (Welden & Cowie 2016), reducing food intake, energy budgets, and growth (Au *et al.* 2015, Blarer & Burkhardt-Holm 2016, Cole *et al.* 2015, Watts *et al.* 2015, Welden & Cowie 2016). Lower energy levels could, therefore, explain the PLAS treatment's tendency to avoid changing shells. I hope that further studies address the effects of microplastic exposure on specific cognitive processes.

Whilst shell contact and entrance latencies were shorter in the CTRL treatment than the PLAS treatment, shell investigation time did not differ. This may indicate that microplastic exposure impaired the ability to assess shells from a distance (i.e. sensory impairment). To some extent, hermit crabs can assess shell quality without contact. Elwood & Stewart (1985) observed more approach behaviour when shells were high quality than low quality. Alternatively, sample size may explain the null results for shell investigation time, as only nine subjects in the PLAS treatment investigated the new shell.

Although this research was laboratory based, my experimental design was more ecologically relevant than previous exposure studies. Microplastic exposure research typically uses unrepresentative concentrations and particle types (Phuong *et al.* 2016). Environmental microplastic concentrations range from 39-89 particles l^{-1} in effluent (Verschoor *et al.* 2016) to approximately 13 particles l^{-1} in the deep sea (Peng *et al.* 2018). Whereas 100 particles l^{-1} is the highest concentration ever recorded in nature (Burns & Boxall 2018, Leslie *et al.* 2017), 82% of exposure studies test > 100 particles l^{-1} (Bucci *et al.* 2019). My 25 particles l^{-1} concentration was, thus, more realistic than most laboratory-based microplastic research. A recent meta-analysis reported more deleterious effects at higher concentrations (Bucci *et al.* 2019), although others have found little evidence for concentration- or duration-dependent effects (Cunningham & Sigwart 2019, Foley *et al.* 2018). Microparticle shape also influences uptake and effects. Whilst fibres and fragments are more abundant in field observations (Burns & Boxall 2018, De Sá *et al.* 2018), I used spheres, because they have more negative impacts on marine life (Foley *et al.* 2018). However, microplastic pollution encompasses various shapes, sizes, and polymer types (Rochman *et al.* 2019). Future laboratory studies should replicate this heterogeneity.

5.5 | Conclusions

I investigated whether microplastics influence shell selection in hermit crabs, as a model for cognitive assessments. Compared to control animals, hermit crabs exposed to polyethylene spheres were less likely to contact and enter a better-quality shell, and took longer to do so. Time spent investigating the new shell did not differ. This proof-of-concept study indicates that microplastic exposure impairs hermit crabs' information-gathering, resource assessments, and decision-making. However, more research is needed to understand the mechanism. Future studies could also establish the generality of my findings across different species, cognitive processes, and microplastic exposures.

6 | Affective states in animal contests: An integrative review

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Abstract. Using contests as a case-study, I propose that short-term emotions underpin animals' assessments, decision-making, and behaviour. Equating contest assessments to emotional appraisals, I describe how contestants appraise more than resource value and outcome probability. These appraisals elicit the cognition, drive, and neurophysiology that governs aggressive behaviour. I discuss how recent contest outcomes induce longer-term moods, which impact subsequent contest behaviour (winner/loser effects). Finally, I distinguish between integral (objectively relevant) and incidental (objectively irrelevant) affective states. Unlike existing ecological models, my approach predicts that incidental events influence contest dynamics, and that contests become incidental influences themselves, potentially causing maladaptive decision-making. This approach applies to all affective stimuli, including anthropogenic stressors. Conservation biologists should, therefore, investigate whether HIREC impacts incidental affective states, as well as integral cognitive processes.

6.1 | Introduction

Consider this: emotions underpin animal behaviour. As well as acting as the foundation of animal welfare, affective states facilitate flexible responses to dynamic environments (Faustino *et al.* 2015, Nettle & Bateson 2012, Trimmer *et al.* 2013; see Introduction). This mirrors the evolutionary function of cognition (Morand-Ferron *et al.* 2016, Pritchard *et al.* 2016), and suggests that emotions and moods may allow animals to adapt to HIREC. Animal welfare scientists, neuroscientists, and psychopharmacologists routinely study the interplay between affective states, cognition, and behaviour (Mendl *et al.* 2010, Mendl & Paul 2020). However, behavioural ecologists and conservation biologists have not yet embraced emotions and moods (Fraser 2009).

In addition to valence and arousal ("scalability"; see Introduction), Anderson and Adolphs (2014) identified two further characteristics of affective states. First, emotions "generalise": various stimuli and situations can induce a particular affective state, and affective states can be associated with various behavioural responses. Affective states also "persist" after stimulus removal. Thus, emotions do not mediate fixed responses to specific stimuli, because fixed responses neither generalise nor persist. Examples of non-affective behaviours, therefore, include withdrawal reflexes (which are genetically encoded from birth) and sexual imprinting (which is learnt during development and subsequently invariant). Emotions, on the other hand, facilitate flexible behaviour in complex, variable, and novel environments (Faustino *et al.* 2015), such as conditions under HIREC.

I propose that animal contests exemplify affective behaviour. Contests are direct inter-individual interactions that determine access to resources, such as food, mates or territory (i.e. rewards; Hardy & Briffa 2013). Resource value (RV) is the resource's fitness benefit (Arnott & Elwood 2008). Contest costs include energy and time expenditure, injury, and even death (i.e. punishments; Enquist & Leimar 1990). Greater potential benefits justify greater costs, so increasing RV increases investment (Enquist & Leimar 1987, Hammerstein & Parker 1982). However, contest costs and outcomes are not fixed. Resource-holding potential (RHP) is the ability to win contests, comprising traits like size, skill, and weaponry (Arnott & Elwood 2009, Briffa & Lane 2017, Parker 1974). Animals with a higher RHP are better at winning, so they are more likely to keep or gain resources. Contests involve acquiring resources and avoiding punishments (valence), vary in intensity and escalation (arousal), are elicited by diverse stimuli and manifested in various behaviours (generalisation), and continue after the inciting event (persistence). These features imply an internal (i.e. affective) state mediating the link between reward, punishment, and contest behaviour.

Previous researchers have not comprehensively applied affective theory to animal contests. However, conceptualised as responses to rewards, punishments, and their predictors, emotions cover contest information-gathering, decision-making, and behaviour. This novel approach extends and refines contest motivation models. For example, Elwood and Arnott (2012) explained contest dynamics in terms of two dimensions: RV and costs. A contestant engages if RV exceeds costs and withdraws if costs exceed RV. Whereas RV usually remains stable, costs accumulate throughout the contest. If costs exceed RV, a contestant’s strategy switches from engage to withdraw. This model approximates the valence dimension of affective states – RV representing positive valence and costs representing negative valence – except that valence is not specific to contests (Mendl *et al.* 2010, Mendl & Paul 2020, Nettle & Bateson 2012, Trimmer *et al.* 2013).

In this review, I use contests as a case-study for applying emotion theory to behavioural ecology. I argue that contestants evaluate contest benefits and costs, and that these “appraisals” elicit emotional episodes encompassing contest decisions and behaviour. I describe how the affective outcome of contests might produce experience effects: prior winners' tendency to initiate and win (and prior losers' tendency to avoid and lose) subsequent contests. Unlike traditional ecological models, my perspective predicts that affective states previously induced in other behavioural contexts will impact contest dynamics. These objectively irrelevant influences could mediate contest decisions and cause maladaptive behaviour. Applying this affective framework to animal behaviour more broadly, incidental affective states may cause anthropogenic stressors to disrupt objectively irrelevant behaviour.

6.2 | Initiating, Escalating, and Quitting Contests

Contest theorists emphasise two key assessments: animals assess RV (which determines fitness benefits and motivation) and RHP (which predicts fitness costs and outcome likelihood; Arnott & Elwood 2008, 2009). Contestants may assess only their own RHP (self-assessment; Maynard Smith 1974, Mesterton-Gibbons *et al.* 1996) or compare their RHP to their opponent's (mutual assessment; Enquist & Leimar 1983, 1990, Hammerstein & Parker 1982). In a meta-analysis of 36 species' assessment strategies, Pinto *et al.* (2019) found that self-assessment is more common than mutual assessment.

Appraisal theory articulates and extends contest theory. The former predicts broader evaluations of the resource, opponent, and context, all related back to the individual's own goals. Under Scherer's (2001) sequential theory (see Introduction), contestants would first appraise novelty. Familiar resources are valued above novel resources (e.g. residency effects; Fuxjager *et al.* 2009, Kemp & Wiklund 2004), whilst dominance hierarchies reduce aggression towards familiar rivals (Hobson 2020). Second, contestants would appraise the resource's intrinsic valence (objective RV; e.g. the calories in food). Third, contestants would appraise whether the resource contributes to their goals (subjective RV; e.g. starving animals value food most; Hansen 1986, Millsopp & Laming 2008). Fourth, contestants would appraise outcome probability (which covers RHP assessments). Animals avoid or de-escalate contests they will probably lose (Arnott & Elwood 2009). Fifth, contestants would appraise discrepancy from expectations. Compared to unconditioned controls, animals trained that a stimulus signals reward become more aggressive when the stimulus is unrewarded (Duncan & Wood-Gush 1971, Papini & Dudley 1997, Vindas *et al.* 2012). Sixth, contestants would appraise their response's compatibility with social context. Observer presence can modify animals' behaviour (audience effects; Darden *et al.* 2019, Miles & Fuxjager 2019, Montroy *et al.* 2016), and watching contests can modify the observers' subsequent behaviour (bystander effects; Darden *et al.* 2019, Oliveira *et al.* 2001). During ongoing contests, animals also reappraise assessments, adjusting their behaviour as information and costs accumulate (Enquist & Leimar 1983, Parker 1974). These appraisals have all been empirically documented, but several are not incorporated into current contest theory.

I further postulate that appraisals unify reward and punishment inputs into a decision-making common currency (Cabanac 1992, Levy & Glimcher 2012). This facilitates cross-context comparisons between competing emotions, moods, sensations, and interoceptive stimuli. For instance, food-deprived goldfish (*Carassius auratus*) endure more electric shocks to feed than well-fed goldfish (Millsopp & Laming 2008). Following shocks, fewer hermit crabs evacuate preferred *Littorina* shells than non-preferred *Gibbula* shells (Elwood & Appel 2009). I conceptualise valence as the common currency in these reward/punishment trade-offs. Contestants likewise weigh RV against potential contest costs and outcome likelihood (Elwood & Arnott 2012). In self-assessment, contestants' affective states integrate RV and own RHP information. Animals persist until they reach a negative-valence threshold: the maximum cost they will pay for the resource. This threshold may be energetic (Payne &

Pagel 1996, 1997) or include injury costs as well (Payne 1998). In mutual assessment, affective states integrate RV, own RHP, and opponent RHP information. Animals withdraw when they establish that their opponent has a higher RHP (Enquist & Leimar 1983), perhaps when they tip below neutral valence. Both self- and mutual assessment models require unidimensional (valence) comparisons of fitness-relevant information.

Affective states may also determine assessment strategy. Researchers traditionally viewed assessment strategies as fixed (e.g. Arnott & Elwood 2009, Elwood & Arnott 2012, Taylor & Elwood 2003), but now recognise individual- and population-level variation (Camerlink *et al.* 2017, Chapin *et al.* 2019, Mesterton-Gibbons & Heap 2014). For example, green anoles (*Anolis carolinensis*; Garcia *et al.* 2012), mangrove killifish (*Kryptolebias marmoratus*; Hsu *et al.* 2008), and fiddler crabs (*Uca mjoebergi*; Morrell *et al.* 2005) use mutual assessment when deciding whether to escalate a contest, and self-assessment during the fight. Humans in positive affective states rely on heuristics (i.e. rules of thumb) more than humans in negative affective states (Blanchette & Richards 2010). When assessing the strength of an argument, for instance, people experiencing positive emotions use the author's expertise, whereas people in neutral states judge the content (i.e. deeper processing; Mackie & Worth 1989, Worth & Mackie 1987). In animal contests, positive valence may also promote less cognitively demanding assessment strategies, such as self-assessment or heuristics (e.g. "resident wins"; see Hutchinson & Gigerenzer 2005). Future research could manipulate affective states to test this. I hypothesise that prior reward will lead to self-assessment, whereas prior punishment will lead to mutual assessment.

Having defined emotions as functional responses to reward and punishment, we can say that contest assessments (i.e. appraisals) elicit emotions. I propose that positive emotions about potential contests indicate that fitness benefits outweigh perceived costs, activating a reward acquisition system (Mendl *et al.* 2010, Mendl & Paul 2020; see Introduction). This system covers (1) cognition: information gathering and decisions to enter and escalate contests; (2) drive: work invested to attack; (3) neurophysiology: dopamine and opioid activity; and (4) behaviour: threat displays and aggression. By contrast, negative emotions indicate that perceived contest costs outweigh fitness benefits, activating a punishment avoidance system. This system covers (1) cognition: information gathering and decisions to avoid and withdraw; (2) drive: work invested to escape; (3) neurophysiology: reduced serotonergic activity; and (4) behaviour: submission and retreat.

From a human perspective, linking positive valence and aggressive behaviour may seem counterintuitive. Anger, for instance, *feels* negative (Harmon-Jones *et al.* 2011), but causes aggression (Cabral & de Almeida 2019, Veenstra *et al.* 2018). However, this perspective is based on our conscious experience of emotion (i.e. the feeling component). The non-feeling components indicate that anger is a reward acquisition emotion (i.e. positive valence), not a punishment avoidance emotion (i.e. negative valence; Carver & Harmon-Jones 2009). Anger drives approach towards the inducing stimulus, whereas negative-valence emotions drive withdrawal (Carver & Harmon-Jones 2009). As a result, my functional definition of emotion – which does not require conscious feeling – categorises anger as positively valenced. Negative-valence emotions can lead to aggressive behaviour, but only when withdrawal is not an option (e.g. cornered animals lashing out). In the present manuscript, I only consider positive-valence aggression, where the aim is resource acquisition.

This review focuses on contest initiation, winning, and losing, but affective states might also govern behavioural transitions within contests, such as levels of display or escalated aggression (e.g. Garcia *et al.* 2012, Hsu *et al.* 2008, Morrell *et al.* 2005). From an emotion standpoint, the transitions at either end of contests are more empirically tractable. Applying an emotional event pre-contest indicates how emotions influence initiation, for example, whereas applying an emotional event between contests indicates how emotions disrupt experience effects. Tracking emotions during contests is more challenging, as contests are ongoing emotional events. To resolve this issue, I propose startling contestants at set points during a contest (Arnott & Elwood 2009, Elwood *et al.* 1998). Motivation theorists interpret faster contest resumption (i.e. shorter startle latencies) as stronger motivation to fight (Moors *et al.* 2013). However, affective state influences the startle reflex (Crump *et al.* 2018; see Chapter Four). In humans (Koch 1990), macaques (Winslow *et al.* 2002), and rats (Koch 1990), negative-valence states increase startle duration and magnitude. Future researchers could use startle duration to understand how valence relates to within-contest behavioural transitions.

To summarise, emotion theory correctly predicts that contest assessments cover more than RV and RHP. Animals assess the resource, opponent, and context, in relation to individual circumstances. I hope researchers investigate whether additional human appraisals influence contest dynamics in other species. For example, perhaps agency appraisals (who was responsible? what did they intend?) influence contest decision-making. Under my definition of emotion, these appraisals elicit emotional responses that reflect personal circumstances and prevailing conditions. Conceptualising cognition, drive, and neurophysiology as a unified affective state underpinning behaviour explains existing results and generates new hypotheses.

6.3 | Contest Outcome and Experience Effects

Contest outcomes indicate how an individual’s RHP compares to the population’s RHP (Fawcett & Johnstone 2010, Mesterton-Gibbons 1999). Assuming self-assessment, wins signal relatively high personal RHP and losses signal relatively low personal RHP. Winners, therefore, initiate, escalate, and win more subsequent contests (winner effects), whereas losers avoid and lose more subsequent contests (loser effects; Hsu *et al.* 2006, 2009, Rutte *et al.* 2006). I conceptualise contests as emotional events, so winning induces positive-valence emotions that increase aggressive behaviour and losing induces negative-valence emotions that reduce aggressive behaviour (even if actual RHP does not change). By reflecting cumulative emotional outcomes, winner and loser effects represent longer-term moods (Figure 17).

Both emotions and moods cause cognitive changes, such as judgement biases (Paul *et al.* 2005; see Chapter Two). Assuming reward and punishment experience predicts likely outcomes in the present, moods indicate whether ambiguous stimuli signal positive or negative outcomes, leading to judgement biases (Mendl *et al.* 2009, Nettle & Bateson 2012). I, therefore, suggest that mood-induced judgement bias underlies contest experience effects. Winners gain fitness-enhancing resources, so winning is positively valenced. Thus, previous winners should be relatively optimistic about unknown rewards (RV) and outcome likelihood (RHP), and correspondingly more aggressive. Losing, meanwhile, is negatively valenced, so losers should be more pessimistic and less aggressive. Indeed, perceived RHP, rather than actual RHP, influences winner and loser effects (Hsu *et al.* 2006, 2009; cf. Kasumovic *et al.* 2010).

Empirical evidence suggests that contests induce judgement biases. In judgement bias tasks, dominant animals respond faster and more frequently to probe stimuli than subordinates (rats: Barker *et al.* 2017; pigs: Horback & Parsons 2019; tufted capuchins: Schino *et al.* 2016; see Chapters Two and Four). The dominants' optimism may reflect wins inducing positive valence. In similar tasks, rats (Papciak *et al.* 2013) and Murray cod (*Maccullochella peelii*;

Rogers *et al.* 2020) that repeatedly lose contests make relatively pessimistic responses to the probes. Equivalent opponent-directed behaviour – reduced likelihood of attacking an ambiguous rival – would constitute a loser effect. As judgement biases influence responses to ambiguity more than responses to predictable outcomes (Mendl *et al.* 2009, Mendl & Paul 2020), I hypothesise that judgement biases impact behaviour in contests with unpredictable outcomes (where opponents have similar RHP) more than contests with predictable outcomes (where opponents' RHP differs markedly).

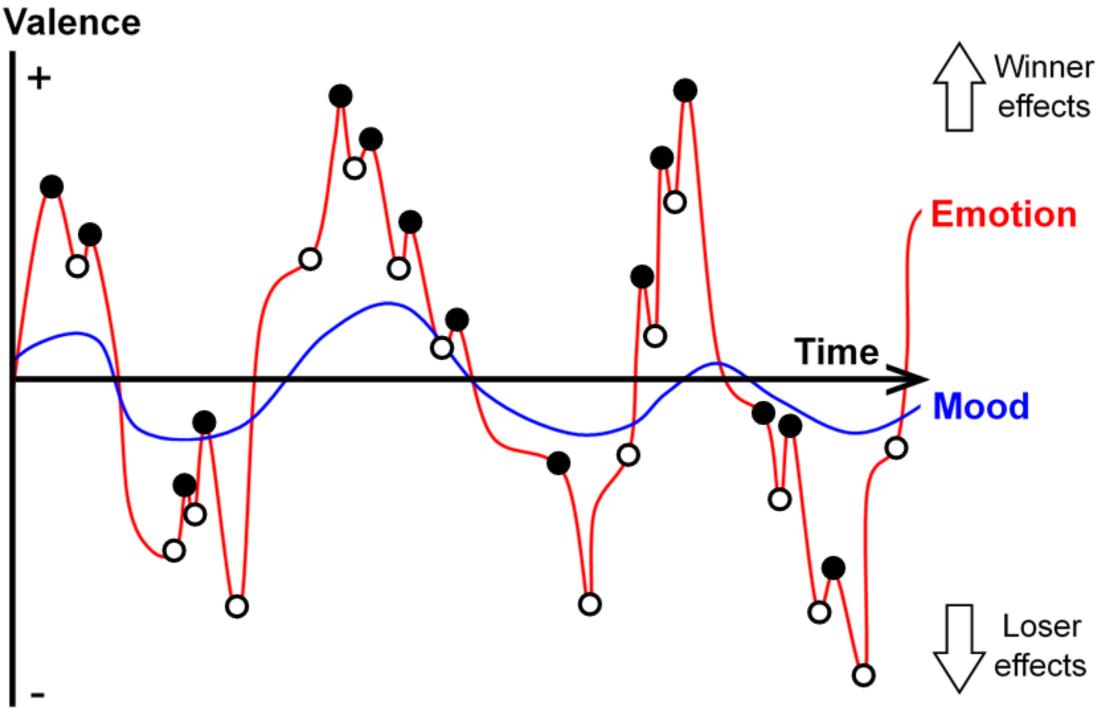

Figure 17. Cumulative emotional valence determines mood (Crump *et al.* 2020a, Webb *et al.* 2018; manifested in aggression). Considering only integral (objectively contest-relevant) influences, white dots are wins and black dots are losses. Considering both integral and incidental (objectively contest-irrelevant) influences, white dots are rewards and black dots are punishments.

Experience effects also suggest that contests can be intrinsically rewarding (May 2011). In addition to yielding external reward, aggressive behaviour itself (and particularly winning) seems to induce positive affective states, which may inform future decisions. For example, mice learn instrumental responses to access and attack submissive opponents (Falkner *et al.* 2016). Responses decline for non-submissive opponents, revealing that outcome matters. Moreover, winning induces conditioned place preference in mice (Martínez *et al.* 1995), Syrian hamsters (*Mesocricetus auratus*; Meisel & Joppa 1994), and green anoles (Farrell & Wilczynski 2006). From an affective state perspective, positive emotions reward this conditioning. Affective reinforcement might also occur within a single contest. For instance, accurate strikes (Briffa & Lane 2017) or appropriate assessments (Reichert & Quinn 2017) may be rewarding.

To recap, I suggest that moods, which reflect contest outcome experience, mediate expectations about unknown RV and future outcomes. Mood-induced judgement bias and affective reinforcement may underpin these experience effects. To investigate judgement bias, contest researchers could measure optimism pre- and post-contest. I predict that wins induce optimism and losses induce pessimism, with state optimism producing winner effects and state pessimism producing loser effects. Exploring the role of neurotransmitters linked to reward, such as opioids, could reveal whether contests are intrinsically rewarding.

6.4 | Crossing Behavioural Contexts

So far, I have considered adaptive affective states. There are clear fitness benefits to cumulative experience informing reliable assessments, but existing optimality models already predict these effects. How do emotions and moods advance our understanding?

Integral affective states are objectively relevant to a cognitive process. In humans, for example, sunshine (stimulus) induces positive valence (emotion) that causes a decision (cognition) to go outside (behaviour). Incidental affective states, on the other hand, influence objectively unrelated cognitive processes (Blanchette & Richards 2010, George & Dane 2016, Lerner *et al.* 2015, Västfjäll *et al.* 2016, Wyer *et al.* 2019). For example, people rate their overall life satisfaction higher on sunny days than rainy days (Schwarz & Clore 1983). Sunshine (stimulus) induces positive valence (emotion) that causes an objectively unrelated assessment (cognition) to be reported positively (behaviour). Incidental affective states, thus, distinguish optimal and affective decision-making. Optimality models only use integral information, whereas affective states incorporate incidental influences as well.

Although understudied in behavioural ecology, incidental affective states influence animal cognition and behaviour. Starlings with enriched housing judge unrelated temporal stimuli more optimistically (Matheson *et al.* 2008), whilst honeybees shaken aversively judge unrelated olfactory stimuli more pessimistically (Bateson *et al.* 2011). Moreover, isolating rats improves recall of unrelated light and sound stimuli (Takatsu-Coleman *et al.* 2013). It follows that incidental information may influence contest behaviour, and that rewards and punishments in general – not wins and losses specifically – induce “winner” and “loser” effects (Figure 17). For instance, positive-valence female interactions increase aggressive behaviour in male speckled wood butterflies (*Pararge aegeria*; Bergman *et al.* 2010) and wolf spiders (*Venonia coruscans*; Zhang *et al.* 2019), whereas negative-valence predator exposure decreases aggressive behaviour in daffodil cichlids (*Neolamprologus pulcher*; Reddon *et al.* 2019). However, a note of caution: apparently incidental influences may be functionally integral. Presence of a potential mate, for example, increases contest benefits, and predation risk increases contest costs (Bergman *et al.* 2010, Reddon *et al.* 2019, Zhang *et al.* 2019). We must understand a species’ ecology to determine whether cross-context variables are objectively relevant, and hence whether they are integral or incidental. I welcome new research to fill this knowledge-gap. Contest researchers could borrow affective state research methods from animal welfare science and psychopharmacology. Exposing fish to antidepressants and anxiolytics in wastewater has produced equivocal results: venlafaxine increases aggression (Parrott & Metcalfe 2018), but fluoxetine reduces aggression (Perreault *et al.* 2003). To test whether incidental affective states influence contest behaviour, we need controlled interventions in more species.

Incidental affective states not only influence contests; contests might also induce incidental affective states and influence objectively unrelated cognitive processes (see Niemelä & Santostefano 2015). For example, rats that repeatedly lose contests develop anhedonia: reduced reward sensitivity, expressed in non-contest situations and linked to depression in humans (Treadway & Zald 2011). Giving the rats unrelated but signalled food rewards reverses this effect (van der Harst *et al.* 2005). Compared to tufted capuchins with subordinate bystanders, capuchins exposed to aggressive bystanders allocate more attention towards humans (Boggiani *et al.* 2018; see Chapter Four). Dominant capuchins (Schino *et al.* 2016) and pigs (Horback & Parsons 2019) expect more positive outcomes from ambiguous spatial stimuli (i.e. optimistic judgement bias), whilst subordinate cod expect fewer positive outcomes from ambiguous spatial stimuli (i.e. pessimistic judgement bias; Rogers *et al.* 2020). Contest-induced incidental affective states may influence virtually any decision. Is brightly-coloured prey toxic or a mimic? Are rustling leaves a predator or the wind? When moods bias decisions, the most encountered emotional stimuli with the longest duration and most polar valence might determine behaviour, regardless of objective relevance. It is possible that frequently winning contests, for example, may induce optimism that rare prey is edible, even if the prey is usually toxic. This example illustrates how decision-making using incidental information can negatively impact fitness. Incidental affective states may cause maladaptive behaviour (Lerner *et al.* 2015).

Given their maladaptive potential, I suggest two reasons for incidental affective states. First, to be selected, cross-context affective states must increase fitness *on average* – not necessarily *every time*. Nettle and Bateson (2012) noted that recent environment and physical condition persist across behavioural contexts. Lame animals, for instance, cannot fight, forage or flee from predators, so information from each of these contexts is integral to the others. Cross-context affective states will be selected if most are integral, even if some are incidental. In humans, various measures increase the likelihood that cross-context affective states influence relevant cognition (Västfjäll *et al.* 2016, Wyer *et al.* 2019). For example, people associate their affective states with concurrent cognitive processes (Clore *et al.* 2001). Incidental emotional influences are also less common than incidental moods, because emotions usually have an obvious eliciting stimulus or event (Västfjäll *et al.* 2016). Animal research may reveal similar mechanisms to limit incidental affective states.

The second possible explanation is that incidental affective states dominate when animals lack reliable information, or when acquisition and storage costs outweigh the benefits (Hobson 2020, Schneeberger & Taborsky 2020). This is why humans evaluating ambiguous stimuli (e.g. brand names without product details) rely on incidental affective states (Bakamitsos 2006). In animal contests, a fight indicates rival RHP most accurately, but entails substantial investment and potential injury (Darden *et al.* 2019, Oliveira *et al.* 2001). Assessments in other contexts carry their own cost/accuracy trade-offs. Bystander effects avoid fight costs and reflect individual RHP, but they require individual discrimination and recall (Elwood & Arnott 2012). Winner and loser effects are less cognitively demanding, but based on previous opponents' RHP. This measure will predict future opponents' RHP less accurately than individual assessments. I hypothesise that mood does not even distinguish between behavioural contexts, further reducing both cognitive requirements and accuracy. Incidental affective states may, therefore, influence decisions when contestants have less reliable information or face high information-gathering costs (e.g. intruders). From this perspective, incidental affective states are the "best of a bad job".

Incidental affective states may magnify the impact of anthropogenic stressors. Conservation biologists typically focus on HIREC's direct effects: habitat destruction, invasive species, overharvesting, pollution, and climate change can all impact objectively relevant (i.e. integral) cognition and behaviour (Sih *et al.* 2011). In turtle hatchlings, for example, artificial light (stimulus) causes a decision (cognition) to move inland (behaviour; Truscott *et al.* 2017, Tuxbury & Salmon 2005). Although the stimulus is misleading and the behaviour is maladaptive, light is objectively relevant to this decision, so the cognitive process is integral. I argue that behavioural ecologists and conservation biologists should also investigate whether human activity influences objectively irrelevant (i.e. incidental) cognition in other animals. Addressing this knowledge-gap may reveal that HIREC impacts biodiversity loss more widely than currently recognised.

In summary, integral affective states are objectively relevant and adaptive, whereas incidental affective states are objectively irrelevant and potentially maladaptive. Incidental influences may nonetheless seep in when integral information is unavailable or costly. Despite preliminary evidence, we do not yet know the extent of incidental affective states in animal decision-making. I hope that future researchers test whether objectively unrelated stimuli impact contest dynamics. Without integral influences, I predict that generic rewards increase aggression and generic punishments decrease aggression. This approach also applies to anthropogenic rewards and punishments, so incidental affective states may contribute to biodiversity loss.

6.5 | Conclusions

An affective states approach generates novel predictions and opens new avenues for behavioural ecology (Table 7). Both emotions and contest behaviour rely on assessments of stimuli and their personal significance; both enlist cognition, drive, and neurophysiology; and both reflect reward and punishment experience. I equate contest assessments to emotional appraisals, which determine contest decision-making and behaviour. I explain experience effects as wins inducing positive moods and losses inducing negative moods. This hypothesis, and my conception of contests as emotional episodes, predicts that manipulating affective state will modify contest behaviour. As well as integral influences, incidental affective states may impact contests, and contest-induced affective states may impact objectively unrelated behaviours. I hypothesise that high-frequency, long-lasting, polar-valence events disproportionately influence animal decision-making and behaviour, even if incidental. Moreover, despite my focus on contests, emotion theory may underpin all non-reflexive behaviour – from signalling to mate choice to parental care. Behavioural ecologists study these fields separately, but affective states transcend boundaries. As a result, HIREC may disrupt animal cognition in unexpected ways. We need a more holistic ethology to understand this affective cognition and behaviour.

Table 7. Major predictions and outstanding questions that arise from applying emotion theory to animal contests.

Major Predictions	**Outstanding Questions**
Contest appraisals cover more variables than traditionally recognised (i.e. RV and RHP)	Are contest appraisals sequential? Do untested human appraisals (e.g. perceived agency) modify contest dynamics in animals?
Positive affective states induce self-assessment; negative states induce mutual assessment	Do assessment strategies vary with affective state? How might this influence the outcome?
Winner effects are associated with optimistic responses to judgement bias tasks; loser effects are associated with pessimistic responses	What neurocognitive mechanisms underpin judgement bias? Are they equivalent to the mechanisms underpinning winner/loser effects
Incidental affective influences modify contest behaviour	Do incidental affective states commonly impact contests in nature? Why evolve a generalised (rather than domain-specific) affective system?
Humans and animals share rules that increase the likelihood of incidental influences (e.g. concurrence, ambiguity, and link to moods)	What mechanisms minimise incidental influences? How do these impact fitness?
The above predictions apply only to animals with a central nervous system	Do all animals with a central nervous system have affective states? Are contest dynamics fundamentally different in organisms without a central nervous system?

7 | General discussion

Cognition and emotion have been comparatively overlooked in animal welfare science and conservation biology. Despite cognitive biases being the “gold standard” for assessing psychological wellbeing (Bateson & Nettle 2015), behaviour and physiology are better studied welfare indicators (Paul *et al.* 2005). Some also resist emotions in animal welfare (e.g. Arlinghaus *et al.* 2020, Dawkins 2017), although this raises the question of why an emotionless welfare concept does not cover plants, bacteria or non-living objects. In conservation science, too, cognition is rarely studied (Greggor *et al.* 2020) and emotion is practically taboo (cf. compassionate conservation; Bekoff 2013, Wallach *et al.* 2018). Instead of internal mental states, researchers focus on their overt external indicators (e.g. physical health and behaviour; Hing *et al.* 2016, Sutherland 1998). As this thesis illustrates, however, studying cognition and emotion can reveal insights that allow us to improve animal welfare and highlight conservation issues. This is essential in a period of unprecedented anthropogenic change.

7.1 | Real-World Impact

Although HIREC can harm individual animals and biodiversity, humans can also reverse the damage. “Top-down” interventions involve governments legislating against detrimental practices and incentivising sustainable alternatives, such as through subsidies. “Bottom-up” approaches involve the public collectively acting more sustainably and pressuring larger bodies to follow suit. Well-publicised scientific research can galvanise both policy-makers (top-down) and the public (bottom-up), ensuring an evidence-based approach to animal welfare (Dawkins 2006, Melfi 2009) and biodiversity conservation (Klein *et al.* 2016, Kowarik & von der Lippe 2018, Svancara *et al.* 2005).

Chapters Two and Three highlighted the importance of pasture access for dairy cattle welfare. Despite this and previous studies, European and North American farmers are increasingly housing cattle indoors all year round (Robbins *et al.* 2016, van den Pol-van Dasselaar *et al.* 2020). In the United States, only 20% of lactating cows and 34% of dry cows accessed pasture in 2013 (USDA 2016). In Denmark, Greece, and Poland, under a quarter of dairy cows went out to pasture in 2019 (van den Pol-van Dasselaar *et al.* 2020). However, welfare studies, such as the one described in Chapters Two and Three, can change perceptions and practice (Dawkins 2006). Finland, Norway, and Sweden, for example, have banned full-time housing on welfare grounds (Jordbruksverket 2017, van den Pol-van Dasselaar *et al.* 2020). Over 90% of British and Irish dairy cows also went out to pasture in 2019, although this number is decreasing (van den Pol-van Dasselaar *et al.* 2020). Brexit is an historic opportunity. The Department for the Environment, Food, and Rural Affairs (Defra) are exploring ways to extend and strengthen welfare laws (e.g. the Animal Welfare Act 2006; Birch *et al.* 2020a). Legislating against housing dairy cattle indoors full-time would help to ensure that the United Kingdom remains a global leader in animal welfare.

The hermit crab results outlined in Chapter Five likewise contribute to previous research demonstrating the adverse effects of microplastic pollution (Au *et al.* 2015, Blarer & Burkhardt-Holm 2016, Cole *et al.* 2015, Watts et al. 2015, Welden & Cowie 2016). Such findings are a global concern. Microplastics have reached the remotest regions of Earth, including Antarctica and the deep sea (Cunningham *et al.* 2020), sparking enormous public and political concern (e.g. Davis 2019, Douglas 2019, Horton 2019). This has serious real-world applications: more than 10 nations have banned cosmetic microbeads since 2015, including the United States, United Kingdom, France, Italy, New Zealand, and South Korea (Lam *et al.* 2018, Nelson *et al.* 2019).

Although microplastic legislation has focused on primary (industry-made) microplastics, secondary (degraded) microplastics are a bigger issue. Lassen *et al.* (2015) attributed > 99% of Danish microplastic pollution to secondary sources and estimated that cosmetic microbeads account for only 0.1%. At 60%, tyre dust was by far the biggest contributor (see also Eunomia 2016, Gouin *et al.* 2015, Sundt *et al.* 2014). Both top-down and bottom-up efforts have attempted to tackle this issue. Banning single-use plastic bags is a popular top-down intervention (Macintosh *et al.* 2020). China's ban slashed usage by two thirds (Zhu 2011), although alternative bag consumption can neutralise the benefits (Macintosh *et al.* 2020). A bottom-up example is the 2018 #StopSucking campaign, which led to corporations from Ikea to SeaWorld eliminating plastic straws (Kessler 2019). Global plastic production is nonetheless increasing by 8% per year (Geyer *et al.* 2017). Further efforts, particularly targeting secondary microplastics, are necessary (Burns & Boxall 2018, Gouin *et al.* 2015).

In both examples of HIREC – housing cattle full-time and coastal microplastic pollution – we are only beginning to understand the environmental impacts. Unfortunately, these changes have already occurred. Most milk now comes from dairy cows without any pasture access (EFSA 2009), and 6.3 billion tonnes of plastic already pollute the oceans, including some of the world's wildest and most pristine environments (Geyer *et al.* 2017). Both figures are rising. If sustainable HIREC is possible, it requires more proactive science (Sánchez-Suárez *et al.* 2020). Protecting animal welfare and biodiversity means pre-emptively mitigating the environmental consequences of anthropogenic change. It is easier to preserve than piece back together.

7.2 | Limitations

My research highlights the importance of studying cognition and emotion to improve animal welfare and address biodiversity loss, but it had limitations. In the dairy cattle experiment (Chapters Two and Three), I did not control for grass intake in the PAS treatment, despite diet influencing cow behaviour (O'Driscoll *et al.* 2019, Webster 2001). Cattle also find cognitive tasks rewarding (Hagen & Broom 2004, Mandel *et al.* 2016), so the judgement bias task itself may have impacted subjects' affective state. More generally, both external (e.g. weather conditions; Charlton *et al.* 2013, Falk *et al.* 2012) and internal factors (e.g. experience of pasture access; Charlton *et al.* 2011a, b) mediate preference for pasture. It is unclear whether my results generalise to different herds on different farms at different times. Comparative observational studies are also necessary to understand how pasture and indoor housing influence welfare (e.g. Armbrecht *et al.* 2019, De Graaf *et al.* 2017, Wagner *et al.* 2018).

The hermit crab study (Chapter Five) did not rule out non-cognitive explanations. Assessment and decision-making underpin shell selection behaviour, causing previous authors to treat disrupted shell selection as a model for compromised cognition (e.g. Walsh *et al.* 2017). In my study, however, this inference was circumstantial. Microplastic exposure may have reduced general activity, explaining why hermit crabs in the plastic treatment were less inclined to approach and enter a new, higher-quality shell. Further studies from our lab indicate that microplastics do not reduce activity and that microplastics disrupt cognitive processes (associative learning; Crump *et al.*, in prep, McDaid *et al.*, in prep), although these are not yet published. Going forward, we plan to explore the proximate mechanism behind the observed behaviour change. This will involve observing subjects in the home tank (i.e. during microplastic exposure) and investigating their physiology and behaviour.

7.3 | Future Directions

Anthropogenic change is accelerating (Steffen *et al.* 2006, 2015). As agriculture intensifies and pollution proliferates, research on the welfare and biodiversity impacts must keep pace.

As their behaviour indicated that cows with pasture access had better welfare, I hope future research identifies the factors responsible (Beaver *et al.* 2019, Robbins & Beck 2018, Smid *et al.* 2020). This could lead to design and management practices that replicate the benefits of pasture in indoor housing (Charlton & Rutter 2017). For example, I linked restlessness to uncomfortable surfaces and competition for cubicles. These issues can be partially addressed without pasture access. Tucker *et al.* (2003) offered dairy cows three cubicle lying surfaces: deep-bedded sand, deep-bedded sawdust, and a rubber-filled mattress. Given the choice, subjects spent longer lying on sand and sawdust, and lying durations were shorter when only the mattress was available. Furthermore, increasing stocking densities reduces lying durations and increases cubicle displacements (Fregonesi *et al.* 2007). Fully- or understocking cubicle housing can ameliorate this (Huzzey *et al.* 2006, Telezhenko *et al.* 2012, Winckler *et al.* 2016). Additionally, enrichment could compensate for under-stimulating living conditions (Mandel *et al.* 2016). Brushes, for instance, increase total scratching time by over 500% in cubicle-housed cows, which may reduce boredom (DeVries *et al.* 2007). These findings indicate that cow welfare can be improved in indoor housing.

Nevertheless, going outdoors has health and welfare benefits, such as exposure to natural light (Arnott *et al.* 2017). Exercise yards have been proposed as an intensive alternative to pasture, because they require less space but allow cattle outside. However, compared to cows with exercise yards, cows with pasture access spend around twice as long outdoors (Kismul *et al.* 2018, Smid *et al.* 2018). This indicates that not all of pasture's welfare benefits are transferable to more intensive production systems. For example, pastures are larger than exercise yards and allow natural grazing behaviour (Smid *et al.* 2020). Restricted pasture access, as in my study, offers a practical alternative (Chapinal *et al.* 2018, Kismul *et al.* 2018, 2019). Using the Welfare Quality® assessment protocol for dairy cattle (Welfare Quality Network 2009), Wagner *et al.* (2018) identified many of the same advantages for cows with 6-12 h of pasture access per day as for cows with > 12 h per day. Some features of indoor housing could also alleviate welfare issues at pasture, such as providing shade structures (Van Iaer *et al.* 2014).

From an experimental design perspective, I hope that future animal welfare research uses more indicators of wellbeing. My dairy cow study assessed cognition (judgement bias) and behaviour (lying and walking). Although most human and animal emotion research adopts a componential view of emotion, neither literature regularly measures multiple components simultaneously (Scherer & Moors 2019). This is problematic, because emotions exist even if one component is removed (Fanselow 2018). For example, humans still experience fear when lateral hypothalamus lesions prevent hypertension (Iwata *et al.* 1986). Likewise, if I had only measured judgement bias in dairy cows, my findings would have indicated that pasture access did not impact welfare. The behavioural data, however, suggested the opposite. Assessing multiple components of emotion gives a more accurate and holistic picture of animals' welfare status (Mendl *et al.* 2010, Briefer *et al.* 2015).

Based on Chapter Four's conclusion that affect-driven attention bias is a promising indicator of animal emotions, it would also be interesting to explore whether pasture access influences attention in dairy cows. Lee *et al.* (2018) recorded beef steers' attention towards a dog, a potential predator. Steers treated with anxiogenic drugs spent longer looking at the dog, looking at the door where the dog had been, and took longer to resume feeding. However, we may not expect full-time indoor housing to induce anxiety-like states. Indoor housing may even minimise the perception of threats like potential predators. Instead, I recommend that future researchers investigate whether full-time housing induces depression-like states. Such states may manifest themselves in attention biases away from positive stimuli (e.g. in humans: Duque & Vázquez 2015). However, my reward anticipation results suggest that cows in negative affective states may allocate more attention towards positive stimuli, such as food, because they have few positive events in their lives (Spruijt *et al.* 2001; see Chapter Two). More research is necessary to distinguish between these hypotheses.

For my hermit crab study (Chapter Five), it is unclear whether the results generalise to hermit crab behaviour in nature. I hope future researchers establish the effects of environmentally accurate microplastic levels in real coastal environments (Cunningham & Sigwart 2019). Such studies could reveal whether microplastics impact hermit crab cognition and behaviour *in situ*, how this might affect fitness, and whether it could cause population declines. Microplastics may also have synergistic effects with other extinction drivers. For example, non-polar plastic adsorbs toxic ions, such as heavy metals (Godoy *et al.* 2019). Microplastics, therefore, cause very high localised heavy metal concentrations, and act as a vector for their consumption (Brennecke *et al.* 2016). Laboratory experiments such as mine, which used virgin microplastics, cannot predict such effects. Beyond hermit crabs, my findings raise the possibility that microplastics affect cognition and behaviour in other taxa. The extent to which this occurs, and its possible effects on coastal diversity, are unknown.

Whilst welfare scientists have embraced animal emotions, behavioural ecologists, pure ethologists, and conservation biologists remain circumspect (Crump *et al.* 2020a). Historically, fundamental animal behaviour research informed the nascent science of animal welfare (Fraser 2009). Welfare science has now matured such that the roles are reversed.

Animal welfare researchers have demonstrated emotions' key role in animal cognition (Mendl *et al.* 2010, Mendl & Paul 2020), so other fields should recognise their importance. Chapter Six highlighted an example: incidental affective states. I argued that affective states not only underpin animal behaviour, but also cross contexts, causing irrelevant stimuli to influence animals' assessments and decision-making. In effect, animals' past experiences function as generalised Bayesian priors, which guide behaviour when more reliable information is unavailable (Weary 2019). Whilst tentative, this hypothesis generates fascinating predictions (Crump *et al.* 2020a). Is animal behaviour influenced by: (1) Similar appraisals to human emotions? (2) Physical and pharmacological affective state manipulations? (3) Incidental valenced stimuli? I hope subsequent studies address these questions.

7.4 | Thesis Structure and Impact of COVID-19

The theme unifying my PhD was originally intended to be cognitive bias. Unfortunately, the 2020 COVID-19 pandemic derailed this plan. My thesis is, therefore, less cohesive than I had intended. Whilst I am extremely proud of completing my PhD during a once-a-century health crisis, I would like to summarise my original plan and explain why I have such disparate chapters.

Throughout my PhD, the working title was: "Affective states and animal welfare: Validating novel cognitive bias tasks". In this plan, the current Chapters Two and Three were combined, so Chapter Two would have covered both dairy cow datasets (judgement bias and behaviour). Chapter Three was then envisaged as an experiment on judgement bias in hermit crabs (details below). The current Chapter Four (attention bias review) was unchanged in the original plan, but the current Chapter Five (hermit crab microplastic study) was not intended as a thesis chapter. Instead, following on from Chapter Four, the planned Chapter Five would have been an attention bias experiment on dairy cows (details below). The current Chapter Six was always planned to conclude my thesis, hence this chapter's focus on the role of cognitive biases in animal behaviour. Thus, in addition to a narrower focus, the main deviations from my planned thesis were losing chapters on hermit crab judgement bias and dairy cow attention bias.

To my knowledge, judgement bias has never been investigated in crustaceans (for other arthropod studies, see Bateson *et al.* 2011, Deakin *et al.* 2018, Perry *et al.* 2016). My planned hermit crab experiment would have used judgement bias as an indicator of pain. There is no consensus on whether invertebrates feel pain (Birch *et al.* 2020, Diggles 2018, Elwood 2019), and most welfare legislation excludes crustaceans (e.g. Directive 2010/63/EU). However, pessimistic judgement biases have been linked to painful procedures (hot iron disbudding in dairy calves; Lecorps *et al.* 2019, Neave *et al.* 2013; see Chapter Two) and painful pathologies (mucositis in rats; George *et al.* 2018; syringomyelia in dogs; Cockburn *et al.* 2018). Humans in chronic pain also exhibit biased interpretations of ambiguous stimuli (Lau *et al.* 2018, Pincus *et al.* 1996, Schoth & Liossi 2017). I, therefore, planned to test electroshocked and control hermit crabs on a Go/No-go spatial judgement bias task (Burman *et al.* 2008), where approaching the P location was rewarded with food and approaching the N location was punished with bright light. My hypothesis was that electric shocks would induce pessimistic judgement biases – potential evidence that hermit crabs feel pain.

I also planned a chapter on attention bias in dairy cattle. Unlike previous work using pharmacological treatments (Lee *et al.* 2017), this experiment would have measured attention to threat after an invasive veterinary procedure. Following routine rectal examinations (part of routine fertility assessment), cows would have been isolated in a testing arena and exposed to a dog (a potentially threatening stimulus) for 10 s (Lee *et al.* 2016, 2017, Monk *et al.* 2018b; see Chapter Four). I planned to record head orientation and eye gaze whilst the dog was visible and for three minutes afterwards. To test recommendations from my attention bias review (see Chapter Four), I would also have measured ear position and movements (Proctor & Carder 2014, Lambert & Carder 2019), as well as subjects' tendency to use the left eye (a lateralised response to threat; Robins & Phillips 2010). I hypothesised that, after the veterinary procedure, cows would orient their ears towards the dog more than cows that had not undergone the procedure. I also predicted a left-eye bias when cows were viewing the dog, and expected the veterinary procedure to strengthen this effect, reflecting subjects' heightened attention to threat.

These carefully laid plans were upended by COVID-19, which emerged one year before my submission deadline. Queen's University Belfast closed its laboratories and postponed non-essential research, so I could not complete the hermit crab and dairy cow experiments. To finish on-time, flexibility was required and I decided to compile the thesis from my existing datasets and papers. I retrospectively linked these disparate chapters under the broad theme of how anthropogenic stressors affect animal cognition and emotion. Nonetheless, I hope to return to my work on judgement bias in hermit crabs and attention bias in dairy cows later in my career.

7.5 | Conclusions

Scientific research is vital to understand and mitigate humans' environmental impact – both to individual animals and entire populations. Animal cognition and emotions have been poorly studied in this regard. I investigated the effects of pasture access on emotional wellbeing in dairy cows. Despite no treatment differences in judgement bias, pasture access was linked to reduced anticipatory behaviour, and increased lying and walking behaviour. These findings suggest that pasture is a more rewarding and comfortable environment. I then reviewed another cognitive bias, attention bias, as an animal welfare indicator. Attention biases to threat are a promising measure of negative affective states, but more research is needed on attention biases to positive stimuli. Next, I tested whether microplastic pollution compromises hermit crab behaviour and cognition. Hermit crabs exposed to microplastics were less likely to touch and enter a shell upgrade, suggesting that microplastic pollution disrupts this crucial survival behaviour. Finally, using contests as a case-study, I applied emotion research to behavioural ecology and conservation biology. Preliminary evidence suggests that valenced stimuli influence unrelated cognition in other behavioural contexts, potentially causing maladaptive behaviour. I hope these findings inspire future research on how anthropogenic change impacts animal cognition and emotions.

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