

1 **From Pigs to Silkworms: Cognition and Welfare across 10 Farmed Taxa**

2
3 **Advanced Review**

4
5 **Authors:**

6

*Rachael Miller, Anglia Ruskin University, UK and University of Cambridge, UK, Email: rh87@aru.ac.uk ORCID: 0000-0003-2996-9571 *Corresponding author
--

Martina Schiestl, University of Veterinary Science Brno, Czech Republic Email: m.schiestl@hotmail.de
--

Anna Trevarthen, Independent Researcher, UK Email: anna.c.trevarthen@gmail.com ORCID: 0000-0001-9575-7150
--

Leigh Gaffney, University of Victoria, Canada Email: gaffney.leigh@gmail.com ORCID: 0000-0002-9516-482X
--

J. Michelle Lavery, University of Guelph, Canada Email: lavery.j.m@gmail.com ORCID: 0000-0003-1179-1445

Bob Fischer, Rethink Priorities, USA and Texas State University, USA Email: bob@rethinkpriorities.org ORCID: 0000-0001-9605-393X

Alexandra Schnell, University of Cambridge, UK Email: alex.k.schnell@gmail.com ORCID: 0000-0001-9223-0724

7

8

9 **Conflict of interest**

10 The authors declare no competing interests.

11

12 **Keywords:** cognition, animal welfare, learning, behavioural flexibility, welfare range

13 **Abstract**

14

15 Billions of animals across many taxa are extensively farmed, with critical impacts on animal welfare.
16 Societal efforts to reduce animal suffering lack rigorous and systematic approaches that facilitate
17 maximising welfare improvements, such as informed funding allocation decisions. We present a multi-
18 measure, cross-taxa framework for modelling differences in pain, suffering, and related cognition to
19 assess whether certain animals have larger welfare ranges (how well or badly animals can fare).
20 Measures include behavioural flexibility, cognitive sophistication, and general learning. We evaluated
21 90 empirically detectable proxies for cognition and welfare range (henceforth 'proxies') in pigs,
22 chickens, carp, salmon, octopus, shrimp, crabs, crayfish, bees, and silkworms. We grouped a subset
23 of proxies into: A) 10 ideal proxies and B) 10 less ideal proxies but with sufficient data for interspecies
24 comparisons. We graded the strength of evidence per proxy across taxa, and constructed a cognition
25 and welfare range profile, with overall judgement scores (ranging from likely no/low confidence to
26 yes/very high confidence). We discuss the implications of comparisons and highlight key avenues for
27 future research. This work is timely, given recent indications of significant political will towards
28 reducing animal suffering, such as the inclusion of cephalopods and decapods in the Animal Welfare
29 (Sentience) Bill following a UK government-commissioned research review. Given the novelty and
30 robustness of our review, we believe it sets a new standard for investigating interspecies comparisons
31 of cognition and welfare ranges and helps inform future research. This should help streamline funding
32 allocations and improve the welfare of millions of farmed animals.

33

34 **Graphical/ Visual Abstract and Caption**



35

36 Caption: Cognition and welfare in farmed animals - from pigs to silkworms (Free stock images:
37 www.pixabay.com)

38

39 **1. INTRODUCTION**

40

41 Do certain animals have a greater capacity for suffering? This article presents and applies a multi-
42 measure framework to understand variation in cognition and welfare ranges, i.e. how well or badly
43 animals can fare, across farmed taxa. Every year, billions of animals worldwide are subject to farming
44 practices that impact welfare, such as tail docking in pigs, beak trimming in chicken, and fin clipping in
45 fish (Allen & Perry, 1975; Sutherland et al., 2008; Uglem et al., 2020; Franks et al., 2021). Given
46 limited resources and the complexity of the challenge, societal efforts and decisions around funding
47 allocations to reduce animal suffering are largely ad-hoc, lacking the rigorous and systematic
48 approach critical to maximising welfare improvements. Insofar as the decision requires comparing
49 welfare impacts across taxa, decision-makers need tools that are not currently available, including a
50 framework for modelling differences in pain, suffering, and related cognition. However, making robust
51 interspecies comparisons about cognition and welfare is exceptionally complex, owing to often-
52 contending ethical, methodological, and practical considerations. As this knowledge is scattered
53 across a broad literature, a key starting point is a comprehensive synthesis across species. While
54 within-species taxa reviews exist (e.g., Marino, 2017; Lambert et al., 2017), they are not sufficiently
55 broad in scope to address the present challenge of comparing between taxa.

56

57 To remedy this, the present review takes an interdisciplinary approach across animal welfare,
58 comparative psychology, veterinary science, and philosophy (with an author from each field) to
59 provide a comprehensive multi-taxa and multi-measure review of the empirical evidence on cognition
60 and welfare ranges. This work is particularly timely because such reviews can lead to critical changes
61 in animal welfare legislation. For example, in 2020, the UK government commissioned a report
62 highlighting the compelling evidence for sentience in cephalopods and decapods (Birch et al., 2021,

63 Sidebar 1), which led to the Animal Welfare (Sentience) Bill being extended to include both
64 invertebrate groups. Here, we evaluate cognition and welfare ranges across 10 of the most
65 extensively farmed animals: pigs, chickens, carp, salmon, octopus, shrimp, crabs, crayfish, bees, and
66 silkworms. To investigate interspecies variation, we defined and assessed 90 empirically detectable
67 proxies of cognition and welfare ranges (henceforth 'proxies') relating to behavioural flexibility,
68 cognitive sophistication, and general learning. The result of this literature assessment was a
69 comprehensive table of ratings based on references relevant, where available, for each proxy and
70 taxa, giving an overall output of >1000 references (details in section 3.2). Fewer than 20 of 90 proxies
71 identified had been tested across the majority of the 10 taxa, so we refined our review into a subset of
72 these proxies in two overlapping catalogues (A and B). Catalogue A contains 10 ideal proxies,
73 providing an optimal suite of proxies most closely linked to welfare. However, as the empirical data for
74 these proxies were lacking for many taxa this negated interspecies comparisons. We thus created
75 Catalogue B, containing a less-optimal suite of 10 proxies, some with weaker links to welfare. The
76 Catalogue B proxies were selected as those with sufficient empirical data to enable interspecies
77 comparisons.
78

Sidebar 1: Example of interdisciplinary animal welfare review with legislation impacts - Birch et al. (2021)

The UK government recently commissioned a team of scientists to review the evidence of sentience – the capacity to experience emotions, with a focus on pain – in two invertebrate groups, cephalopods and decapods. The scientists used eight interdisciplinary criteria for determining sentience. The first four focused on whether the animal's nervous system could support sentience. Specifically, whether the groups could (i) detect harmful stimuli; (ii) transmit those signals to the brain; (iii) process the signals in integrative brain regions; and (iv) change the nervous system's response when exposed to painkillers or anaesthetics. The four remaining criteria focused on behaviour and cognition. Specifically, whether the groups could (v) trade-off risks of injury against opportunities for reward; (vi) tend to specific sites of injury using self-protective behaviours; (vii) learn to avoid harmful stimuli; and (viii) learn to value painkillers or anaesthetics when injured. After reviewing over 300 studies, the researchers found strong and diverse evidence of sentience in both groups. For example, exposure to acid caused crabs and octopuses to scratch and shield the affected area but self-protective behaviours ceased when exposed to an anaesthetic; crayfish exposed to repeated electrical fields showed anxiety-like mental states; and injured octopuses learned to favour locations where they could self-administer an anaesthetic. Results from this review led to including both cephalopods and decapods in the UK's Animal Welfare (Sentience) Act 2022. Other countries including Norway, Sweden, and New Zealand have already given invertebrates legal protection, but many countries remain to recognise invertebrates as sentient.

79
80 Our review adapted the rating methods developed by Rethink Priorities (2020) and Birch et al. (2021)
81 to compare the strength of the evidence against each proxy. For each taxa, we thus constructed a
82 cognition and welfare range profile, with an overall judgement score based on current evidence, and
83 discussed the implications of comparisons across the taxa. This process identified which proxies are
84 supported by quantitative evidence and which should be prioritised for future research and funding.
85 From this analysis, we proposed future research experiments for specific proxies to enable
86 informative comparative research, including cognitive bias and inhibitory control related paradigms.
87 We believe this approach will assist researchers, including potentially big-team science collaborations
88 (Sidebar 2), to efficiently target existing knowledge gaps. We hope it will help streamline funding
89 allocations and other key decisions that are required to improve the welfare of farmed animals.
90

Sidebar 2: Big-team Science (BTS) Collaborations

There is a recent drive for the development of large collaborative, international networks aiming to promote Open Science practices, pool resources, and enable greater cross-species comparisons, with larger sample sizes and species representations to help remedy potential reproducibility and generalisation issues (Coles et al., 2022; Lambert et al., 2022). Examples of big-team science (BTS) projects focusing on non-human species include: [ManyPrimates](#), [ManyBirds](#), [ManyDogs](#), [ManyGoats](#) and [ManyFishes](#). These projects vary in terms of their study focus, however, efforts are being made to devise 'ManyMany' studies, where BTS projects plan to combine efforts in

collaboration with [ManyBabies](#) and [Psychological Science Accelerator](#) to facilitate comparisons across humans, non-human primates, birds, fish, and others (Coles et al., 2022). Some current topics include: ManyPrimates on working memory (ManyPrimates et al. 2021), delay of gratification and inference by exclusion; ManyBirds on neophobia (responses to novelty; Miller et al., 2022); ManyGoats on responses to human attentional states; ManyDogs on dog-human social communication. These studies result in huge samples and greater statistical power compared to smaller studies that traditionally include several researchers and a single lab. For example, 400+ subjects across 40+ species and 30+ sites in ManyPrimates et al. (2021). Future studies may be driven by project core teams or collaborators. There is potential and scope to consider future studies of relevance to applied welfare and conservation, such as proxies highlighted in the current review, either through existing BTS projects, cross-BTS studies or development of a new BTS projects focusing on welfare, for instance, across farmed taxa.

91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119

2. COGNITION AND WELFARE

2.1 What is animal welfare and cognition?

Welfare may be defined as an animal's state while responding to environmental challenges (Broom, 1996). There are various theories of animal welfare, but here we focus on hedonism, i.e., welfare determined by positively and negatively valenced experiences (Bruckner, 2020). In order to assess an animal's welfare, it is necessary to make an objective assessment of a subjective state (Sandøe & Jensen, 2012), largely requiring reliance on measurable proxies for welfare. It is broadly agreed that no single proxy measure is sufficient for determining welfare (Botreau et al., 2009; Mellor & Beausoleil, 2015). As such, we integrate a variety of different proxies to create a welfare range profile (i.e., how well or badly an animal can fare) for each of our farmed taxa. Whether welfare ranges vary across taxa intersects with the theory that different species vary in their capacity to experience emotions. This concept has been referred to as the 'emotional capacities claim', which implies that animals with stronger emotional capacities possess larger welfare ranges (Višak 2017). In a similar vein, welfare often refers to both physical and mental needs, for example, the extent of awareness of an internal state when in pain, may determine how much the animal is actually suffering (Duncan & Petherick, 1991). This definition highlights the need to consider cognition, which can be broadly defined as including perception, learning, decision-making, and memory (Shettleworth, 2010). Cognition, therefore, includes the animal's perspective when assessing welfare (Ferreira et al., 2021). For this reason, we also include cognitive assays to create our welfare range profiles. Cognitive assays of particular relevance to welfare include learning ability, preference tests, memory workload, capacity to recollect memories, behaviours associated with noxious stimuli, and cognitive bias (Brydges & Braithwaite, 2008). Some examples of research linking cognitive measures with welfare implications in chickens are included in Table 1; however, it is important to note that there is a general lack of fundamental, cognitive research addressing welfare issues (Fijn et al., 2020).

Table 1. Examples linking cognition and welfare in chickens

Proxy	Finding	Reference
Individual differences	More fearful/ anxious chickens show reduced space use	Campbell et al., 2016
Learning/ Individual differences	Low-ranging chickens show stronger food conditioning (place preference conditioning). Application: train to associate food or conspecifics with range	Ferreira et al., 2020
Learning	Social learning of feather plucking in chickens. Application: increased use of visual barriers between plucking and non-plucking individuals, remove feather plucking individuals from flock, train 'demonstrator' birds that peck appropriate stimuli to encourage natural alternative	Zeltner et al., 2000; Freire, 2020

	behaviour to plucking	
Learning/ Taste aversion	Spray feathers to reduce plucking in chickens. Application: alter taste/smell with sucrose vs quinine	Harlander-Matauschek et al., 2008
Learning	Chronic hunger reduces learning in chickens (Y-maze)	Buckley et al., 2011
Learning/ Navigation/ Individual differences	Adult hens that do not use outdoor areas were slower to learn the T-maze task compared to outdoor-preferring hens	Campbell et al., 2018
Mental representation (of missing resources)	Rearing in a spatially complex environment leads to increased space use in chickens	Freire, 2020

120

121

122

2.2 What is a cognition and welfare range?

123

124

125

126

127

128

129

130

131

132

133

134

A cognition and welfare range (CWR) essentially refers to how well or badly animals can fare. It describes animals' respective capacities for valenced experiences and can be used to assign relative moral weights to different species based on those capacities. For instance, one could understand a moral weight as the amount or range of welfare a species can realise, produce, or generate, from the best to worst welfare states possible. Therefore, CWR relates to how much welfare can be realised by individuals within a given species. This approach suggests that while every unit of realised welfare counts the same, some species may possess a larger number of possibly realised welfare units than others, i.e. a larger welfare range. In order to assess CWR, it is necessary to measure variation in capacities of relevance to welfare, for which the proxies provide some evidence. It assumes that animals with relatively large welfare ranges can be harmed to greater degrees (e.g., experience greater suffering) than animals with relatively small welfare ranges (outlined in Gaffney et al., 2022).

135

2.3 How to and why make interspecies comparisons

136

137

138

139

140

141

142

143

144

145

146

147

148

Resources for improving animal welfare in farming, laboratory, and other captive settings are often limited. As such, decisions need to be made around prioritisation of species and the focus of research and management protocols. These decisions are often made largely without rigorous evidence, as relevant tools are lacking. There remains a need for interspecies comparative tools that are grounded in empirical data, such as those relating to cognitive differences. For example, there has been a recent drive for the reduction of the use of non-human primates in invasive research as well as increased legal protection in several countries. This shift is partly due to increasing evidence for complex cognition and behaviour in these animals (Padrell et al., 2021). However, invasive work continues with many other taxa, such as rats and dogs, which arguably show similarly high levels of cognitive abilities, for instance, metacognition (rats: Foote & Crystal, 2007; dogs: Belger & Bräuer, 2018).

149

150

151

152

153

154

155

156

157

158

159

160

161

There are evident ethical, methodological, and practical considerations to be accounted for when making interspecies comparisons of cognition and welfare (Gaffney et al., 2022; Fischer, in press). One starting place is to utilise the field of comparative psychology, which investigates the evolution of cognition, for instance, involving comparisons of performance in cognitive tasks across different taxa (Chittka et al., 2012). Ideally, comparisons should utilise similar experimental paradigms and measures, while accounting or adapting for physical, social, and ecological differences between species. Large-scale cross-species comparisons of cognition are limited. Nevertheless, within the past decade there has been a drive to conduct big-team science collaborations with comprehensive comparisons of specific cognitive abilities across species. For example, short-term memory has been compared in 41 primate species (ManyPrimates et al., 2022), neophobia (responses to novelty) in 10 corvid species (Miller et al., 2022) and self-control (specifically inhibitory control) across 36 mammal and bird species (MacLean et al., 2014).

162 As it stands, many studies include single-species investigations or cross-species comparisons with a
163 small number of taxa. Making comparisons between species where methodologies differ considerably
164 is problematic. Nevertheless, providing limitations are acknowledged and conclusions are tentative,
165 interspecies comparisons can be made on existing research through focused literature reviews, as we
166 outline below.

167

168 **3. METHODS**

169

170 **3.1 Species/ Taxa and Reviewers**

171

172 We included a wide range of commonly farmed species and their families, namely: Suidae (inc pigs),
173 Phasiandae (inc chickens), Cyprinidae (inc carp), Salmonidae (inc salmon), Octopodidae (inc
174 octopus), Penaeidae (inc shrimps), Portunidae (inc crabs), Cambaridae (inc crayfish), Apidae (inc
175 bees), and Bombycidae (inc silkworm). There were six reviewers (RM, MS, AKS, LPG, JML, AT),
176 each responsible for 1-4 taxa, and all were experienced in differing areas of animal welfare and
177 comparative cognition or had related research and practical experience. Literature reviews for all
178 target taxa, except Octopodidae, were completed in June 2022, with Octopodidae completed in
179 August 2022.

180

181 **3.2 Literature Review**

182

183 **3.2.1 Full Review: 90 Proxies**

184

185 To investigate interspecies variation, we assessed 90 empirically detectable proxies of cognition and
186 welfare ranges (henceforth proxies) relating to cognition, behaviour, anatomy, physiology, and
187 welfare. We used a variation of Delphi method (Linstone & Turoff, 1975), a form of structured
188 deliberation involving a panel of five experts (philosophers, comparative psychologists,
189 neuroscientists), to select the full set of proxies. Each panel expert provided a list of proxies, which
190 were then discussed regarding their merits and relevance, and the final lists were combined to create
191 the full 90 proxy list in Dec 2021. For each combination of taxon and proxy, we reviewed the existing
192 literature across 10 taxa to determine whether there was sufficient scientific data and, based on this,
193 whether it was possible to assess the likelihood of whether a taxon possessed a proxy. We used: 1)
194 Google Scholar (soft search) and 2) Web of Science (hard search), as well as recent taxa-specific
195 reviews and cited references.

196

197 Taxa were listed at the family level. If, for a given proxy, the target family had not been studied, we
198 expanded the search to similar families in the same order that had been studied. Similarly, if a given
199 proxy had not been studied, though a similar proxy had been, we included the latter, though noted
200 clearly if this occurred. An example of search terms for chickens included: '*Phasianidae*', 'chicken',
201 'junglefowl', 'pheasant', 'bird'. An example of search terms for the proxy self-control included: 'self-
202 control', 'delay of gratification', 'inhibitory control', 'behavioural flexibility', 'reversal learning'. Fifteen of
203 the 90 proxies (17%) within each taxa were reviewed independently by a second person (not involved
204 with initial lit review for that taxon) and cross-checked to ensure inter-rater reliability.

205

206 **3.2.2 Reduced Review: 'Catalogues A and B'**

207

208 A large number of proxies had missing data for at least one taxon (fewer than 20 of 90 proxies had
209 been tested across the majority of the 10 taxa) so we refined our review to a) focus on the most
210 welfare relevant proxies and b) enable interspecies comparisons using existing research. We grouped
211 a subset of the 90 proxies into two overlapping catalogues (A and B, Figure 1). Catalogue A
212 contained 10 ideal proxies, providing an optimal suite most closely linked to welfare. The selection for
213 Catalogue A was based on a combination of criteria typically used to assess consciousness (Birch et
214 al., 2020) and sentience (Birch et al., 2021; Sidebar 1) in non-verbal animals. Such criteria are
215 relevant because the question of interspecies comparisons is largely about the comparative level of
216 consciousness or sentience of different animals, since we assume that animals with stronger
217 emotional capacities have larger cognitive and welfare ranges (i.e., emotional capacities claim, Višak,
218 2017). Several cognitive measures that have been linked to emotional capacities include learning
219 ability, preference tests, and cognitive bias (Brydges & Braithwaite, 2008). However, as the empirical
220 data for these proxies were lacking for many taxa, this negated interspecies comparisons. We thus
221 created Catalogue B, containing a less-optimal suite of 10 proxies, some with weaker links to welfare.

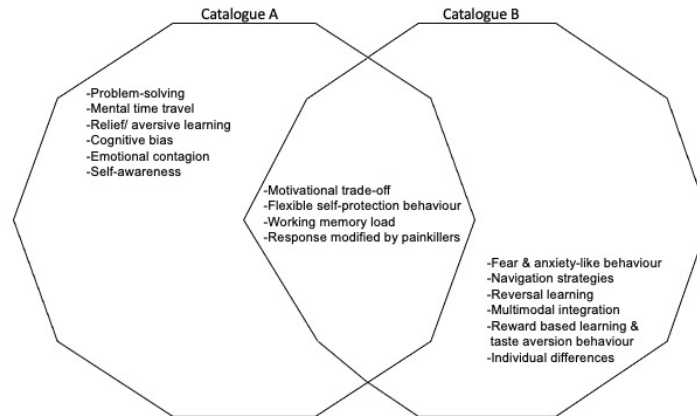
222 The Catalogue B proxies were selected as those with sufficient empirical data to enable intra- and
 223 interspecies comparisons. As such, we selected only those proxies that had been tested in the
 224 majority of the 10 taxa, regardless of rating, after filtering out those with many 'unknown' (i.e.
 225 insufficient evidence) ratings. The proxies in both catalogues tend to fall within the larger categories of
 226 behavioural flexibility, cognitive sophistication, and general learning. See Table 2 (glossary) for proxy
 227 definitions and Figure 1.
 228
 229

Table 2. Glossary of Catalogue A and B proxies

Catalogue	Category and Proxy	Definition
A	Cognitive sophistication: Mental time travel (incl. episodic-like memory, source memory, self-control, future planning, and memory integration)	Mental time travel is the ability to travel backwards and forwards in time in the mind's eye, to remember the past based on what happened, where and when (i.e., episodic-like memory, also consider source memory); and plan for the future (Tulving, 1983). Episodic-like memory is considered to be the precursor for future planning, as it functions as a memory database to predict future scenarios (Clayton et al., 2003; Schacter et al., 2012). Self-control, which is part of executive function, is an integral part of future planning because an individual must overcome immediate gratification to fulfil future needs (Schnell et al., 2021).
A	General learning: Relief/ aversive learning	Relief learning involves the ability to associate that a specific stimulus results in relief from a negative state (e.g., pain) or results in the offset of a negative reinforcer. In a similar way, aversive learning involves the ability to avoid aversive stimuli that causes a negative state. There is a type of relief-memory that relates to something that happens after a painful event finishes, at the moment of the so-called relief. This relief can both increase the learning of the cues associated with the disappearance of the threat and reinforce those behaviours that helped to escape it (Gerber et al., 2014).
A	Cognitive sophistication: Cognitive bias (incl. judgement, attention, memory)	Cognitive bias in animals is a pattern of deviation whereby inferences about new situations might be affected by irrelevant information or emotional states. There are several types of cognitive bias, which are measured using different methods. These include assessing whether individuals experiencing negative affect make more pessimistic judgements about ambiguous stimuli (i.e., judgement bias), pay more attention to negative stimuli (i.e., attention bias), and are more likely to remember negatively valenced memories (memory bias) than positively valenced memories (Eysenck et al., 1991; Wright & Bower, 1992; Paul et al., 2005).
A	Behavioural flexibility: Problem-solving	The ability to solve problems is important for animals to respond to a rapidly changing environment. Specifically, animals use problem-solving skills to avoid predators and obtain access to important food sources, shelter, or mates (Pérez Fraga et al., 2021). Problem-solving does not have to be a complicated process, and can rely on animals exploring their environment, learning and remembering information. However, problem-solving can also involve complex cognitive abilities such as logical reasoning, causal reasoning, and future planning (Andrews, 2021). Notice that different species, populations, or even individuals can solve problems in different ways.
A	Cognitive sophistication: Emotional contagion	Emotional contagion occurs when an individual matches the emotional state with another individual or when emotions are transferred between individuals (Perez-Manrique & Gomila, 2022). It can be seen as evidence of more sophisticated emotions, and perhaps as a precursor to the capacity for

		empathy, which indicates social cognition or even theory of mind (Reimert et al., 2013).
A	Cognitive sophistication: Self-awareness (incl. self-recognition i.e., MMR, knowledge of own mental states, knowledge of others' mental states i.e., theory of mind, body awareness, experience projection)	Self-awareness suggests an understanding or recognition of self. Self-recognition in non-human animals is generally measured via the mirror mark test (Gordon, 1970). One complementary avenue to measure self-recognition is to investigate body self-awareness. Body awareness is the ability to discriminate between body and non-self-stimuli, specifically understanding that an individual's body is distinctly different from the surroundings (Moore et al., 2007; Brownell et al., 2007; Dale & Plotnik, 2017). Self-awareness is often linked to other complex forms of cognition including empathy and perspective-taking. Perspective-taking, also termed theory of mind, is the ability to understand and consider another individual's mental state i.e., 'mind-reading' (Premack & Woodruff, 1978), including knowledge, desires and beliefs that motivate others' action (Krupenye, 2021).
A & B	Behavioural flexibility: Flexible self-protective behaviour	Flexible protective behaviour is a type of non-reflexive reaction to injury in which an injured animal attempts to guard, groom, or otherwise tend to the injured body part. Examples include limping, wound rubbing, wound licking, and wound guarding (Elwood, 2019). Protective behaviour, in our sense, must be carefully distinguished from reflexive reactions known (in humans) that operate subconsciously, such as grimacing, rapid withdrawal, postural adjustments, and some paralinguistic features of vocalisation (Sekhon et al., 2017).
A & B	Cognitive sophistication: Working memory load	Working memory load is a short-term memory system, describing a limited capacity to hold information temporarily. Working memory load is important for reasoning and guiding decision-making as well as executing behaviour (Miyake & Shah, 1997; Diamond, 2013). It is also responsible for following goals and keeping track of multiple goals, by integrating a variety of information sources (Miyake & Shah, 1997).
A & B	General learning: Response modified by painkillers	Painkillers such as local anaesthetics, analgesics (i.e., opioids), anxiolytics or anti-depressants modify an animal's response to noxious stimuli in a way that suggests that these compounds attenuate the experience of negative affective states (i.e., pain or distress).
A & B	Behavioural flexibility: Motivational trade-off	Motivational trade-off involves an animal having to flexibly trade-off between two competing motivations. Specifically, an animal must be motivated to avoid a noxious stimulus, and this motivation must be weighed (traded-off) against other motivations (e.g., thirst, hunger, the need for shelter) in a flexible decision-making process. Motivational trade-off has been demonstrated in hermit crabs who were offered an opportunity to hide from an electric shock in either their preferred <i>Littorina</i> shells or their non-preferred <i>Gibbula</i> shells, meaning the crabs had to trade shock avoidance against shell preference (Magee & Elwood, 2016).
B	Cognitive sophistication: Fear-like and anxiety-like behaviour	The experience of fear is associated with certain physiological and behavioural responses. Behavioural markings of fear include fleeing, hiding, freezing, and suspending unnecessary bodily functions. Physiological reactions to fear can include elevated heart rate, hyperventilation, increased muscle tension, constriction of blood vessels, nausea, and dizziness (Stankowich & Blumstein, 2005). Anxiety is related to but distinct from fear.

		Anxiety is sometimes said to be the result of danger that is perceived to be unavoidable (Öhman, 2008) or situations in which the threat is ambiguous or unknown (Belzung & Philippot, 2007).
B	Behavioural flexibility: Individual differences/ 'personality'	Personality refers to individual differences in characteristic patterns of behaving. Temperaments and personalities are integrated behavioural phenotypes and stable traits that are consistent over time and across situations, which are broad and consistent dimensions of individuality (Budaev, 1997).
B	Cognitive sophistication: Navigation strategies	Animals need to avoid environmental hazards and locate food, water, and mates. Many animals need to return to fixed sites (such as dens, hives, breeding grounds, food caches, watering holes, foraging sites, or nesting beaches) multiple times over the course of their lives. To do so requires navigational skills. Notice that navigation strategies can vary from simple associative processes and innate behaviours to complex cognitive mapping and memory recollection. Navigational skills are relevant for welfare ranges insofar as some strategies indicate advanced forms of cognition, which is correlated with increased welfare range. Importantly, the evolutionary function of consciousness is thought to produce an integrated and egocentric spatial model to guide an animal as it navigates a complex environment (Barron & Klein, 2016).
B	General learning: Reversal learning	Reversal learning is the ability to change behaviour rapidly and flexibly in response to changing circumstances, which is an important tool for survival in a rapidly changing environment (Izquierdo et al., 2017).
B	Cognitive sophistication: Multimodal integration	Multimodal integration is the ability to process different sensory modalities (e.g., light, touch, smell, sound) and integrate them via the nervous system (New, 2002).
B	General learning: Reward based learning and taste aversion behaviour	Learning based on reward is one type of associative learning, which involves learning about a relationship between two separate stimuli. Associative learning can be differentiated into classical and operant conditioning (Pearce & Bouton, 2001). Taste aversion learning is a form of associative learning, which involves a learned pattern of aversion to a specific food after it has been paired with an aversive stimuli (e.g., radiation exposure, injection of some toxic drug such as lithium chloride, exposure to a high intensity magnet, etc.) (Bernstein, 1999). Specifically, the animal associates a transient state of illness to the taste, odour, or other characteristic of a specific food item, which ultimately results in a long-term change in its perception of palatability (Snijders et al., 2021).



231
232 **Figure 1: Catalogues A and B consisted of 16 proxies representing cognition and welfare**
233 **range. Catalogue A provided an optimal framework, containing proxies most closely linked to**
234 **welfare. Catalogue B provided a less-optimal framework, containing some proxies that are**
235 **more weakly linked to welfare but are useful nonetheless as they facilitate direct interspecies**
236 **comparisons via the availability of empirical data. Some proxies overlap both catalogues.**
237

238 3.3 Evidence Rating

239
240 Our review adapted the rating methods developed by Rethink Priorities (2020) and Birch et al. (2021)
241 to compare the strength of the evidence and probability against each proxy. In our reduced review,
242 each proxy was rated per taxa using two approaches, whereas in the full review, each proxy was
243 ranked using the probability rating scale per Rethink Priorities (2020). The rating systems lend to
244 similar outputs, though we used both approaches for continuity and to enable comparison with
245 previous studies:
246

247 1. Rethink Priorities (2020) use a probability rating scale with 5 grades to assess whether the
248 evidence suggests a taxon possesses a proxy: 'likely no' (0–25% credences), 'lean no' (>25–<50%),
249 'unknown' (50%), 'lean yes' (>50–<75%) and 'likely yes' (>75–100%). Note that these 5 'credence
250 assessments' represent the evaluation of whether a taxon displays or fails to demonstrate the proxy
251 rather than the *extent* to which the animals possessed the proxy. 'Unknown' was the default
252 assessment in cases where insufficient evidence was found for a particular taxon/proxy combination.
253

254 2. Birch and colleagues (2021) use a level of confidence to grade the quantity, reliability and quality of
255 the available evidence. There are six confidence levels in this rating method: (i) very high confidence,
256 (ii) high confidence, (iii) medium confidence, (iv) low confidence, (v) very low confidence, and (vi) no
257 confidence. The 'very high' confidence rating illustrates that the weight of scientific evidence leaves
258 no room for reasonable doubt that the proxy is present or absent. The 'high' confidence rating
259 illustrates that the animals convincingly display or fail to demonstrate the proxy but there is some
260 room for reasonable doubt. The 'medium' confidence rating illustrates that there are some concerns
261 about the reliability of the evidence. The 'low' confidence rating illustrates that there is little evidence
262 that the animals display or fail to demonstrate the proxy. Finally, the 'very low' and 'no' confidence
263 ratings illustrate that the evidence is either considerably inadequate or non-existent, respectively.
264

265 We calculated an overall judgement score per taxa and across proxies, using a comparable approach
266 to Birch et al. (2021), comprising the total percentage of 'very high' and 'high' ratings. The grading
267 scheme allocates 'very high' or 'high' confidence that a taxon satisfies 87.5% of proxies as **very**
268 **strong**, 62.5% as **strong**, 38.5% as **substantial** and < 38.5 % as **weak** evidence for a larger
269 cognition and welfare range, indicating a greater capacity to experience enhanced negative (e.g.,
270 greater suffering) and positive (e.g., greater enjoyment) emotions. Note that Birch et al. (2021) focus
271 on evidence for sentience, specifically pain, and proxies of particular relevance for this, with overall
272 judgements determined by percentage of criteria met per taxa, whereas we focus on proxies relevant
273 to cognition and welfare rather than sentience (See Sidebar 1 for more detail).
274

275 4. RESULTS

276
277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295
296
297
298
299

4.1 Full Review Output: 90 proxies

The final table comprised 90 proxies across 10 taxa (Fischer, 2022; Table S1 and S2). We note that, across these 90 proxies, there were only 7 'likely no' and 8 'lean no' ratings - most of which were for proxies that had not been tested in many taxa (other than parental care), therefore this was not a useful alternative means of reducing the table, i.e., based on range of rating.

4.2 Reduced Review: Catalogue A and B

We outline Catalogue A (ideal proxies, with limited empirical data) and B (less-optimal proxies, with empirical data) output and ratings in Table 3, Figure 2 (Catalogue A and B combined) and Figure 3 (a: Catalogue A & B combined, Catalogue B alone; b: Categories - behavioural flexibility, cognitive sophistication, general learning). Please note, we provide only 1 citation per taxa and proxy in Table 3 as an example as the primary goal was to establish trait presence and also due to the sheer number of references generated by the review (123 references with only 1 reference example). The full 90-proxy review output identified >1000 references.

Table 3. Cognition and welfare range proxies for Catalogue A and B per taxa. Code: **VH/ Very high**: Large amount high-quality, reliable evidence; **H/ High**: Convinced based on evidence, with room for reasonable doubt; **M/ Medium**: Some concerns about reliability of evidence; **L/Low**: Little evidence; **VL/ Very low**: Seriously inadequate or non-existent evidence (per Birch et al., 2021 rating). Rating translates to: VH = yes, H = likely yes, M = lean yes, L = lean no, VL = unknown (per Rethink Priorities 2020 rating). Overall judgement (% of VH & H out of overall ratings): 87.5% = **Very strong**; 62.5% = **Strong**; 38.5% = **Substantial**; < 38.5% = **Weak** (Birch et al., 2021).

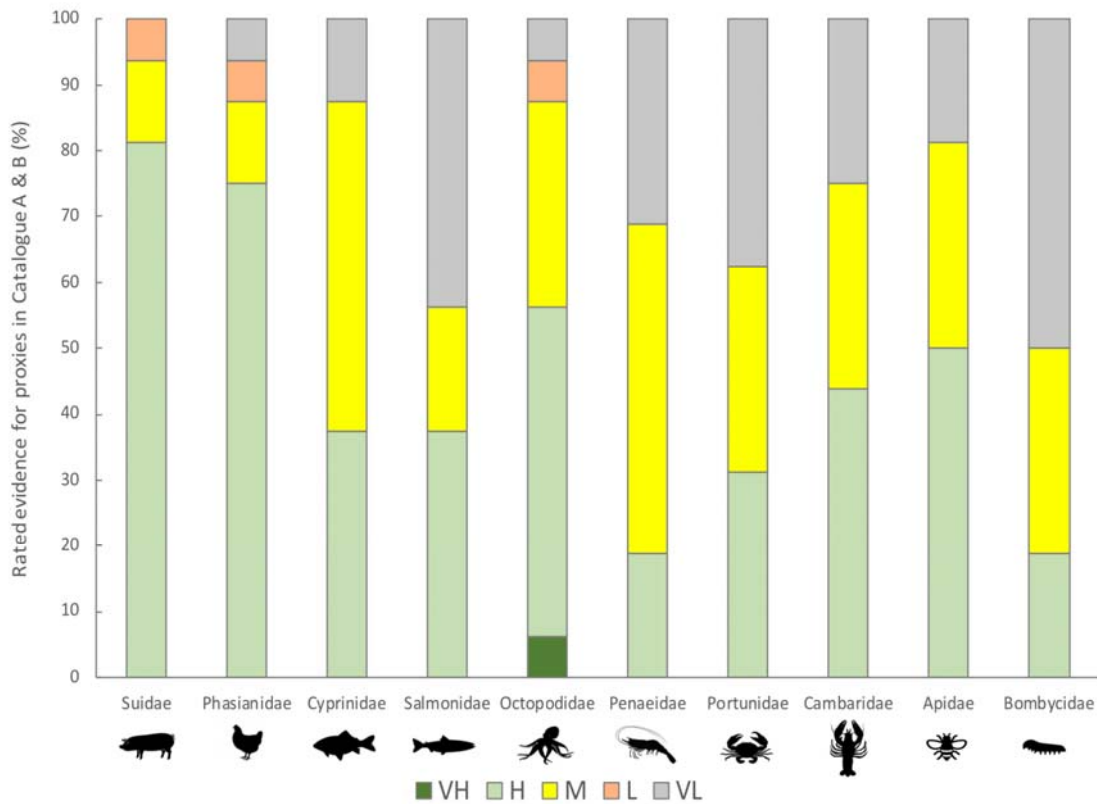
Catalogue	Taxa/ Proxy	Suidae	Phasianidae	Cyprinidae	Salmonidae	Octopodidae	Penaeidae	Portunidae	Cambaridae	Apidae	Bombycidae
A	Mental time travel	H ¹	H ²	M ³	VL	M ⁴	VL	VL	VL	VL	VL
A	Relief/ aversive learning	L ^b	VL	M ^b	VL	H ^c	M ⁵	M ⁹	M ¹⁰	M ¹¹	VL
A	Cognitive bias	H ¹²	H ¹³	M ¹⁴	VL	M ¹⁵	VL	VL	M ¹⁶	H ¹⁷	VL
A	Problem-solving	H ¹⁸	H ¹⁹	VL	VL	H ²⁰	M ²¹	VL	VL	H ²²	VL
A	Emotional contagion	H ²³	M ²⁴	M ²⁵	VL	VL	VL	VL	VL	VL	VL
A	Self-awareness	H ²⁶	L ²⁷	VL	VL	L ²⁸	VL	VL	VL	VL	VL
A & B	Flexible self-protective behaviour	H ²⁹	H ³⁰	H ³¹	H ³²	VH ³	M ³⁴	H ³⁵	M ³⁶	M ³⁷	M ³⁸
A & B	Working memory load	H ³⁹	H ⁴⁰	M ⁴¹	M ⁴²	M ⁴³	VL	VL	M ⁴⁴	H ⁴⁵	M ⁴⁶

Catalogue	Taxal Proxy	Suidae	Phasianidae	Cyprinidae	Salmonidae	Octopodidae	Penaeidae	Portunidae	Cambaridae	Apidae	Bombycidae
A & B	Response modified by painkillers	H ⁴⁷	H ⁴⁸	H ⁴⁹	H ⁵⁰	H ⁵¹	H ⁵²	M ⁵³	H ⁵⁴	H ⁵⁵	VL
A & B	Motivational trade-off	M ⁵⁶	M ⁵⁷	M ⁵⁸	M ⁵⁹	M ⁶⁰	M ⁶¹	H ⁶²	H ⁶³	M ⁶⁴	M ⁶⁵
B	Fear and anxiety-like behaviour	H ⁶⁶	H ⁶⁷	H ⁶⁸	H ⁶⁹	H ⁷⁰	M ⁷¹	M ⁷²	H ⁷³	M ⁷⁴	VL
B	Individual differences	H ⁷⁵	H ⁷⁶	H ⁷⁷	H ⁷⁸	H ⁷⁹	H ⁸⁰	H ⁸¹	H ⁸²	M ⁸³	M ⁸⁴
B	Navigation strategies	H ⁸⁵	H ⁸⁶	H ⁸⁷	H ⁸⁸	H ⁸⁹	M ⁹⁰	H ⁹¹	H ⁹²	H ⁹³	H ⁹⁴
B	Reversal learning	H ⁹⁵	H ⁹⁶	M ⁹⁷	M ⁹⁸	H ⁹⁹	M ¹⁰⁰	M ¹⁰¹	M ¹⁰²	H ¹⁰³	M ¹⁰⁴
B	Multimodal integration	M ¹⁰⁵	H ¹⁰⁶	M ¹⁰⁷	VL	M ¹⁰⁸	M ¹⁰⁹	M ¹¹⁰	H ¹¹¹	H ¹¹²	H ¹¹³
B	Reward based learning and taste aversion behaviour	H ¹¹⁴	H ¹¹⁵	H ¹¹⁶	H ¹¹⁷	H ¹¹⁸	H ¹¹⁹	H ¹²⁰	H ¹²¹	H ¹²²	H ¹²³
Total (H/VH) of 16 proxies: Catalogue A & B		13	12	6	6	9	3	5	7	8	3
Total (H/VH) of 10 proxies: Catalogue B		8	9	6	6	7	3	5	7	6	3
Overall Judgement (%): Catalogue A & B		81.3	75	37.5	37.5	56.3	18.8	31.3	43.8	50	18.8
Overall Judgement (%): Catalogue B		80	90	60	60	70	30	50	70	60	30

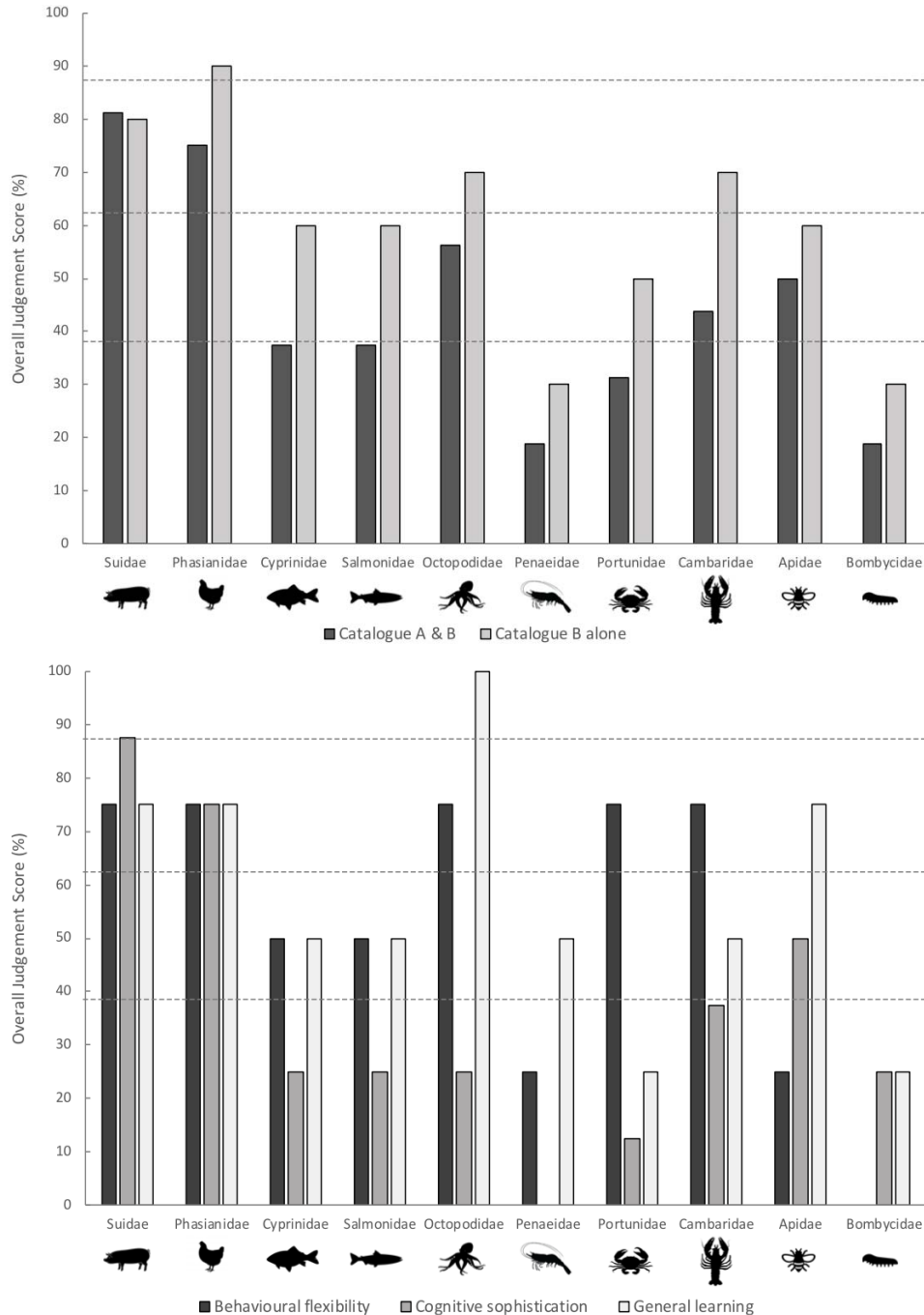
300
301
302
303
304
305
306
307
308
309
310
311

Table 3 Citations: ¹ Kouwenberg et al., 2009, ² Marino 2017, ³ Hamilton et al., 2016, ⁴ Jozet-Alves et al. 2013, ⁵ Imfeld-Mueller et al., 2011, ⁶ Sneddon et al., 2014, ⁷ Crook 2020, ⁸ Bool et al., 2011, ⁹ Magee & Elwood, 2013, ¹⁰ Okada et al., 2021, ¹¹ Yarali et al., 2012, ¹² Döpjan et al., 2013, ¹³ Crump et al., 2018, ¹⁴ Espigares et al., 2021, ¹⁵ Schnell & Vallortigara 2019, ¹⁶ Bacqué-Cazenave et al., 2017, ¹⁷ Bateson et al., 2011, ¹⁸ Pérez Fraga et al., 2021, ¹⁹ Daisley et al., 2010, ²⁰ Fiorito et al., 1998; Kuba et al., 2006, ²¹ Duffield et al., 2015, ²² Loukola et al., 2017, ²³ Reimert et al., 2013, ²⁴ Edgar & Nicol 2018, ²⁵ Oliveirs et al., 2017, ²⁶ Broom et al., 2009, ²⁷ Gallup Jr 1975, ²⁸ Amodio & Fiorito 2022, ²⁹ Bracke 2011, ³⁰ Duncan et al., 1989, ³¹ Reilly et al., 2008, ³² Reilly et al., 2008, ³³ Alupay et al., 2014, ³⁴ Bauer 1981, ³⁵ McCambridge et al., 2016, ³⁶ Puri & Faulkes 2010, ³⁷ Breed et al., 1990, ³⁸ Walters et al., 2001, ³⁹ Arts et al., 2009, ⁴⁰ Nordquist et al., 2011, ⁴¹ Bloch et al., 2019, ⁴² Sovrano et al., 2018, ⁴³ Borrelli & Fiorito 2008, ⁴⁴ Tierney & Andrews 2013, ⁴⁵ Siviter et al., 2018, ⁴⁶ Blackiston et al., 2008, ⁴⁷

312 McGlone & Hellman, 1988,⁴⁸ Singh et al. 2017,⁴⁹ Chervova & Lapshin 2000,⁵⁰ Nordgreen et al.,
 313 2013,⁵¹ Butler-Struben et al., 2018,⁵² Taylor et al., 2004,⁵³ Barr & Elwood 2011,⁵⁴ Buřič et al., 2018,
 314 ⁵⁵Groening et al., 2017,⁵⁶ Kratzer 1969,⁵⁷ Appleby et al., 2004,⁵⁸ Dunlop et al., 2006,⁵⁹ Dunlop et al.,
 315 2006,⁶⁰ Crook et al., 2011,⁶¹ Maskrey et al., 2018,⁶² Magee & Elwood 2013,⁶³ Mergler et al., 2020,⁶⁴
 316 Gibbons et al., 2022,⁶⁵ Mir & Qamar 2018⁶⁶ Arroyo et al., 2016,⁶⁷ Duncan & Petherick 1991,⁶⁸ Stabell
 317 et al., 2010,⁶⁹ Geller & Brady 1961,⁷⁰ Bennett & Toll 2011,⁷¹ Takahashi 2022,⁷² Wilson et al.,
 318 2021,⁷³ Wood & Moore 2020,⁷⁴ Tan et al., 2013,⁷⁵ O'Malley et al., 2019,⁷⁶ Favati et al., 2014,⁷⁷
 319 Huntingford et al., 2010,⁷⁸ Vaz-Serrano et al., 2011,⁷⁹ Mather & Anderson 1993,⁸⁰ Bardera et al.,
 320 2021,⁸¹ Su et al., 2019,⁸² Zhao & Feng 2015,⁸³ Muller et al., 2010,⁸⁴ Obara & Tamazawa 1982,⁸⁵
 321 Morelle et al., 2015,⁸⁶ Denzau et al., 2013,⁸⁷ Moorman 2001,⁸⁸ Dittman & Quinn 1996,⁸⁹ Forsythe &
 322 Hanlon 1997,⁹⁰ Reaka 1980,⁹¹ Keller et al., 2003,⁹² Kamran & Moore 2015,⁹³ Chittka & Geiger 1995,
 323 ⁹⁴Namiki et al. 2018,⁹⁵ Bolhuis et al., 2004,⁹⁶ Wascher et al., 2021,⁹⁷ Kuroda et al., 2017,⁹⁸ de
 324 Lourdes Ruiz-Gomez et al., 2011,⁹⁹ Boycott & Young 1957,¹⁰⁰ Ventura & Mattel 1977,¹⁰¹ Abramson
 325 & Feinman 1990,¹⁰² Tierney et al., 2019,¹⁰³ Raine & Chittka 2012,¹⁰⁴ Rodrigues et al. 2010,¹⁰⁵
 326 Statham et al., 2020,¹⁰⁶ Verhaal & Luksch 2016,¹⁰⁷ Wang & Chittka 2011,¹⁰⁸ Gutnick et al., 2011,¹⁰⁹
 327 Heberts & Rundus 2010,¹¹⁰ Sneddon et al., 2003,¹¹¹ Aquiloni & Gherardi 2008,¹¹² Ostwald et al.,
 328 2019,¹¹³ Yamada et al. 2021¹¹⁴ Hemsworth et al., 1996,¹¹⁵ Ferreira et al., 2020,¹¹⁶ Wright & Eastcott
 329 1982,¹¹⁷ Paspatis & Boujard 1996,¹¹⁸ Mackintosh & Mackintosh 1963,¹¹⁹ Ventura & Mattel 1977,¹²⁰
 330 Davies et al., 2019,¹²¹ Imeh-Nathaniel et al., 2016,¹²² de Brito Sanchez 2011,¹²³ Takahashi et al.,
 331 2021
 332



333
 334 **Figure 2. Rated evidence for proxies* listed in Catalogue A and B per taxa.**
 335 **Code: VH/ Very high: Large amount high-quality, reliable evidence; H/ High: Convinced based**
 336 **on evidence, with room for reasonable doubt; M/ Medium: Some concerns about reliability of**
 337 **evidence; L/Low: Little evidence; VL/ Very low: Seriously inadequate or non-existent evidence**
 338 **(per Birch et al., 2021 rating). Rating translates to: VH = yes, H = likely yes, M = lean yes, L =**
 339 **lean no, VL = unknown (per Rethink Priorities 2020 rating). * Table 3 lists the specific proxies**
 340



341
342
343
344
345
346
347
348
349
350
351
352
353

Figure 3: Percentage overall judgement scores (rated as high-very-high confidence out of all ratings) per taxa arranged across (a) Catalogues (A & B combined; B alone)* (b) Categories (behavioural flexibility, cognitive sophistication, general learning). Horizontal dotted lines reflect very high-high confidence in strength of evidence in descending order: at least 87.5% = Very strong; at least 62.5% = Strong; at least 38.5% = Substantial; values below the lowest horizontal dotted line < 38.5% = weak (Birch et al., 2021).* Catalogue A alone is not represented in the graph because empirical data for these proxies were lacking for many taxa, thus it was not possible to make reliable interspecies comparisons with this catalogue alone at present.

4.3 Overall Judgement Score per Taxa

354 For Catalogue A & B combined (16 proxies), five of ten taxa meet criteria for either 'strong' or
355 'substantial' evidence for a larger cognition and welfare range, whereas for Catalogue B alone, eight
356 taxa meet these criteria, one of which scored as 'very strong' (Table 3; Figure 3a). Specifically, for
357 Catalogue A & B, *Suidae* (inc pigs) and *Phasianidae* (inc chickens) had a 'strong' overall judgement
358 score, while *Octopodidae* (inc octopus), *Cambaridae* (inc crayfish), and *Apidae* (inc bees) had a
359 'substantial' score, and *Cyprinidae* (inc carp), *Salmonidae* (inc salmon), *Penaeidae* (inc shrimp),
360 *Portunidae* (inc crabs), and *Bombycidae* (inc silk moths) only attained a 'weak' overall judgement
361 score. For Catalogue B (10 proxies), *Phasianidae* had a 'very strong' score, *Suidae*, *Octopodidae*,
362 *Cambaridae* had a 'strong' score, *Cyprinidae*, *Salmonidae*, *Portunidae*, and *Apidae* had a 'substantial'
363 score, and *Penaeidae* and *Bombycidae* had a 'weak score'.

364

365 5. DISCUSSION

366

367 5.1 Interspecies Comparisons: Similarities and Differences

368

369 The overall number of taxa with 'strong' to 'substantial' evidence supporting larger cognition and
370 welfare ranges differed across our catalogues. We found stronger evidence for larger cognition and
371 welfare ranges across taxa in Catalogue B alone, compared to Catalogue A & B combined. However,
372 this is invariably because of a lack of research that focuses on proxies listed in Catalogue A, rather
373 than clear evidence that some of the Catalogue A proxies are absent in our taxa. Given the lack of
374 research in some taxa across the Catalogue A proxies, we propose that the Catalogue B is a more
375 reliable catalogue at present. Within our target vertebrate taxa, there is 'very strong' to 'strong'
376 evidence for larger cognition and welfare ranges in chickens and pigs, respectively. There is
377 somewhat less evidence concerning carp and salmon, with the evidence in Catalogue B alone graded
378 as 'substantial' and the evidence for Catalogue A & B combined graded as 'weak'. Some of our target
379 invertebrate taxa scored similarly to some of our higher scoring vertebrates in their cognition and
380 welfare ranges. Indeed, for Catalogue B, pigs, octopus, and crayfish attained a 'strong' overall
381 judgement score and chickens attained a 'very strong' overall judgement score.

382

383 Overall judgement scores for Catalogue A & B (Table 3) were more variable across the
384 aforementioned taxa: pigs (81.3 %), chickens (75 %), octopus (56.3 %), and crayfish (43.8 %); but
385 again, this is invariably because of a lack of positive evidence, rather than because of clear evidence
386 that some of our taxa do not possess specific proxies in Catalogue A & B. Comparable scores, at
387 least within Catalogue B, also exist between our target fish species (i.e., carp, 60 %; and salmon, 60
388 %), crabs (50 %), and bees (60 %). These findings add to existing evidence supporting
389 recommendations for the audit and amendment of current housing, treatment, and other management
390 decisions across *all* farmed animals, particularly fish and invertebrates, which tend to be amongst the
391 least protected under legislation (e.g., Brown, 2014; Chittka, 2022).

392

393 We can assume that humans generally score the maximum possible judgement score on each proxy
394 selected (i.e., 100%) as proposed by Rethink Priorities (2020). This would correspond with 'very
395 strong' evidence under our rating system for a larger cognition and welfare range. In comparison, we
396 also find 'very strong' evidence in chickens, at least for Category B proxies where more empirical
397 evidence exists. These findings imply that at least some basic proxies measuring how well or badly a
398 species may fare are comparable to some degree between humans and other species. Moreover, our
399 data suggests that the same pattern exists between some of our vertebrate and invertebrate taxa
400 (e.g., pigs, octopus, and crayfish). Attaining a similar cognitive and welfare range implies that these
401 animals have comparable capacities for a wide range of valanced experiences, from negative (e.g.,
402 greater suffering) to positive (e.g., greater enjoyment).

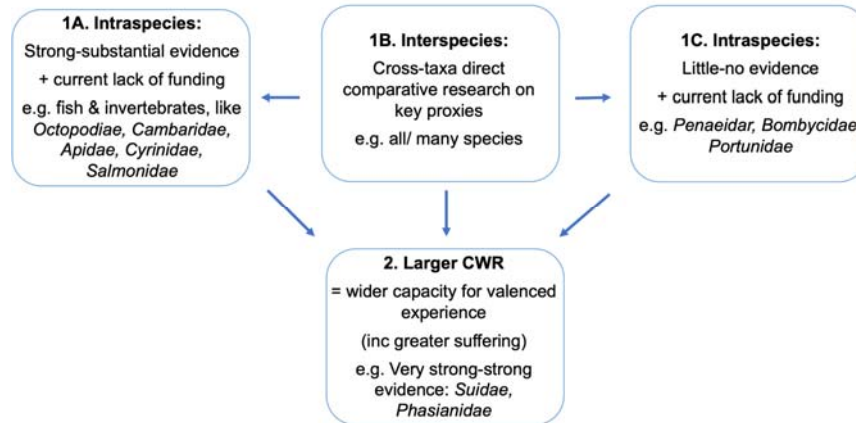
403

404 5.2 Potential Implications and Recommendations

405

406 There are several implications and tentative recommendations from these findings with regard to
407 prioritising funding and future research to improve welfare, as outlined in Figure 4. We highlight 'key
408 proxies' in Catalogue A and elaborate on these in the 'future research' section.

409



410
411
412

Figure 4: Recommendations for prioritising future funding and research

413 Recommendations 1A) to 1C) should be prioritised first to inform generally as well as on
414 recommendation 2) i.e., prioritising species with larger cognitive and welfare ranges (CWR).
415 Recommendation 1B (interspecies comparisons) can inform on 1A, 1C and 2, though multi-species
416 comparisons may require simplified experimental paradigms and take longer to complete given that
417 large-scale multi-species studies typically require multiple collaborators and sites, compared to single-
418 species studies. Therefore, 1A and 1C are also vital steppingstones to facilitate in-depth interspecies
419 studies. The decision to prioritise species with some evidence ('strong' – 'substantial') compared with
420 little to no evidence ('weak') of CWR may be further informed by current levels of funding allocations
421 and other existing empirical data. For example, there is currently relatively little evidence for
422 Portunidae (including crabs) to demonstrate a larger CWR.

423
424
425
426
427

These recommendations are not mutually exclusive. We advocate prioritising all farmed species to
improve welfare. However, we also recognise that with limited financial support, funding and research
allocation decisions have to be made and where possible, would benefit from being empirically based.

428
429

5.3 Limitations and Considerations

430
431
432
433
434
435
436
437
438
439
440
441
442
443

We highlight several potential limitations of our review; some of which are specific to the review, and
others are more generally widespread across animal-related research though may impact the review
findings. Within this review, one issue was the selection of suitable proxies for cognition and welfare
range, which differentially influenced the overall judgement scores. For instance, overall judgement
scores differed across catalogues for some taxa, i.e. *Phasianidae*, *Cyprinidae*, *Salmonidae*,
Octopodidae, *Portunidae* and *Cambaridae* all obtained higher scores in Catalogue B alone compared
to Catalogue A & B combined. Given that the scores are sensitive to proxy selection, our judgement
scores should be treated with caution. It might be worthwhile placing more weight on the Catalogue B
proxies, given that this is where more research has been conducted. However, we do not recommend
dismissing the proxies listed in Catalogue A. It is widely suggested that evidence of psychological
abilities such as mental time travel, problem-solving, and theory of mind suggests the animal
possesses complex cognition (Emery & Clayton, 2004) and indicates a presence of sentience
(Proctor, 2012). As such, these proxies are likely to be important for estimating CWR.

444
445
446
447
448
449
450
451
452
453
454
455

We took a two-pronged approach to ensure that we recorded a widespread search of the literature to
gain the best possible overview of the current evidence for each proxy and taxa. However, it is
possible that our literature reviews have not captured every relevant, existing study. Many studies,
even within proxy, used different measures, designs and outputs, and thus, it was not possible to
compare data directly. We were therefore required to make an informed judgement to provide a
rating, with a subset of ratings cross-checked across two observers. We recognise that the current
output (Table 3) will need to be updated as new studies are published or updated, however, we
provide a necessary and comprehensive starting place (and potential methodologies) within this
review article. One possible downside of the Birch et al. (2021) strength of evidence rating system is
that it leans towards favouring presence, without allowing for indication of doubt in whether evidence
for a proxy exists, as included in the Rethink Priorities (2020) rating system. For this reason, we used
both rating systems and found similar outputs overall. Also, it is worth noting that our literature

456 reviewers were aware of the study's general theory and purpose (i.e. quantifying welfare ranges)
457 when reviewing and rating proxies, and where possible, reviewed taxa that they were highly familiar
458 with (e.g., experience conducting research and/or animal care). In the present study, interobserver
459 reliability was conducted and confirmed; however going forward, we recommend that replication
460 efforts conduct literature reviews while blind to study purpose.

461

462 Although some of the proxies have been tested in different species, they are rarely done so
463 comparatively, which severely limits direct comparisons. For example, similar paradigms have been
464 used to test for delay of gratification across species, but researchers often focus on differing
465 measures and procedures that limit cross-species comparability (outlined in Miller et al., 2019 review
466 of self-control in crows, parrots, and non-human primates). Efforts to expand on multi-species
467 comparisons, for instance short-term/working memory in primates (ManyPrimates et al., 2019,
468 Sidebar 2), may be a step towards remedying this in the future.

469

470 It is critical to keep in mind that 'absence of evidence is not evidence of absence' (Birch, 2017;
471 Kuntsson & Munthe, 2017). Specifically, lack of evidence is likely to reflect lack of existing
472 publications, rather than necessarily a confirmed lack of positive or negative evidence. The publication
473 bias against negative findings leads to many studies that fail or show negative results not being
474 published. Of the 90 proxies identified in the full table (Fischer, 2022; Table S1 and S2), fewer than 20
475 had been tested across the majority of the 10 taxa of focus. These areas highlight possible avenues
476 for future empirical research and cross-species comparisons.

477

478 Similarly, as with many areas of science, the fields of animal cognition, behaviour, welfare science
479 and others face some concerns and issues regarding replicability, low statistical power and sample
480 sizes, as well as generalisation (Beran, 2018; Farrar et al., 2021; Open Science Collaboration, 2015).
481 In response to this replication crisis, there is a push for greater use of Open Science practices
482 (Munafò et al., 2017). This has also driven the development of big-team science projects (Coles et al.,
483 2022; Sidebar 2). These issues impact on the reliability in interpreting some of the existing studies
484 both within-species and between-species. For example, as outlined in Farrar et al. (2021) using
485 inhibitory control (specifically the 'cylinder' task) as a case study.

486

487 We note that poor welfare can impact on cognition and behaviour, and thus it is possible that low
488 cognitive performance in farmed animals may be a result of overall management practices, as
489 opposed to being representative of typical species-level capacities. Similarly, study animals may be
490 'STRANGE' (e.g., their social background, rearing history) or 'CRAMPED' (e.g., have compromised
491 health and development) hampering generalizability (Webster & Rutz, 2020; Cait et al., 2022). We
492 remedied this to some extent by including a wider family focus (i.e., *Phasianidae*, as opposed to only
493 chickens) to gather, where available, a wider representation of species and studies. Furthermore, at
494 least for chickens, evidence is lacking for domestication leading to reduced cognitive or perceptual
495 abilities in domestic chickens compared with their wild counterparts (i.e., red junglefowl) (Marino,
496 2017).

497

498 **5.4 Future Research**

499

500 Catalogues A & B represent outlines of proxies for prioritising in future (particularly comparative)
501 research aimed at targeting welfare-relevant measures. In particular, cognitive bias, mental time travel
502 (including self-control), relief/ aversive learning, emotional contagion, problem-solving, and self-
503 awareness are all Catalogue A measures that are currently lacking in empirical data for most selected
504 taxa (see Table 2 for proxy definitions). Furthermore, there are several Catalogue B measures that
505 would benefit from direct comparative approaches, such as reversal learning and motivational trade-
506 off, and expanding on memory related measures, such as episodic-like memory. For instance,
507 episodic-like memories bring a past moment into the present, providing opportunity for individuals to
508 recall details of these personal experiences. In this regard, negative memories can be especially
509 powerful if an animal has the capacity to collect the emotions that are linked to the experience,
510 which is likely to lead to a larger welfare range.

511

512 We expand on two proxies, one per Catalogue, that may benefit from future research focus. Within
513 cognitive bias (Catalogue A) tests, multiple study designs may be used, such as go/no-go, go/go (or
514 active choice), or active choice with negative reinforcement methods (see reviews by Bethell et al.,
515 2015 and Baciadonna & McElligott, 2015). Each method has various critiques, such as a large

516 amount of training and confounding aspects of an animal's internal state, like motivation or arousal, in
517 go/no-go tasks. Go/go tasks may be more robust to such differences, though still require extensive
518 training (Bethell et al., 2015). Tasks can also be adapted for cross-species comparisons by requiring
519 different behavioural responses (e.g., nose poking, lever pressing, screen pecking) and varying
520 sensory modalities (e.g., visual, auditory, textural cues) that are most appropriate for the study
521 species. For instance, play related experiments have been tested across mammals, birds and insects,
522 including recently using ball-rolling in bees (Dona et al., 2022). While modifications are necessary to
523 support diverse taxa, it is important to design translatable tasks that facilitate cross-taxa comparisons.
524 For instance, judgement bias tasks in humans commonly use secondary reinforcers (e.g., money -
525 see Neville et al. 2021a) whereas judgement bias tasks in animals tend to use primary reinforcers
526 (e.g., food - see Neville et al. 2020), making it challenging to compare results. Studies on humans
527 should aim to use primary reinforcers (e.g., juice/salty tea) to make judgement bias tasks translatable
528 between humans and animals (Neville et al. 2021b). By designing a series of translatable tasks, we
529 can better draw conclusions about susceptibility to cognitive bias across taxa in the future.

530
531 Within reversal learning (Catalogue B) tests – a method for measuring inhibitory control – the
532 methodologies often differ considerably despite being adapted for many species, making comparisons
533 problematic. For example, the output measure may be learning speed, accuracy or error rates, or
534 number of trials to reach criterion (acquisition and/or reversal phases). Similarly with cognitive bias
535 tests, it can be easily modified to suit modality (e.g., colour or shape discriminations) and behavioural
536 response. The complexity can also be increased, since some studies use additional reversals i.e.,
537 serial reversals tasks. Future research may look to standardise a methodology, including type of
538 stimulus, criteria and output measures, and test across taxa. These outputs can then also be
539 correlated with other factors, such as brain-to-body ratio and neuronal density (Olkowicz et al., 2016).
540 For example, three North American corvid species differing in sociality were tested using a reversal
541 learning colour discrimination task. Results revealed that highly social pinyon jays outperformed more
542 solitary Clark's nutcrackers and California scrub jays (Bond et al., 2007).

543
544 Further research should aim to directly correlate a) across different measures, such as cognition and
545 welfare, and b) within related mechanisms, such as learning proxies such as social and contextual
546 learning, or classical and operant conditioning. Cross-team collaborative approaches focusing on
547 measures relevant and testable across a wide range of species will allow for more reliable inter-
548 species comparisons of cognition, welfare, and other measures.

549 **Conclusion**

550
551 Do certain animals have a greater capacity for suffering? This article presents and applies a multi-
552 measure framework to understand variation in cognition and welfare range across 10 farmed taxa. For
553 each taxon, we constructed a cognition and welfare range profile, with an overall judgement score,
554 and discussed the implications of comparisons across the taxa. This process identified which proxies
555 are supported by quantitative evidence and which should be prioritised for future research and
556 funding. Our results reveal some variation in CWR across farmed taxa. Animals with larger cognitive
557 and welfare ranges should be prioritised because we assume they have a greater capacity to
558 experience enhanced negative (e.g., greater suffering) and positive (e.g., greater enjoyment)
559 emotions. That being said, the research gaps are large, particularly in the proxies listed in Catalogue
560 A; and thus, we are not yet in a position to construct comprehensive (i.e., data completeness) CWR
561 profiles for all of our target taxa. Nevertheless, our analysis allows us to make broad, evidence-based
562 comparisons with the data that is available. For example, evidence for proxies linked to behavioural
563 flexibility is comparable across pigs, chickens, octopus, crabs, and crayfish (i.e., 75 %). Comparisons
564 of this type can be made along all categories. Evidence for proxies linked to general learning is
565 comparable across carp, salmon, shrimp, and crayfish (i.e., 50 %), whereas octopuses obtained a
566 much stronger score in this category (i.e., 100 %). These conjectures may be overturned as
567 researchers collect more detailed evidence, but it is a starting point.

568
569
570 Our analysis of current evidence also highlights gaps in the literature. To help bridge these gaps, we
571 propose some future research experiments for specific proxies, which will enable informative
572 comparative research. These include cognitive bias and inhibitory control related paradigms, both of
573 which have been proposed as welfare-relevant measures. We believe this approach will assist
574 researchers, including Big-Team Science collaborations (Sidebar 2), to efficiently target existing

575 knowledge gaps and accelerate these objectives. Ultimately, this approach should help streamline
576 funding allocations for welfare improvements and increase the overall welfare of farmed species.

577

578 **Funding Information**

579

580 This work was funded by a grant from Open Philanthropy (182 Howard Street #225, San Francisco,
581 CA 94105), awarded to Rethink Priorities (RP), which supported all authors (BF as RP employee;
582 other authors on temporary consultancy basis). No authors were employed by Open Philanthropy
583 (OP) at the time of conducting this review work; one author (JML) commenced employment with OP in
584 Oct 2022.

585

586 **Acknowledgements**

587

588 We would like to thank Richard Bruns, Marcus Davis, Adam Shriver, and Michael St. Jules for their
589 discussion of the ideas that facilitated this approach to making interspecies welfare comparisons.

590

591 **References**

592

593 Abramson, C. I., & Feinman, R. D. (1990). Lever-press conditioning in the crab. *Physiology &*
594 *behavior*, 48(2), 267-272.

595

596 Adamo, S. A. (2016). Consciousness explained or consciousness redefined?. *Proceedings of the*
597 *National Academy of Sciences*, 113(27), E3812-E3812.

598

599 Adamo, S. A., & McMillan, L. E. (2019). Listening to your gut: immune challenge to the gut sensitises
600 body wall nociception in the caterpillar *Manduca sexta*. *Philosophical Transactions of the Royal*
601 *Society B*, 374(1785), 20190278.

602

603 Allen, J., & Perry, G. C. (1975). Feather pecking and cannibalism in a caged layer flock. *British Poultry*
604 *Science*, 16(5), 441-451.

605

606 Alupay, J. S., Hadjisolomou, S. P., & Crook, R. J. (2014). Arm injury produces long-term behavioral
607 and neural hypersensitivity in octopus. *Neuroscience Letters*, 558, 137-142.

608

609 Amodio, P., & Fiorito, G. (2022). A preliminary attempt to investigate mirror self-recognition in *Octopus*
610 *vulgaris*. *Frontiers in Physiology*, 1651.

611

612 Andrews K., & Monsó S. (2021), "Animal Cognition", *The Stanford Encyclopedia of Philosophy*
613 (Spring 2021 Edition), Edward N. Zalta (ed.).

614

615 Aquiloni, L., & Gherardi, F. (2008). Assessing mate size in the red swamp crayfish *Procambarus*
616 *clarkii*: effects of visual versus chemical stimuli. *Freshwater Biology*, 53(3), 461-469.

617

618 Appleby, M. C., Mench, J. A., & Hughes, B. O. (2004). Poultry behaviour and welfare. Cabi.

619

620 Arroyo, L., Carreras, R., Valent, D., Peña, R., Mainau, E., Velarde, A., Sabrià, J. and Bassols, A.,
621 (2016). Effect of handling on neurotransmitter profile in pig brain according to fear related behaviour.
622 *Physiology & Behavior*, 167, 374-381.

623

624 Arts, J. W., van der Staay, F. J., & Ekkel, E. D. (2009). Working and reference memory of pigs in the
625 spatial holeboard discrimination task. *Behavioural Brain Research*, 205(1), 303-306.

626

627 Baciadonna, L., & McElligott, A. G. (2015). The use of judgement bias to assess welfare in farm
628 livestock. *Animal Welfare*, 24: 81-91

629

630 Bacqué-Cazenave, J., Cattaert, D., Delbecque, J. P., & Fossat, P. (2017). Social harassment induces
631 anxiety-like behaviour in crayfish. *Scientific reports*, 7(1), 1-7.

632

- 633 Bardera, G., Owen, M. A., Façanha, F. N., Alcaraz-Calero, J. M., Sloman, K. A., & Alexander, M. E.
634 (2020). Assessing feed attractability in Pacific white shrimp (*Litopenaeus vannamei*) using an
635 automated tracking software. *Aquaculture*, 529, 735692.
636
- 637 Bardera, G., Owen, M. A., Façanha, F. N., Alcaraz-Calero, J. M., Alexander, M. E., & Sloman, K. A.
638 (2021). The influence of density and dominance on Pacific white shrimp (*Litopenaeus vannamei*)
639 feeding behaviour. *Aquaculture*, 531, 735949.
640
- 641 Barr, S., & Elwood, R. W. (2011). No evidence of morphine analgesia to noxious shock in the shore
642 crab, *Carcinus maenas*. *Behavioural Processes*, 86(3), 340-344.
643
- 644 Barron, A. B., & Klein, C. (2016). What insects can tell us about the origins of consciousness.
645 *Proceedings of the National Academy of Sciences*, 113(18), 4900-4908.
646
- 647 Bateson, M., Desire, S., Gartside, S. E., & Wright, G. A. (2011). Agitated honeybees exhibit
648 pessimistic cognitive biases. *Current biology*, 21(12), 1070-1073.
649
- 650 Bauer, R. T. (1981). Grooming behavior and morphology in the decapod Crustacea. *Journal of*
651 *Crustacean Biology*, 1(2), 153-173.
652
- 653 Belger, J., & Bräuer, J. (2018). Metacognition in dogs: Do dogs know they could be wrong?. *Learning*
654 *& behavior*, 46(4), 398-413.
655
- 656 Belzung, C., & Philippot, P. (2007). Anxiety from a phylogenetic perspective: is there a qualitative
657 difference between human and animal anxiety?. *Neural plasticity*, 2007.
658
- 659 Bennett, H., & Toll, R. B. (2011). Intramantle inking: A stress behavior in *Octopus bimaculoides*
660 (Mollusca: Cephalopoda). *Journal of the American Association for Laboratory Animal Science*, 50(6),
661 943-945.
662
- 663 Beran, M. (2018). Replication and pre-registration in comparative psychology. *International Journal of*
664 *Comparative Psychology*, 31.
665
- 666 Bernstein, I. L. (1999). Taste aversion learning: a contemporary perspective. *Nutrition*, 15(3), 229-234.
667
- 668 Bethell, E. J. (2015). A "how-to" guide for designing judgment bias studies to assess captive animal
669 welfare. *Journal of Applied Animal Welfare Science*, 18(sup1), S18-S42.
670
- 671 Birch, J. (2017). Animal sentience and the precautionary principle. *Animal sentience*, 2(16), 1.
672
- 673 Birch, J., Schnell, A. K., & Clayton, N. S. (2020). Dimensions of animal consciousness. *Trends in*
674 *cognitive sciences*, 24(10), 789-801.
675
- 676 Birch, J., Burn, C., Schnell, A., Browning, H & Crump, A. (2021). Review of the evidence of sentience in
677 cephalopod molluscs and decapod crustaceans. LSE Consulting. LSE Enterprise Ltd. The London
678 School of Economics and Political Science. Available at: [https://www.lse.ac.uk/News/News-Assets/PDFs/2021/ Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-](https://www.lse.ac.uk/News/News-Assets/PDFs/2021/Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-November-2021.pdf)
679 [November-2021.pdf](https://www.lse.ac.uk/News/News-Assets/PDFs/2021/Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-November-2021.pdf).
680
- 681
- 682 Blackiston, D. J., Silva Casey, E., & Weiss, M. R. (2008). Retention of memory through
683 metamorphosis: can a moth remember what it learned as a caterpillar? *PloS one*, 3(3), e1736.
684
- 685 Bloch, S., Froc, C., Pontiggia, A., & Yamamoto, K. (2019). Existence of working memory in teleosts:
686 Establishment of the delayed matching-to-sample task in adult zebrafish. *Behavioural brain research*,
687 370, 111924.
688
- 689 Bolhuis, J. E., Schouten, W. G., de Leeuw, J. A., Schrama, J. W., & Wiegant, V. M. (2004). Individual
690 coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behavioural brain*
691 *research*, 152(2), 351-360.
692

- 693 Bool, J. D., Witcomb, K., Kydd, E., & Brown, C. (2011). Learned recognition and avoidance of invasive
694 mosquitofish by the shrimp, *Paratya australiensis*. *Marine and Freshwater Research*, 62(10), 1230-
695 1236.
696
- 697 Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of
698 behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*,
699 *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, 121(4), 372.
700
- 701 Borrelli L., & Fiorito G. (2008) Behavioral analysis of learning and memory in cephalopods. In: Byrne
702 JJ (ed) *Learning and memory: a comprehensive reference*. Academic Press, Oxford, pp 605–627.
703
- 704 Botreau, R., Veissier, I., & Perny, P. (2009). Overall assessment of animal welfare: strategy adopted
705 in Welfare Quality®. *Animal Welfare*, 18(4), 363-370.
706
- 707 Boycott, B. B., & Young, J. Z. (1957). Effects of interference with the vertical lobe on visual
708 discriminations in *Octopus vulgaris* Lamarck. *Proceedings of the Royal Society of London. Series B-
709 Biological Sciences*, 146(925), 439-459.
710
- 711 Bracke, M. B. (2011). Review of wallowing in pigs: implications for animal welfare. *Animal Welfare*,
712 20(3), 347-363.
713
- 714 Breed, M. D., Robinson, G. E., & Page, R. E. (1990). Division of labor during honey bee colony
715 defense. *Behavioral Ecology and Sociobiology*, 27(6), 395-401.
716
- 717 Broom, D. M. (1996). Attempts to Cope with the Environment. *Acta Agric. Scand. Sec. A. Anim. Sci.
718 Suppl*, 27, 22-28.
719
- 720 Broom, D. M., Sena, H., & Moynihan, K. L. (2009). Pigs learn what a mirror image represents and use
721 it to obtain information. *Animal Behaviour*, 78(5), 1037-1041.
722
- 723 Brown, C. (2015). Fish intelligence, sentience and ethics. *Animal cognition*, 18(1), 1-17.
724
- 725 Brownell, C. A., Zerwas, S., & Ramani, G. B. (2007). "So big": The development of body
726 self-awareness in toddlers. *Child development*, 78(5), 1426-1440.
727
- 728 Bruckner, D. W. (2020). Animal welfare science, varieties of value and philosophical methodology.
729 *Animal Welfare*, 29(4), 387-397.
730
- 731 Brydges, N. M., & Braithwaite, V. A. (2008). Measuring animal welfare: what can cognition contribute.
732 *Annual Review of Biomedical Sciences*, 10, 91-103.
733
- 734 Buckley, L. A., Sandilands, V., Tolkamp, B. J., & D'Eath, R. B. (2011). Quantifying hungry broiler
735 breeder dietary preferences using a closed economy T-maze task. *Applied Animal Behaviour
736 Science*, 133(3-4), 216-227.
737
- 738 Budaev, S. V. (1997). " Personality" in the guppy (*Poecilia reticulata*): A correlational study of
739 exploratory behavior and social tendency. *Journal of Comparative Psychology*, 111(4), 399.
740
- 741 Budolfson, M., & Spears, D. (2019). Quantifying animal well-being and overcoming the challenge of
742 interspecies comparisons. In *The Routledge Handbook of Animal Ethics*(pp. 92-101). Routledge.
743
- 744 Buřič, M., K. Grabicová, J. Kubec, A. Kouba, I. Kuklina, P. Kozák, R. Grabic, and T. Randák. (2018).
745 Environmentally relevant concentrations of tramadol and citalopram alter behaviour of an aquatic
746 invertebrate. *Aquatic Toxicology*, 200, 226-232.
747
- 748 Burman, O. H., Parker, R., Paul, E. S., & Mendl, M. (2008). A spatial judgement task to determine
749 background emotional state in laboratory rats, *Rattus norvegicus*. *Animal Behaviour*, 76(3), 801-809.
750

- 751 Butler-Struben, H. M., Brophy, S. M., Johnson, N. A., & Crook, R. J. (2018). In vivo recording of neural
752 and behavioral correlates of anesthesia induction, reversal, and euthanasia in cephalopod molluscs.
753 *Frontiers in physiology*, 9, 109.
754
- 755 Cait, J., Cait, A., Scott, R. W., Winder, C. B., & Mason, G. J. (2022). Conventional laboratory housing
756 increases morbidity and mortality in research rodents: results of a meta-analysis. *BMC biology*, 20(1),
757 1-22.
758
- 759 Campbell, D. L., Hinch, G. N., Downing, J. A., & Lee, C. (2016). Fear and coping styles of outdoor-
760 preferring, moderate-outdoor and indoor-preferring free-range laying hens. *Applied Animal Behaviour*
761 *Science*, 185, 73-77.
762
- 763 Campbell, D. L., Talk, A. C., Loh, Z. A., Dyall, T. R., & Lee, C. (2018). Spatial cognition and range use
764 in free-range laying hens. *Animals*, 8(2), 26.
765
- 766 Chambers, K. C. (1990). A neural model for conditioned taste aversions. *Annual review of*
767 *neuroscience*, 13(1), 373-385.
768
- 769 Chervova, L. S., & Lapshin, D. N. (2000). Opioid modulation of pain threshold in fish. In *Doklady*
770 *Biological Sciences* (Vol. 375, No. 1-6, pp. 590-591). Kluwer Academic/Plenum Publishers.
771
- 772 Chittka, L., & Geiger, K. (1995). Can honey bees count landmarks? *Animal Behaviour*, 49(1), 159-
773 164.
774
- 775 Chittka, L., Rossiter, S. J., Skorupski, P., & Fernando, C. (2012). What is comparable in comparative
776 cognition?. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1603), 2677-
777 2685.
778
- 779 Chittka, L. (2022). *The Mind of a Bee*. Princeton University Press.
780
- 781 Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the
782 future?. *Nature Reviews Neuroscience*, 4(8), 685-691.
783
- 784 Coles, N. A., Hamlin, J. K., Sullivan, L. L., Parker, T. H., & Altschul, D. (2022). Build up big-team
785 science. *Nature* 601, 505-507
786
- 787 Crook, R. J., Lewis, T., Hanlon, R. T., & Walters, E. T. (2011). Peripheral injury induces long-term
788 sensitization of defensive responses to visual and tactile stimuli in the squid *Loligo pealeii*, Lesueur
789 1821. *Journal of Experimental Biology*, 214(19), 3173-3185.
790
- 791 Crook, R. J. (2020). Conditioned place preference reveals tonic pain in Octopus. bioRxiv.
792
- 793 Crump, A., Arnott, G., & Bethell, E. J. (2018). Affect-driven attention biases as animal welfare
794 indicators: review and methods. *Animals*, 8(8), 136.
795
- 796 Davies, R., Gagen, M. H., Bull, J. C., & Pope, E. C. (2019). Maze learning and memory in a decapod
797 crustacean. *Biology letters*, 15(10), 20190407.
798
- 799 Daisley, J. N., Vallortigara, G., & Regolin, L. (2010). Logic in an asymmetrical (social) brain: transitive
800 inference in the young domestic chick. *Social Neuroscience*, 5(3), 309-319
801
- 802 Dale, R., & Plotnik, J. M. (2017). Elephants know when their bodies are obstacles to success in a
803 novel transfer task. *Scientific reports*, 7(1), 1-10.
804
- 805 de Brito Sanchez, M. G. (2011). Taste perception in honey bees. *Chemical senses*, 36(8), 675-692.
806
- 807 de Lourdes Ruiz-Gomez, M., Huntingford, F. A., Øverli, Ø., Thörnqvist, P. O., & Höglund, E. (2011).
808 Response to environmental change in rainbow trout selected for divergent stress coping styles.
809 *Physiology & behavior*, 102(3-4), 317-322.
810

- 811 Denzau, S., Nießner, C., Rogers, L. J., & Wiltschko, W. (2013). Ontogenetic development of magnetic
812 compass orientation in domestic chickens (*Gallus gallus*). *Journal of Experimental Biology*, 216(16),
813 3143-3147.
- 814
- 815 Diamond, A. (2013). Executive functions. *Annual review of psychology*, 64, 135.
- 816
- 817 Dittman, A., & Quinn, T. (1996). Homing in Pacific salmon: mechanisms and ecological basis. *The*
818 *Journal of experimental biology*, 199(1), 83-91.
- 819
- 820 Dona, H. S. G., Solvi, C., Kowalewska, A., Mäkelä, K., MaBouDi, H., & Chittka, L. (2022). Do bumble
821 bees play?. *Animal Behaviour*.
- 822
- 823 Duffield, C., Wilson, A. J., & Thornton, A. (2015). Desperate prawns: Drivers of behavioural innovation
824 vary across social contexts in rock pool crustaceans. *PLoS One*, 10(10), e0139050.
- 825
- 826 Duncan, I. J. H., Slee, G. S., Seawright, E., & Breward, J. (1989). Behavioural consequences of
827 partial beak amputation (beak trimming) in poultry. *British Poultry Science*, 30(3), 479-488.
- 828
- 829 Duncan, I. J., & Petherick, J. C. (1991). The implications of cognitive processes for animal welfare.
830 *Journal of animal science*, 69(12), 5017-5022.
- 831
- 832 Dunlop, R., Millsopp, S., & Laming, P. (2006). Avoidance learning in goldfish (*Carassius auratus*) and
833 trout (*Oncorhynchus mykiss*) and implications for pain perception. *Applied Animal Behaviour Science*,
834 97(2-4), 255-271.
- 835
- 836 Döpjan, S., Ramp, C., Kanitz, E., Tuchscherer, A., & Puppe, B. (2013). A design for studies on
837 cognitive bias in the domestic pig. *Journal of Veterinary Behavior*, 8(6), 485-489.
- 838
- 839 Eckert, J., Bohn, M., & Spaethe, J. (2022). Does quantity matter to a stingless bee?. *Animal*
840 *Cognition*, 25(3), 617-629.
- 841
- 842 Edgar, J. L., & Nicol, C. J. (2018). Socially-mediated arousal and contagion within domestic chick
843 broods. *Scientific Reports*, 8(1), 1-10.
- 844
- 845 Edwards, D. D., Rapin, K. E., & Moore, P. A. (2018). Linking phenotypic correlations from a diverse
846 set of laboratory tests to field behaviors in the crayfish, *Orconectes virilis*. *Ethology*, 124(5), 311-330.
- 847
- 848 Ehrensing, R. H., Michell, G. F., & Kastin, A. J. (1982). Similar antagonism of morphine analgesia by
849 MIF-1 and naloxone in *Carassius auratus*. *Pharmacology Biochemistry and Behavior*, 17(4), 757-761.
- 850
- 851 Elwood, R. W. (2019). Assessing the potential for pain in crustaceans and other invertebrates. *The*
852 *Welfare of Invertebrate Animals*, 147-177.
- 853
- 854 Elwood, R. W. (2022). Hermit crabs, shells, and sentience. *Animal cognition*, 1-17.
- 855
- 856 Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in
857 corvids and apes. *Science*, 306(5703), 1903-1907.
- 858
- 859 Espigares, F., Martins, R. R., & Oliveira, R. F. (2022). A Behavioural Assay to Investigate Judgment
860 Bias in Zebrafish. *Bio-protocol*, 12(4), e4327-e4327.
- 861
- 862 Eysenck, M. W., Mogg, K., May, J., Richards, A., & Mathews, A. (1991). Bias in interpretation of
863 ambiguous sentences related to threat in anxiety. *Journal of abnormal psychology*, 100(2), 144.
- 864
- 865 Farrar, B. G., Voudouris, K., & Clayton, N. S. (2021). Replications, comparisons, sampling and the
866 problem of representativeness in animal cognition research. *Animal behavior and cognition*, 8(2), 273.
- 867
- 868 Favati, A., Leimar, O., & Løvlie, H. (2014). Personality predicts social dominance in male domestic
869 fowl. *PLoS One*, 9(7), e103535.
- 870

- 871 Fazekas, P., & Overgaard, M. (2016). Multidimensional models of degrees and levels of
872 consciousness.
873
- 874 Ferreira, V. H. B., Germain, K., Calandreau, L., & Guesdon, V. (2020). Range use is related to free-
875 range broiler chickens' behavioral responses during food and social conditioned place preference
876 tests. *Applied Animal Behaviour Science*, 230, 105083.
877
- 878 Ferreira, V. H. B., Barbarat, M., Lormant, F., Germain, K., Brachet, M., Løvlie, H., Calandreau, L., &
879 Guesdon, V. (2020). Social motivation and the use of distal, but not local, featural cues are related to
880 ranging behavior in free-range chickens (*Gallus gallus domesticus*). *Animal Cognition*, 23(4), 769-780.
881
- 882 Ferreira, V. H. B., Guesdon, V., & Calandreau, L. (2021). How can the research on chicken cognition
883 improve chicken welfare: a perspective review. *World's Poultry Science Journal*, 77(3), 679-698.
884
- 885 Fijn, L. B., van der Staay, F. J., Goerlich-Jansson, V. C., & Arndt, S. S. (2020). Importance of basic
886 research on the causes of feather pecking in relation to welfare. *Animals*, 10(2), 213.
887
- 888 Fiorito, G., Biederman, G. B., Davey, V. A., & Gherardi, F. (1998). The role of stimulus preexposure in
889 problem solving by *Octopus vulgaris*. *Animal cognition*, 1(2), 107-112.
890
- 891 Fischer, B. (in press). How to express improvements in animal welfare in DALYs-averted. *Kennedy*
892 *Institute of Ethics Journal*.
893
- 894 Fischer, B. (2022). The welfare range table - Effective Altruism forum. Available online at:
895 <https://forum.effectivealtruism.org/posts/tNsg6o7cRcHFLc395/the-welfare-range-table> (Accessed on
896 November 7th, 2022)
897
- 898 Foote, A. L., & Crystal, J. D. (2007). Metacognition in the rat. *Current Biology*, 17(6), 551-555.
899
- 900 Forsythe, J. W., & Hanlon, R. T. (1997). Foraging and associated behavior by *Octopus cyanea* Gray,
901 1849 on a coral atoll, French Polynesia. *Journal of Experimental Marine Biology and Ecology*, 209(1-
902 2), 15-31.
903
- 904 Franks, B., Ewell, C., & Jacquet, J. (2021). Animal welfare risks of global aquaculture. *Science*
905 *Advances*, 7(14), eabg0677.
906
- 907 Freire R. (2020). Understanding chicken learning and cognition and implications for improved
908 management. In *Understanding the behaviour and improving the welfare of chickens* (pp. 1-27).
909 Burleigh Dodds Science Publishing Limited.
910
- 911 Friel, M., Kunc, H. P., Griffin, K., Asher, L., & Collins, L. M. (2016). Acoustic signalling reflects
912 personality in a social mammal. *Royal Society open science*, 3(6), 160178.
913
- 914 Gaffney, L., Lavery, J. M., Schiestl, M., Trevarthen, A., Schukraft, J., Miller, R., Schnell, A., Fischer, B.
915 A. (2022). Method for Improving Interspecies Welfare Comparisons. *Preprints 2022*, 2022100012 (doi:
916 10.20944/preprints202210.0012.v1).
917
- 918 Gallup Jr, G. G. (1975). Towards an operational definition of self-awareness. *Socioecology and*
919 *psychology of primates*, 309-341.
920
- 921 Geller, I., & Brady, J. V. (1961). Effect of Electroconvulsive Shock on an Extinguished" Fear"
922 Response. *Science*, 133(3458), 1080-1081.
923
- 924 Gerber, B., Yarali, A., Diegelmann, S., Wotjak, C. T., Pauli, P., & Fendt, M. (2014). Pain-relief learning
925 in flies, rats, and man: basic research and applied perspectives. *Learning & Memory*, 21(4), 232-252.
926
- 927 Gibbons, M., Versace, E., Crump, A., Baran, B., & Chittka, L. (2022). Motivational trade-offs in
928 bumblebees. bioRxiv.
929
- 930 Gordon, G. G. (1970). Chimpanzees: self-recognition. *Science*, 167(3914), 86-87.

- 931
932 Groening, J., Venini, D., & Srinivasan, M. V. (2017). In search of evidence for the experience of pain
933 in honeybees: A self-administration study. *Scientific Reports*, 7(1), 1-8.
934
935 Gutnick, T., Byrne, R. A., Hochner, B., & Kuba, M. (2011). Octopus vulgaris uses visual information to
936 determine the location of its arm. *Current biology*, 21(6), 460-462.
937
938 Hamilton, T. J., Myggland, A., Duperreault, E., May, Z., Gallup, J., Powell, R. A., ... & Digweed, S. M.
939 (2016). Episodic-like memory in zebrafish. *Animal Cognition*, 19(6), 1071-1079.
940
941 Harlander-Matauschek, A., Wassermann, F., Zentek, J., & Bessei, W. (2008). Laying hens learn to
942 avoid feathers. *Poultry Science*, 87(9), 1720-1724.
943
944 Heberts, E. A., & Rundus, A. (2010). Chemical communication in a multimodal context. In Chemical
945 communication in crustaceans (pp. 335-354). Springer, New York, NY.
946
947 Hemsworth, P. H., Verge, J., & Coleman, G. J. (1996). Conditioned approach-avoidance responses to
948 humans: the ability of pigs to associate feeding and aversive social experiences in the presence of
949 humans with humans. *Applied Animal Behaviour Science*, 50(1), 71-82.
950
951 Huntingford, F. A., Andrew, G., Mackenzie, S., Morera, D., Coyle, S. M., Pilarczyk, M., & Kadri, S.
952 (2010). Coping strategies in a strongly schooling fish, the common carp *Cyprinus carpio*. *Journal of*
953 *Fish Biology*, 76(7), 1576-1591.
954
955 Imeh-Nathaniel, A., Adedeji, A., Huber, R., & Nathaniel, T. I. (2016). The rewarding properties of
956 methamphetamine in an invertebrate model of drug addiction. *Physiology & behavior*, 153, 40-46.
957
958 Imfeld-Mueller, S., Van Wezemaal, L., Stauffacher, M., Gygax, L., & Hillmann, E. (2011). Do pigs
959 distinguish between situations of different emotional valences during anticipation? *Applied Animal*
960 *Behaviour Science*, 131(3-4), 86-93.
961
962 Izquierdo, A., Brigman, J. L., Radke, A. K., Rudebeck, P. H., & Holmes, A. (2017). The neural basis of
963 reversal learning: an updated perspective. *Neuroscience*, 345, 12-26.
964
965 Jozet-Alves, C., Bertin, M., & Clayton, N. S. (2013). Evidence of episodic-like memory in cuttlefish.
966 *Current Biology*, 23(23), R1033-R1035.
967
968 Kamran, M., & Moore, P. A. (2015). Comparative homing behaviors in two species of crayfish,
969 *Fallicambarus fodiens* and *Orconectes rusticus*. *Ethology*, 121(8), 775-784.
970
971 Keller, T. A., Powell, I., & Weissburg, M. J. (2003). Role of olfactory appendages in chemically
972 mediated orientation of blue crabs. *Marine Ecology Progress Series*, 261, 217-231.
973
974 Khan, W., Khan, M. I., Hussain, S., Masood, Z., Shadman, M., Baset, A., Rahman, A., Mohsin, M. &
975 Alfarraj, S. (2021). Comparative analysis of brain in relation to the body length and weight of common
976 carp (*Cyprinus carpio*) in captive (hatchery) and wild (river system) populations. *Brazilian Journal of*
977 *Biology*, 82.
978
979 Knutsson, S., & Munthe, C. (2017). A virtue of precaution regarding the moral status of animals with
980 uncertain sentience. *Journal of Agricultural and Environmental Ethics*, 30(2), 213-224.
981
982 Kouwenberg, A. L., Walsh, C. J., Morgan, B. E., & Martin, G. M. (2009). Episodic-like memory in
983 crossbred Yucatan minipigs (*Sus scrofa*). *Applied Animal Behaviour Science*, 117(3-4), 165-172.
984 Chicago.
985
986 Krause, A., Kreiser, M., Puppe, B., Tuchscherer, A., & Döpjan, S. (2021). The effect of age on
987 discrimination learning and self-control in a marshmallow test for pigs. *Scientific Reports*, 11(1), 1-10.
988
989 Kratzer, D. D. (1969). Effects of age on avoidance learning in pigs. *Journal of Animal Science*, 28(2),
990 175-179.

- 991
992 Krupenye, C. (2021). The evolution of mentalizing in humans and other primates. In *The Neural Basis*
993 *of Mentalizing* (pp. 107-129). Springer, Cham.
994
995 Kuba, M. J., Byrne, R. A., Meisel, D. V., & Mather, J. A. (2006). When do octopuses play? Effects of
996 repeated testing, object type, age, and food deprivation on object play in *Octopus vulgaris*. *Journal of*
997 *comparative psychology*, 120(3), 184.
998
999 Kuroda, T., Mizutani, Y., Cançado, C. R., & Podlesnik, C. A. (2017). Reversal learning and
1000 resurgence of operant behavior in zebrafish (*Danio rerio*). *Behavioural Processes*, 142, 79-83.
1001
1002 Linstone, H. A., & Turoff, M. (Eds.). (1975). *The delphi method*(pp. 3-12). Reading, MA: Addison-
1003 Wesley.
1004
1005 Lambert, H., Elwin, A., & D'Cruze, N. (2021). Wouldn't hurt a fly? A review of insect cognition and
1006 sentience in relation to their use as food and feed. *Applied Animal Behaviour Science*, 243, 105432.
1007
1008 Lambert, M., Farrar, B., Garcia-Pelegri, E., Reber, S., & Miller, R. (2022). ManyBirds: A multi-site
1009 collaborative Open Science approach to avian cognition and behavior research. *Animal Behavior and*
1010 *Cognition*, 9(1), 133-152.
1011
1012 Loukola, O. J., Solvi, C., Coscos, L., & Chittka, L. (2017). Bumblebees show cognitive flexibility by
1013 improving on an observed complex behavior. *Science*, 355(6327), 833-836.
1014
1015 Mackintosh, N. J., & Mackintosh, J. (1963). Performance of Octopus over a series of reversals of a
1016 simultaneous discrimination. OXFORD UNIV (ENGLAND).
1017
1018 MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J.M.,
1019 Bania, A.E., Barnard, A.M., ... & Zhao, Y. (2014). The evolution of self-control. *Proceedings of the*
1020 *National Academy of Sciences*, 111(20), E2140-E2148.
1021
1022 Magee, B., & Elwood, R. W. (2013). Shock avoidance by discrimination learning in the shore crab
1023 (*Carcinus maenas*) is consistent with a key criterion for pain. *Journal of Experimental Biology*, 216(3),
1024 353-358.
1025
1026 Magee, B., & Elwood, R. W. (2016). Trade-offs between predator avoidance and electric shock
1027 avoidance in hermit crabs demonstrate a non-reflexive response to noxious stimuli consistent with
1028 prediction of pain. *Behavioural processes*, 130, 31-35.
1029
1030 ManyPrimates, Aguenounoun, G., Allritz, M., Altschul, D. M., Ballesta, S. Beaud, A., Bohn, M.,
1031 Bornbusch, S. L., Brandão, A., Brooks, J., Bugnyar, T., Bustamante, L., Call, J., Canteloup, C.,
1032 Caspar, K. R., de Sousa, A. A., DeTroy, S. E., Eppley, T. M., Fichtel, C., Fischer, J., Gong, C.,
1033 Grange, J. A., Grebe, N. M., Hanus, D., Haus, D., Haux, L. M., Héjja-Brichard, Y., Helman, A.,
1034 Hernadi, I., Hernandez-Aguilar, R. A., Hermann, E., Hopper, L. M., Howard, L. H., Huang, L.,
1035 Huskisson, S. M., Jacobs, I., Jin, Z., Joly, M., Kani, F., Keupp, S., Kiefer, E., Knakker, B., Kóczán, K.,
1036 Kraus, L., Kwok, S. C., Lefrançois, M., Lewis, L., Liu, S., Llorente, M., Lonsdorf, E., Loyant, L.,
1037 Majecka, K., Maurits, L., Meunier, H., Mobili, F., Morino, L., Motes-Rodrigo, A., Nijman, V., Ihome, C.
1038 N., Persson, T., Pietraszewski, D., Parrish, J. F. R., Roig, A., Sánchez-Amaro, A., Sato, Y., Sauciuc,
1039 G-A., Schrock, A. E., Schweinfurth, M. K., Seed, A., Shearer, C. L., Šlipogor, V., Su, Y., Sutherland,
1040 K., Tan, J., Taylor, D., Troisi, C. A., Völter, C. J., Warren, E., Watzek, J., Zablocki-Thomas, P. (2022).
1041 The evolution of primate short-term memory. *Animal Behavior and Cognition*, 9(4), 428-516.
1042 <https://doi.org/10.26451/abc.09.04.06.202>
1043
1044 ManyPrimates, Altschul, D. M., Beran, M. J., Bohn, M., Call, J., DeTroy, S., ... & Watzek, J. (2019).
1045 Establishing an infrastructure for collaboration in primate cognition research. *PLoS One*, 14(10),
1046 e0223675.
1047
1048 Marino, L. (2017). Thinking chickens: a review of cognition, emotion, and behavior in the domestic
1049 chicken. *Animal cognition*, 20(2), 127-147.
1050

- 1051 Maskrey, D. K., White, S. J., Wilson, A. J., & Houslay, T. M. (2018). Who dares does not always win:
1052 risk-averse rockpool prawns are better at controlling a limited food resource. *Animal Behaviour*, 140,
1053 187-197.
- 1054
- 1055 Mather, J. A., & Anderson, R. C. (1993). Personalities of octopuses (*Octopus rubescens*). *Journal of*
1056 *comparative psychology*, 107(3), 336.
- 1057
- 1058 McCambridge, C., Dick, J. T., & Elwood, R. W. (2016). Effects of autotomy compared to manual
1059 declawing on contests between males for females in the edible crab cancer pagurus: Implications for
1060 fishery practice and animal welfare. *Journal of Shellfish Research*, 35(4), 1037-1044.
- 1061
- 1062 McGlone, J. J., & Hellman, J. M. (1988). Local and general anesthetic effects on behavior and
1063 performance of two- and seven-week-old castrated and uncastrated piglets. *Journal of Animal*
1064 *Science*, 66(12), 3049-3058.
- 1065
- 1066 Mehlhorn, J., & Caspers, S. (2020). The Effects of Domestication on the Brain and Behavior of the
1067 Chicken in the Light of Evolution. *Brain, behavior and evolution*, 95(6), 287-301.
- 1068
- 1069 Mellor, D. J., & Beausoleil, N. J. (2015). Extending the 'Five Domains' model for animal welfare
1070 assessment to incorporate positive welfare states. *Anim. Welf*, 24(3), 241.
- 1071
- 1072 Mergler, C. J., Ludwig, A. N., & Gall, B. G. (2020). The effects of satiation level and competition risk
1073 on resource acquisition in red swamp crayfish (*Procambarus clarkii*). *Aquatic Ecology*, 54(3), 889-894.
- 1074
- 1075 Miller, R., Boeckle, M., Jelbert, S. A., Frohnwieser, A., Wascher, C. A., & Clayton, N. S. (2019).
1076 Self-control in crows, parrots and nonhuman primates. *Wiley Interdisciplinary Reviews: Cognitive*
1077 *Science*, 10(6), e1504.
- 1078
- 1079 Miller, R., Lambert, M. L., Frohnwieser, A., Brecht, K. F., Bugnyar, T., Crampton, I., Garcia-Pelegri,
1080 E., Gould, K., Greggor, A. L., Izawa, E. I., Kelly, D. M., Li, Z., Luo, Y., Luong, L., Massen, J., Nieder,
1081 A., Reber, S., Schiestl, M., Sepelri, P., Stevens, J., Taylor, A. H., Wang, L., Wolff, L. M., Zhang, Y., &
1082 Clayton, N. S. (2022). Socio-ecological correlates of neophobia in corvids. *Current Biology*, 32(1), 74-
1083 85.
- 1084
- 1085 Mir, A.H., & Qamar, A. (2018). Effects of starvation and thermal stress on the thermal tolerance of the
1086 silkworm, *Bombyx mori*: Existence of trade-offs and cross-tolerances. *Neotropical Entomology*, 47,
1087 610-618.
- 1088
- 1089 Miyake, A., & Shah, P. (1997). *Models of working memory*. Colorado University at Boulder Dept of
1090 Psychology.
- 1091
- 1092 Moore, C., Mealiea, J., Garon, N., & Povinelli, D. J. (2007). The development of body self-awareness.
1093 *Infancy*, 11(2), 157-174.
- 1094
- 1095 Moorman, S. J. (2001). Development of Sensory Systems in Zebrafish (*Donio rerio*). *ILAR journal*,
1096 42(4), 292-298.
- 1097
- 1098 Morelle, K., Podgórski, T., Prévot, C., Keuling, O., Lehaire, F., & Lejeune, P. (2015). Towards
1099 understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. *Mammal*
1100 *Review*, 45(1), 15-29.
- 1101
- 1102 Muller, H., Grossmann, H., & Chittka, L. (2010). 'Personality' in bumblebees: individual consistency in
1103 responses to novel colours? *Animal Behaviour*, 80(6), 1065-1074.
- 1104
- 1105 Munafò, M. R., Nosek, B. A., Bishop, D. V., Button, K. S., Chambers, C. D., Percie du Sert, N., ... &
1106 Ioannidis, J. (2017). A manifesto for reproducible science. *Nature human behaviour*, 1(1), 1-9.
- 1107
- 1108 Namiki, S., Wada, S. & Kanzaki, R. (2018). Descending neurons from the lateral accessory lobe and
1109 posterior slope in the brain of the silkworm *Bombyx mori*. *Scientific Reports* 8, 9663.
- 1110

- 1111 Neville, V., King, J., Gilchrist, I. D., Dayan, P., Paul, E. S., & Mendl, M. (2020). Reward and punisher
1112 experience alter rodent decision-making in a judgement bias task. *Scientific Reports* 10:11839.
1113
- 1114 Neville, V., Dayan, P., Gilchrist, I. D., Paul, E. S., & Mendl, M. (2021a). Dissecting the links between
1115 reward and loss, decision-making, and self-reported affect using a computational approach. *PLOS*
1116 *Computational Biology* 17(1): e1008555.
1117
- 1118 Neville, V., Dayan, P., Gilchrist, I. D., Paul, E. S., & Mendl, M. (2021b). Using Primary Reinforcement
1119 to Enhance Translatability of a Human Affect and Decision-Making Judgment Bias Task. *Journal of*
1120 *Cognitive Neuroscience*, 33(12):2523-2535.
1121
- 1122 New, J. G. (2002). Multimodal integration in the feeding behaviors of predatory teleost fishes. *Brain,*
1123 *behavior and evolution*, 59(4), 177-189.
1124
- 1125 Nordgreen, J., Bjørge, M. H., Janczak, A. M., Poppe, T., Koppang, E. O., Ranheim, B., & Horsberg, T.
1126 E. (2013). The effect of morphine on changes in behaviour and physiology in intraperitoneally
1127 vaccinated Atlantic salmon (*Salmo salar*). *Applied Animal Behaviour Science*, 145(3-4), 129-137.
1128
- 1129 Nordquist, R. E., Heerkens, J. L., Rodenburg, T. B., Boks, S., Ellen, E. D., & van der Staay, F. J.
1130 (2011). Laying hens selected for low mortality: behaviour in tests of fearfulness, anxiety and cognition.
1131 *Applied Animal Behaviour Science*, 131(3-4), 110-122.
1132
- 1133 Norscia, I., Collarini, E. & Cordoni, G. (2021) Anxiety behavior in pigs decreases through affiliation
1134 and may anticipate threat. *Frontiers Veterinary Sciences* 8:630164
1135
- 1136 Obara, Y., & Tamazawa, S. (1982). A behavioural gynandromorph of *Bombyx mori*. *Royal*
1137 *Entomological Society*, 7(4): 443-448.
1138
- 1139 Öhman, A. (2008). Fear and anxiety: Overlaps and dissociations. In M. Lewis, J. M. Haviland-Jones,
1140 & L. F. Barrett (Eds.), *Handbook of emotions* (pp. 709–728). The Guilford Press.
1141
- 1142 Okada, S., Hirano, N., Abe, T., & Nagayama, T. (2021). Aversive operant conditioning alters the
1143 phototactic orientation of the marbled crayfish. *Journal of Experimental Biology*, 224(6), jeb242180.
1144
- 1145 Oliveira, T. A., Idalencio, R., Kalichak, F., dos Santos Rosa, J. G., Koakoski, G., de Abreu, M. S., ... &
1146 Barcellos, L. J. G. (2017). Stress responses to conspecific visual cues of predation risk in zebrafish.
1147 *PeerJ*, 5, e3739.
1148
- 1149 Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P.
1150 (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National*
1151 *Academy of Sciences*, 113(26), 7255-7260.
1152
- 1153 Open Science Collaboration (2015). Estimating the reproducibility of psychological science. *Science*,
1154 349(6251), aac4716.
1155
- 1156 Ostwald, M. M., Shaffer, Z., Pratt, S. C., & Fewell, J. H. (2019). Multimodal cues facilitate nest
1157 recognition in carpenter bee aggregations. *Animal behaviour*, 155, 45-51.
1158
- 1159 Padrell, M., Llorente, M., & Amici, F. (2021). Invasive Research on Non-Human Primates—Time to
1160 Turn the Page. *Animals*, 11(10), 2999.
1161
- 1162 Paspatis, M., & Boujard, T. (1996). A comparative study of automatic feeding and self-feeding in
1163 juvenile Atlantic salmon (*Salmo salar*) fed diets of different energy levels. *Aquaculture*, 145(1-4), 245-
1164 257.
1165
- 1166 Paul, E. S., Harding, E. J., & Mendl, M. (2005). Measuring emotional processes in animals: the utility
1167 of a cognitive approach. *Neuroscience & Biobehavioral Reviews*, 29(3), 469-491.
1168
- 1169 Pearce, J. M., & Bouton, M. E. (2001). Theories of associative learning in animals. *Annual review of*
1170 *psychology*, 52(1), 111-139.

- 1171
1172 Pérez Fraga, P., Gerencsér, L., Lovas, M., Újváry, D., & Andics, A. (2021). Who turns to the human?
1173 Companion pigs' and dogs' behaviour in the unsolvable task paradigm. *Animal cognition*, 24(1), 33-
1174 40.
1175
1176 Pérez-Manrique, A., & Gomila, A. (2022). Emotional contagion in nonhuman animals: A review. *Wiley*
1177 *Interdisciplinary Reviews: Cognitive Science*, 13(1), e1560.
1178
1179 Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind?. *Behavioral and*
1180 *brain sciences*, 1(4), 515-526.
1181
1182 Proctor, H. (2012). Animal sentience: where are we and where are we heading?. *Animals*, 2(4), 628-
1183 639.
1184
1185 Puri, S., & Faulkes, Z. (2010). Do decapod crustaceans have nociceptors for extreme pH? *PLoS One*,
1186 5(4), e10244.
1187
1188 Raine NE, Chittka L. No trade-off between learning speed and associative flexibility in bumblebees: a
1189 reversal learning test with multiple colonies. *PLoS One*. 2012;7(9):e45096.
1190
1191 Reaka, M. L. (1980). On learning and living in holes by mantis shrimp. *Animal Behaviour*, 28(1), 111-
1192 115.
1193
1194 Reilly, S. C., Quinn, J. P., Cossins, A. R., & Sneddon, L. U. (2008). Behavioural analysis of a
1195 nociceptive event in fish: comparisons between three species demonstrate specific responses.
1196 *Applied Animal Behaviour Science*, 114(1-2), 248-259.
1197
1198 Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. B. (2013). Indicators of positive and negative
1199 emotions and emotional contagion in pigs. *Physiology & behavior*, 109, 42-50.
1200
1201 Rethink Priorities (2020). *Invertebrate Sentience Table*. Available online at:
1202 <https://rethinkpriorities.org/invertebrate-sentience-table> (accessed on October 20, 2022).
1203
1204 Rodrigues, D., Goodner, B.W. & Weiss, M.R. (2010). Reversal Learning and Risk-Averse Foraging
1205 Behavior in the Monarch Butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae). *Ethology*, 116: 270-
1206 280.
1207
1208 Sandøe, P., & Jensen, K. K. (2012). The idea of animal welfare—developments and tensions. In
1209 *Veterinary & Animal Ethics: Proceedings of the First International Conference on Veterinary and*
1210 *Animal Ethics, September 2011*(pp. 19-31). Oxford, UK: Blackwell Publishing Ltd.
1211
1212 Schacter, D. L., Addis, D. R., Hassabis, D., Martin, V. C., Spreng, R. N., & Szpunar, K. K. (2012). The
1213 future of memory: remembering, imagining, and the brain. *Neuron*, 76(4), 677-694.
1214
1215 Schnell, A., & Vallortigara, G. (2019). 'Mind' is an ill-defined concept: Considerations for future
1216 cephalopod research. *Animal Sentience*, 4(26), 16.
1217
1218 Schnell, A. K., Amodio, P., Boeckle, M., & Clayton, N. S. (2021). How intelligent is a cephalopod?
1219 Lessons from comparative cognition. *Biological Reviews*, 96(1), 162-178.
1220
1221 Sekhon, K. K., Fashler, S. R., Versloot, J., Lee, S., & Craig, K. D. (2017). Children's behavioral pain
1222 cues: Implicit automaticity and control dimensions in observational measures. *Pain Research and*
1223 *Management*, 2017.
1224
1225 Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends*
1226 *in cognitive sciences*, 14(11), 477-481.
1227
1228 Singh, P. M., Johnson, C. B., Gartrell, B., Mitchinson, S., Jacob, A., & Chambers, P. (2017). Analgesic
1229 effects of morphine and butorphanol in broiler chickens. *Veterinary anaesthesia and analgesia*, 44(3),
1230 538-545.

- 1231
1232 Siviter, H., Koricheva, J., Brown, M. J., & Leadbeater, E. (2018). Quantifying the impact of pesticides
1233 on learning and memory in bees. *Journal of Applied Ecology*, 55(6), 2812-2821.
1234
1235 Sneddon, L. U., Huntingford, F. A., Taylor, A. C., & Clare, A. S. (2003). Female sex pheromone-
1236 mediated effects on behavior and consequences of male competition in the shore crab (*Carcinus*
1237 *maenas*). *Journal of Chemical Ecology*, 29(1), 55-70.
1238
1239 Sneddon, L. U., Elwood, R. W., Adamo, S. A., & Leach, M. C. (2014). Defining and assessing animal
1240 pain. *Animal behaviour*, 97, 201-212.
1241
1242 Snijders, L., Thierij, N. M., Appleby, R., St. Clair, C. C., & Tobajas, J. (2021). Conditioned taste
1243 aversion as a tool for mitigating human-wildlife conflicts. *Frontiers in Conservation Science*, 2,
1244 744704.
1245
1246 Sovrano, V. A., Baratti, G., & Potrich, D. (2018). A detour task in four species of fishes. *Frontiers in*
1247 *Psychology*, 9, 2341.
1248
1249 Stabell, O. B., Faeravaag, A. C., & Tuvikene, A. (2010). Challenging fear: chemical alarm signals are
1250 not causing morphology changes in crucian carp (*Carassius carassius*). *Environmental biology of*
1251 *fishes*, 89(2), 151-160.
1252
1253 Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: a meta-analysis and review of risk
1254 assessment. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2627-2634.
1255
1256 Statham, P., Hannuna, S., Jones, S., Campbell, N., Robert Colborne, G., Browne, W.J., Paul, E.S.
1257 and Mendl, M., (2020). Quantifying defence cascade responses as indicators of pig affect and welfare
1258 using computer vision methods. *Scientific reports*, 10(1), 1-13.
1259
1260 Su, X., Sun, Y., Liu, D., Wang, F., Liu, J., & Zhu, B. (2019). Agonistic behaviour and energy
1261 metabolism of bold and shy swimming crabs *Portunus trituberculatus*. *Journal of Experimental*
1262 *Biology*, 222(3), jeb188706.
1263
1264 Su, X., Zhu, B., & Wang, F. (2022). Feeding strategy changes boldness and agonistic behaviour in the
1265 swimming crab (*Portunus trituberculatus*). *Aquaculture Research*, 53(2), 419-430.
1266
1267 Sutherland, M. A., Bryer, P. J., Krebs, N., & McGlone, J. J. (2008). Tail docking in pigs: acute
1268 physiological and behavioural responses. *Animal*, 2(2), 292-297.
1269
1270 Sutherland, M. A., Davis, B. L., & McGlone, J. J. (2011). The effect of local or general anesthesia on
1271 the physiology and behavior of tail docked pigs. *Animal*, 5(8), 1237-1246
1272
1273 Tan, K., Hu, Z., Chen, W., Wang, Z., Wang, Y., & Nieh, J. C. (2013). Fearful foragers: honey bees
1274 tune colony and individual foraging to multi-predator presence and food quality. *PLoS One*, 8(9),
1275 e75841.
1276
1277 Takahashi, K. (2022). Changes in the anxiety-like and fearful behavior of shrimp following daily
1278 threatening experiences. *Animal cognition*, 25(2), 319-327.
1279
1280 Takahashi, T., Hasegawa, T., Egi, Y., & Sakamoto, K. (2021). Silkworm larvae (*Bombyx mori*) can
1281 learn cues associated with finding food. *European Journal of Biological Research*, 11(4), 519-523.
1282
1283 Takeshita, F., Murai, M., Matsumasa, M., & Henmi, Y. (2018). Multimodal signaling in fiddler crab:
1284 waving to attract mates is condition-dependent but other sexual signals are not. *Behavioral Ecology*
1285 *and Sociobiology*, 72(9), 1-10.
1286
1287 Taylor, J., Vinatea, L., Ozorio, R., Schuweitzer, R., & Andreatta, E. R. (2004). Minimizing the effects of
1288 stress during eyestalk ablation of *Litopenaeus vannamei* females with topical anesthetic and a
1289 coagulating agent. *Aquaculture*, 233(1-4), 173-179.
1290

- 1291 Tierney, A. J., & Andrews, K. (2013). Spatial behavior in male and female crayfish (*Orconectes*
1292 *rusticus*): learning strategies and memory duration. *Animal cognition*, 16(1), 23-34.
1293
- 1294 Tierney, A. J., Baker, A., Forward, J., Slight, C., & Yilma, H. (2019). Response and place learning in
1295 crayfish spatial behavior. *Learning & Behavior*, 47(1), 80-90.
1296
- 1297 Tulving, E. (1983). *Elements of episodic memory*. New York: Oxford University Press.
1298
- 1299 Uglem, I., Kristiansen, T. S., Mejdell, C. M., Basic, D., & Mortensen, S. (2020). Evaluation of
1300 large-scale marking methods in farmed salmonids for tracing purposes: Impact on fish welfare.
1301 *Reviews in Aquaculture*, 12(2), 600-625.
1302
- 1303 Vaz-Serrano, J., Ruiz-Gomez, M. D. L., GjØen, H. M., Skov, P. V., Huntingford, F. A., Øverli, Ø., &
1304 Höglund, E. (2011). Consistent boldness behaviour in early emerging fry of domesticated Atlantic
1305 salmon (*Salmo salar*): decoupling of behavioural and physiological traits of the proactive stress coping
1306 style. *Physiology & behavior*, 103(3-4), 359-364.
1307
- 1308 Ventura, D. F., & Mattel, R. H. (1977). Visual discrimination in the freshwater shrimp (*Macrobrachium*
1309 *acanthurus*). *Behavioral Biology*, 20(1), 116-121.
1310
- 1311 Verhaal, J., & Luksch, H. (2016). Multimodal integration in the chicken. *Journal of Experimental*
1312 *Biology*, 219(1), 90-95.
1313
- 1314 Višak, T. (2017). Cross-species comparisons of welfare. In *Ethical and Political Approaches to*
1315 *Nonhuman Animal Issues*(pp. 347-363). Palgrave Macmillan, Cham.
1316
- 1317 Walters, E., Illich, P., Weeks, J., & Lewin, M. (2001). Defensive responses of larval *Manduca sexta*
1318 and their sensitization by noxious stimuli in the laboratory and field. *Journal of Experimental Biology*,
1319 204(3), 457-469.
1320
- 1321 Wang, M. Y., & Chittka, L. (2011). Cross-modal learning between visual and vibration signals in
1322 zebrafish *Danio rerio*. *i-Perception*, 2(8), 847-847.
1323
- 1324 Wascher, C. A., Allen, K., & Szimpl, G. (2021). Learning and motor inhibitory control in crows and
1325 domestic chickens. *Royal Society open science*, 8(10), 210504.
1326
- 1327 Webster, M.M., Rutz, C. (2020) How STRANGE are your study animals? *Nature*. 582(7812):337-340.
1328
- 1329 Wilson, C. H., Nancollas, S. J., Rivers, M. L., Spicer, J. I., & McGaw, I. J. (2021). Effects of handling
1330 during experimental procedures on stress indices in the green shore crab, *Carcinus maenas* (L.).
1331 *Marine and Freshwater Behaviour and Physiology*, 54(2), 65-86.
1332
- 1333 Wood, T. C., & Moore, P. A. (2020). Big and bad: how relative predator size and dietary information
1334 influence rusty crayfish (*Faxonius rusticus*) behavior and resource-use decisions. *Canadian Journal of*
1335 *Zoology*, 98(1), 62-72.
1336
- 1337 Woodruff, M. L. (2017). Consciousness in teleosts: There is something it feels like to be a fish. *Animal*
1338 *Sentience*, 2(13), 1
1339
- 1340 Wright, D. E., & Eastcott, A. (1982). Operant conditioning of feeding behaviour and patterns of feeding
1341 in thick lipped mullet, *Crenimugil labrosus* (Risso) and common carp, *Cyprinus carpio* (L.). *Journal of*
1342 *Fish Biology*, 20(6), 625-634.
1343
- 1344 Wright, W.F., & Bower, G. H. (1992). Mood effects on subjective probability assessment.
1345 *Organizational behavior and human decision processes*, 52(2), 276-291.
1346
- 1347 Yamada, M., Ohashi, H., Hosoda, K., Kurabayashi, D., & Shigaki, S. (2021). Multisensory-motor
1348 integration in olfactory navigation of silkworm, *Bombyx mori*, using virtual reality system. *eLife*,
1349 10:e72001.
1350

- 1351 Yarali, A., Nehrkorn, J., Tanimoto, H., & Herz, A. V. (2012). Event timing in associative learning: from
1352 biochemical reaction dynamics to behavioural observations. *PloS one*, 7(3), e32885.
1353
1354 Zeltner, E., Klein, T., & Huber-Eicher, B. (2000). Is there social transmission of feather pecking in
1355 groups of laying hen chicks?. *Animal Behaviour*, 60(2), 211-216.
1356
1357 Zhao, D., & Feng, P. (2015). Temperature increase impacts personality traits in aquatic non-native
1358 species: implications for biological invasion under climate change. *Current Zoology*, 61(6), 966-971.
1359
1360