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What can inactivity (in its various forms) reveal about affective states in non-human animals? A review

ESTEBAN , ARRIBAS REYES

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Corresponding Author: Dr. Carole Fureix, PhD

Corresponding Author's Institution: University of Bristol

First Author: Carole Fureix, PhD

Order of Authors: Carole Fureix, PhD; Rebecca K Meagher, PhD

Abstract: Captive / domestic animals are often described as inactive, with the implicit or explicit implication that this high level of inactivity is a welfare problem. Conversely, not being inactive enough may also indicate or cause poor welfare. In humans, too much inactivity can certainly be associated with either negative or positive affective states. In non-human animals, however, the affective states associated with elevated or suppressed levels of inactivity are still not well understood.

Part of the complexity is due to the fact that there are many different forms of inactivity, each likely associated with very different affective states. This paper has two aims. One is to identify specific forms of inactivity that can be used as indicators of specific affective states in animals. The other is to identify issues that need to be resolved before we could validly use the remaining, not yet validated forms of inactivity as indicators of affective state.

We briefly discuss how inactivity is defined and assessed in the literature, and then how inactivity in its various forms relates to affective (either negative or positive) states in animals, basing our reasoning on linguistic reports of affective states collected from humans displaying inactivity phenotypically similar to that displayed by animals in similar situations, and, when possible, on pharmacological validation. Specific forms of inactivity expressed in response to perceived threats (freezing, tonic immobility, and hiding) appear to be, to date, the best-validated indicators of specific affective states in animals. We also identify a number of specific forms of inactivity likely to reflect either negative (associated with ill-health, boredom-like, and depression-like conditions), or positive states (e.g. 'sun-basking', post-consummatory inactivity), although further research is warranted before we could use those forms as indicators of the affective states. We further discuss the relationship between increased inactivity and affective states by presenting misleading situations likely to yield wrong conclusions. We conclude that more attention should be paid to inactivity in animal welfare studies: specific forms of inactivity identified in this paper are, or have the potential to be, useful indicators of affective (welfare) states in animals.

What can inactivity (in its various forms) reveal about affective states in non-human animals? A review

Carole Fureix, Rebecca K. Meagher

Highlights

Affective states linked with altered inactivity are poorly understood in animals.

Different forms of inactivity are likely to relate to different affective states.

Some specific forms (e.g. freezing) reliably indicate negative affective states.

Other specific forms are *likely to be* linked with either negative or positive states.

We propose further research directions to further validate those forms of inactivity.

1 **What can inactivity (in its various forms) reveal about affective states in non-human**
2 **animals? A review**

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4 Carole Fureix ^{a*}, Rebecca K. Meagher ^b

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6 ^a University of Bristol, School of Veterinary Sciences, Langford House, Langford, Bristol
7 BS40 5DU, United Kingdom

8 ^b University of British Columbia, Faculty of Land and Food System, 2357 Main Mall,
9 Vancouver, BC V6T 1Z4, Canada

10

11

12 * Corresponding author: carole.fureix@bristol.ac.uk; Tel.: +44 (0)117 331 9221; Fax: +44-
13 0117-928-9582. University of Bristol, School of Veterinary Sciences, Langford House,
14 Langford, Bristol BS40 5DU, UK

15 **Abstract**

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17 implication that this high level of inactivity is a welfare problem. Conversely, not being
18 inactive enough may also indicate or cause poor welfare. In humans, too much inactivity can
19 certainly be associated with either negative or positive affective states. In non-human
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36 consummatory inactivity), although further research is warranted before we could use those
37 forms as indicators of the affective states. We further discuss the relationship between
38 increased inactivity and affective states by presenting misleading situations likely to yield
39 wrong conclusions. We conclude that more attention should be paid to inactivity in animal

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41 to be, useful indicators of affective (welfare) states in animals.

42

43 Key-words: inactivity; affective states; indicator; validation; animal welfare; fear

44 **1. Introduction**

45 Captive or domestic animals are often described as inactive, with the implicit (*e.g.*
46 Broom, 1988), or explicit implication that this high level of inactivity is a welfare problem
47 (*e.g.* Zanella et al., 1996; McPhee and Carlstead, 2010). Conversely, not being inactive
48 *enough*, for instance when external demands require increased efforts to cope with challenges
49 and when severely sleep deprived, may also indicate or cause poor welfare; it can have
50 dramatic adverse consequences for organisms (*e.g.* Ferrara and De Gennaro, 2001; Maslach
51 et al., 2001). However, the affective states -- our main focus with regards to welfare¹ --
52 associated with these elevated or suppressed levels of inactivity are still not well understood
53 in non-human animals (henceforth ‘animals’). This is in part because inactivity has rarely
54 been the focus of behavioural studies and is often considered simply a default state rather
55 than a true ‘behaviour’ (see *e.g.* Lima et al., 2005; Levitis et al., 2009).

56 In humans, too much inactivity can be associated with negative affective states (*e.g.*
57 psychological distress, Muhsen et al., 2010). In animals, too, inactivity is elevated (and
58 activity decreased) in a variety of situations where welfare is believed to be poor. In an
59 extreme example, monkeys separated from their mothers after birth and raised alone in bare
60 wire cages ‘sit in their home cages and stare fixedly into space’ (Harlow and Harlow, 1962).
61 Juveniles raised in total isolation until 8 months of age needed as long as 12 to 27 weeks to
62 begin to move at all, when placed with social companions in a room designed to trigger play
63 (Harlow and Harlow, 1962; see Konrad and Bagshaw, 1970 for similar results in cats). Male
64 rats exposed to social defeat become more inactive and less exploratory in novel
65 environments than non-defeated controls (Meerlo et al., 1996a; Meerlo et al., 1996b), while
66 buffalo cows housed in restrictive, high stocking density conditions spend more time in

¹ Defining animal welfare is a complex issue, on which not everyone agrees (see *e.g.* Fraser, 2008). Measures related to affect have however often been raised as relevant measures for assessing animal welfare; we, following *e.g.* Duncan, 2005, are principally concerned about this aspect of animal welfare.

67 inactive ‘idling’ than their counterparts with free access to a large outdoor yard with wallows
68 and grazing opportunities (Tripaldi et al., 2004).

69 However, inactivity is also elevated in a variety of situations where welfare is self-
70 reported (in humans, *e.g.* when receiving a gentle massage, Goats, 1994), or believed, to be
71 good. Animals are often inactive when in familiar, safe environments where all immediate
72 needs are met (*e.g.* Cockram, 2004; Wells, 2005; Nowak, 2006). Meanwhile, frustration of
73 motivations to perform specific activities (deprivation: cf. Dawkins, 1988) tends to increase
74 locomotor activity and to induce stereotypic behaviour, escape attempts and other ‘restless’
75 behaviour, thus likely reducing time spent inactive (*e.g.* migratory birds when caged:
76 Mewaldt and Rose, 1960; laying hens unable to nest: Duncan, 1970; mink blocked from
77 swimming water: Vinke et al., 2005; feed-restricted calves: Vieira et al., 2008, mink: Bildsoe
78 et al., 1991; Hansen and Moller, 2008, horses: Benhajali et al., 2008 and rats: Prescott, 1970).

79 As illustrated in the examples above, the relationship between inactivity and welfare states
80 is far from straightforward. Part of this complexity is due to the fact that inactivity is not a
81 homogeneous category: there are many different forms, expressed in different contexts, and
82 each likely associated with very different affective states. This paper therefore has two aims.
83 One is to identify specific forms of inactivity that can be used as indicators of specific
84 affective states in animals. The second is, for those specific forms of inactivity that are
85 currently not validated as indicators, to identify issues that need to be resolved before we
86 could validly use them as indicators of affective state. It is, however, not our goal here to
87 provide an exhaustive list of specific examples of inactivity being associated with affective
88 states. Instead, we intend to illustrate a rationale and to discuss further research suggestions to
89 achieve a better understanding of the relationship between inactivity and affective states.
90 Neither is our goal to argue that inactivity should be considered as the sole and/or ‘gold
91 standard’ indicator of affective states in animals, but rather to highlight the potential it has,

92 when considered in its specific forms together with contextual information, to help infer
93 animals' affective states. This would be valuable in a wide range of studies, such as those
94 assessing the impact of housing, management, and other procedures on affective states, and to
95 provide practical recommendations for eliciting positive affective states in domestic and
96 captive animals.

97 In animals, linguistic self-reports on specific affective states, *i.e.* the 'gold standard'
98 method to capture conscious affective experiences, are obviously not attainable (discussed in
99 *e.g.* Mendl et al., 2010). Behaviours are thus the only attainable, albeit indirect, measure of
100 putative affective states associated with a given situation. We argue that a partial solution to
101 this problem could be to rely on our own species' experiences (providing face validity and,
102 for some of the states, cf. 3.2.2., etiological validity, *e.g.* Belzung and Lemoine, 2011).
103 Indeed, acknowledging that we cannot be sure what an inactive dog's, rat's or any other
104 animal's affective experiences are, we can still make reasonable assumptions if animals'
105 behavioural patterns in avoided (hence putatively perceived as aversive) situations are similar
106 to those reported by humans feeling *e.g.* fearful or depressed in similarly aversive situations
107 (*e.g.* Mendl et al., 2010). For instance, both a rat exposed to a cat (predator) (Dielenberg and
108 McGregor, 1999), and someone frightened by a stranger entering his/her home late at night
109 (Blanchard et al., 2001), might stay still in a location where s/he is protected behind
110 something. We would argue that the hiding rat is in such a case likely to *feel afraid* of the
111 perceived threat just as the motionless hiding person does. Following the same rationale,
112 animals' behavioural patterns that are expressed in preferred or positive situations and are
113 similar to those exhibited by humans in similar situations where they report feeling
114 positively-valenced states, are likely to reflect positive affective states. For instance, lying in
115 the sun, which does have a hedonic component in humans (*e.g.* Dhaenen, 1996), is likely to
116 also be pleasurable in a diurnal rodent such as a striped mouse that chooses to lie down in the

117 sun when risks of predation are low (Schradin et al., 2007). Beyond analogies with humans
118 self-reporting their feelings, additional evidence to support inferences regarding the affective
119 valence of inactive animals' states can also come from pharmacological corroboration, *e.g.*
120 testing that a specific form of inactivity is reduced by anxiolytics and/or increased by
121 anxiogenics if it is believed to reflect fear. This provides evidence of construct validity and,
122 in cases where a range of treatments was tested, discriminant validity (see *e.g.* Cronbach and
123 Meehl, 1955). In this review, we briefly discuss how inactivity is defined and assessed in the
124 literature, and then discuss how it relates to affective (welfare) states. In humans, affective
125 states can be categorized in terms of two fundamental underlying dimensions: the valence –
126 *i.e.* whether the experience is perceived as negative or positive, punishing or rewarding,
127 unpleasant or pleasant– and the reported activation – *i.e.* high or low arousal (*e.g.* Russell and
128 Barrett, 1999). Theoretical and empirical studies (reviewed in Mendl et al., 2010) suggest that
129 negative high-arousal affective states (*e.g.* feeling fearful) are principally associated with
130 perceiving and reacting to threats or dangers, while negative low-arousal states (*e.g.* feeling
131 sad) are likely to be associated with experiences of loss or lack of reward, and may promote
132 low activity and energy conservation when resources are lacking. Positive high-arousal
133 affective states (*e.g.* excitement) are likely to be associated with appetitive motivational
134 states, and function to facilitate seeking and obtaining rewards; while positive low-arousal
135 affective states (*e.g.* calmness) are instead expected to be associated with low levels of
136 experienced threat, perhaps facilitating the expression of maintenance activities. In this paper,
137 we rely on this framework in order to categorize affective states, and those specific forms of
138 inactivity associated with such states. This classification of specific forms of inactivity
139 displayed by animals will be supported by linguistic self-reports collected in humans
140 displaying phenotypically similar inactivity in similar situations, and, when possible, by
141 pharmacological validation.

142

143 **2. How is inactivity defined and measured?**

144 Although inactivity may seem fairly straightforward to define, there is some variation in
145 exactly what the term encompasses. In some cases, the hypotheses under test relate to specific
146 forms of inactivity (*e.g.* in rats: sleeping, or lying non-alert with both eyes closed: Abou-
147 Ismail et al., 2008; freezing, a complete absence of visible movement except breathing:
148 Fanselow, 1982), and so only those forms are assessed. However, in other cases, its
149 operational definition seems to be a by-product of the methods used to assess activity. This
150 usually occurs when inactivity is not the main focus of the study but is measured simply as a
151 part of the time budget or to control for ‘activity’ levels because they influence the variable of
152 interest. When it is studied in free-living animals, activity is usually assessed using radio-
153 tracking or similar technology, and so any time not in locomotion is called inactivity. Some
154 studies of captive animals similarly equate ‘activity’ with locomotion. Laboratory animal
155 research, for example, often infers activity levels from proxy measures such as the number of
156 entries into closed arms (and therefore locomotion) in the elevated plus maze, a test of
157 anxiety (*e.g.* Louvart et al., 2005), while some agricultural studies use pedometers (*e.g.*
158 O’Callaghan et al., 2003). Therefore, inactivity in those studies would include time spent
159 stationary but performing purposeful movements such as grooming. However, in applied
160 ethology research using video or live observation, any movement is typically considered
161 activity, even if the animal remains in one place; for example, kicking (*e.g.* Rushen et al.,
162 2001) and eating (*e.g.* Rochlitz et al., 1998; Burrell and Altman, 2006) are not categorized as
163 inactive. Thus, the most common definition of inactivity is being relatively motionless, and
164 although it is rarely stated explicitly, this means no movement with an apparent function (*e.g.*
165 grazing or chewing a bite of food) but would include other slight movements (*e.g.* turning the
166 head or shifting positions). Finally, research on anticipatory behaviour sometimes discusses

167 hyperactivity or decreases in activity during anticipation, but actually measures the number of
168 behavioural transitions rather than total amount of time spent moving or stationary (*e.g.* van
169 den Bos et al., 2003). Studies using any of these definitions of inactivity will be discussed
170 here.

171

172 **3. Increased inactivity / decreased activity as a sign of poor affective states**

173 Increased inactivity likely to be associated with negative affective states will be
174 considered here, distinguishing specific forms of inactivity expressed in response to a
175 perceived threat (likely to be associated with negative high-arousal affective states, Mendl et
176 al., 2010, cf. Introduction) from those expressed in situations where threat levels but also
177 chances of getting rewards are low (likely to be associated with negative low-arousal
178 affective states).

179

180 *3.1. Increased inactivity / decreased activity displayed in response to a perceived threat*

181 Inactivity that may occur in response to a perceived (frightening) threat stimulus will be
182 presented here, targeting more specifically the freezing, tonic immobility and hiding
183 responses.

184

185 **Freezing** (sometimes also termed *attentive immobility*) is a common response in the face
186 of an immediate (perceived) threat in various species, where an individual becomes abruptly
187 motionless, monitoring a perceived source of danger (reviewed by Boissy, 1995). A
188 ‘freezing-like’ state, characterised by increased immobility and rigidity (quantified using a
189 force platform) and a reduced heart rate (also termed ‘fear bradycardia’), has been described
190 in humans. This state has been observed in healthy people viewing pictures of mutilation
191 (that they self-rated as negative in valence and high in arousal) compared to neutral or

192 positively rated pictures (Azevedo et al., 2005; Facchinetti et al., 2006), as well as in patients
193 diagnosed with panic disorders when seeing either pictures of mutilation or images that were
194 anxiogenic due to their pathologies (*e.g.* crowded areas for agoraphobic patients), compared
195 to neutral pictures (Lopes et al., 2009).

196 In animals, freezing is used to quantify fearfulness in many behavioural tests (see *e.g.*
197 Bouton and Bolles, 1980; Forkman et al., 2007). It has been particularly well-described in
198 rodents, on which we will focus here, and can be operationally defined as ‘the absence of all
199 visible movement of the body and vibrissae, except for movements necessitated by
200 respiration’ (Fanselow, 1982). The description can also include (species-specific) postural
201 elements, such as a ‘characteristic immobile, crouching posture’ in rats, and autonomic
202 changes, *i.e.* a decreased heart rate (similarly to the ‘fear bradychardia’ recorded in freezing
203 humans) and an increased respiratory rate (Fanselow, 1984). Freezing can be induced by
204 exposing rats to a predator odour (*e.g.* Wallace and Rosen, 2000; Knox et al., 2012), as well
205 as to conditioned stimuli or contexts paired with aversive experiences (electric shocks: *e.g.*
206 Fanselow, 1984; Richmond et al., 1998; Luyten et al., 2011; carbon dioxide inducing
207 dyspnoeic suffocation: Mongeluzi et al., 2003). The more intense the aversive stimuli are, the
208 longer the rats remain frozen (Fanselow and Helmstetter, 1988; Wallace and Rosen, 2000;
209 Mongeluzi et al., 2003; Santos et al., 2005, but see Leaton and Borszcz, 1985 for non-
210 monotonic effects). Freezing is ‘not a simple suppression of activity’ (Fanselow, 1984) but a
211 highly aroused state (Bracha, 2004): rats’ percentage of time spent freezing when exposed to
212 a conditioned stimulus previously paired with electric shock was positively correlated with
213 the amplitude of their acoustic startle response in the presence of that conditioned stimulus
214 (Leaton and Borszcz, 1985). Interestingly, neither food deprivation (an aversive experience
215 but not assumed to induce ‘fear’, Maren and Fanselow, 1998; Heiderstadt et al., 2000), nor
216 exposure to smells unrelated to predation (*e.g.* butyric acid, banana and pear odours, Wallace

217 and Rosen, 2000; Knox et al., 2012) induce freezing responses. Moreover, in rats where the
218 risk of infanticide by unrelated adult males ends around weaning, exposure to a sexually
219 experienced, unrelated male rat induces freezing in young rats only before they reach a
220 natural weaning age (around 26 d), whereas exposure to a cat odour (a predation risk relevant
221 during all life stages) induces the freezing response in rats before and after weaning age
222 (Wiedenmayer and Barr, 2001). Additional evidence that the freezing response is associated
223 with negative valence in rodents comes from pharmacological corroboration: in rats, while
224 freezing in response to a cat exposure was gradually suppressed over repeated daily exposure
225 (Farook et al., 2004), administration of anxiogenic drugs restores the freezing behaviour.
226 Conversely, the administration of anxiolytic drugs (*e.g.* midazolam, diazepam) reduces the
227 duration of rats' place-conditioned freezing response (Fanselow and Helmstetter, 1988;
228 Verleye and Gillardin, 2004; Santos et al., 2005).

229

230 Another specific form of inactivity also displayed in response to a threat in various species
231 is **tonic immobility (TI)** (*e.g.* Gallup et al., 1971b). In humans, 'TI-like' states are
232 characterised by a temporary behavioural state of motor inhibition, associated with tremors,
233 eye closure, increased breathing, and coldness, and have been reported to occur in response to
234 situations involving intense fear and physical restraint such as interpersonal trauma (sexual
235 assault, torture, armed robbery)² (Galliano et al., 1993; Abrams et al., 2009). Although such
236 studies are non-experimental in nature (and therefore results may not be generalised to any
237 human population), TI-like responses appear to be far from uncommon. For example, across
238 several studies reviewed in Galliano et al. (1993), from 12% to 50% of the studied victims of
239 rape/sexual assaults were 'paralyzed' motionless and did not resist their attackers in any way.
240 Displaying TI-like responses during traumatic episodes has also been reported to positively

² Although less studied, intense fear associated with accident-related trauma and the unexpected death of a loved one have also been reported to sometimes induce a TI-like state in humans despite not involving physical restraint.

241 correlate with longer-term psychological impairments such as depression, anxiety and Post-
242 Traumatic Stress Disorder (Abrams et al., 2009; Volchan et al., 2011). In laboratory studies,
243 ‘standing still (paralyzed with fear)’ is one of the defensive strategies subjects predicted they
244 would display in response to threat scenarios involving nearby threat stimuli and
245 inescapability of the threat/situation, such as ‘*Late at night you are alone in an elevator.*
246 *When it stops and the doors open, a rough looking stranger gets in fast to attack you,*
247 *blocking your exit*’ (Blanchard et al., 2001; Shuhama et al., 2008).

248 In animals, TI has been reported in several taxa (see *e.g.* Forkman et al., 2007), and is
249 particularly well-described in birds, where it has been defined as a ‘reversible state of
250 (‘catatonic-like’) profound motor inactivity following brief exposure to physical restraint
251 (*e.g.* 15s), which may last from a few seconds to over several hours’ (*e.g.* Gallup et al.,
252 1971b). It is also characterised by a suppression of vocalisation, as well as TI-specific (not
253 observed in freezing) muscle tremors in the extremities and intermittent eye closures. As for
254 freezing, physiological correlates include bradycardia and increased respiratory rate, as well
255 as a TI-specific (not reported in freezing) decrease in body temperature (*e.g.* Gallup et al.,
256 1971b; Nash et al., 1976). TI is an aroused state: electroencephalographic activity in animals
257 displaying TI has been reported to be often the same as that of waking animals (*e.g.* in
258 rabbits: Klemm, 1966; in opossum *Didelphis virginiana*: Barratt, 1965, review in Gallup,
259 1974; Whishaw et al., 1982). A ‘TI-like’ response has also been described in certain domestic
260 goats, known as ‘fainting’ goats becoming ‘perfectly rigid when suddenly surprised or
261 frightened’ (Lush, 1930). This response is caused by a hereditary genetic disorder (*congenital*
262 *myotonia*, Clark, 1939), although physiological correlates of this state have not been
263 investigated. In birds (chicks unless otherwise specified), a variety of aversive manipulations
264 before TI induction increase the TI duration and/or propensity of the bird to display the TI
265 state, including exposure to electric shocks or to conditioned stimulus signalling shocks

266 (Gallup et al., 1970; Gallup, 1973), rough handling (bird inverted for 30s: laying hens and
267 broilers, Jones, 1992), and exposure to loud noise (Gallup et al., 1970). While freezing in
268 rodents appears to be a risk-assessment behaviour to a (perceived) distant threat (Blanchard et
269 al., 2011), TI happens *following physical restraint*, and has been suggested to be an anti-
270 predation response even after the animal has been captured. Such ‘death-feigning’ might
271 induce the predator to loosen its hold (Gilman et al., 1950; Engel and Schmale, 1972;
272 Sargeant and Eberhardt, 1975; see Thompson et al., 1981 for evidence TI can deter
273 predators). This response seems specific to fear-inducing situations: food-depriving chickens,
274 which is aversive but not likely frightening, does not increase these animals’ TI duration
275 (Gallup and Williamson, 1972). Additional evidence supporting the negative valence and
276 high arousal of the TI response in birds comes from pharmacological validation: in chicks,
277 pre-TI-induction administration of adrenaline (Braud and Ginsburg, 1973) and corticosterone
278 (Jones et al., 1988) increases the TI duration and/or the propensity of birds to display TI,
279 while a pre-TI-induction tranquilizer injection reduces the duration of the TI response (Gallup
280 et al., 1971a).

281

282 Another -- perhaps less species-specific -- form of inactivity that can be displayed in
283 response to a perceived threat is **hiding**. In humans, hiding (protecting oneself behind
284 something) is one of the defensive strategies chosen by subjects in laboratory studies in
285 response to fearful threat scenarios such as ‘*Late at night... you are sleeping alone in your*
286 *bed. You suddenly wake up feeling that you heard a suspicious noise*’. Not surprisingly, the
287 presence of a place of concealment or protection in the scenario promoted the hiding choice;
288 so did distant (rather than close) threat stimuli (Blanchard et al., 2001; Shuhama et al., 2008).

289 In animals, hiding can be defined operationally using location (provided that there are
290 locations suitable for hiding in the environment): hiding animals are ‘remaining stationary

291 and out of sight or camouflaged using any kind of shelter or visual barrier' (Meagher et al.,
292 2013). In rodents, exposure to a predator or to its odour initially induces a hiding response
293 (e.g. rats exposed to a worn cat collar: Dielenberg and McGregor, 1999; mice repeatedly
294 exposed to a rat moving around on top of their cages: Dalm et al., 2009). In laboratory cats,
295 exposure to complex stressors (involving unpredictable mildly aversive procedures) increases
296 time spent awake/alert and attempting to hide, and suppresses active exploratory and play
297 behaviour (Carlstead et al., 1993b). Translocation to novel environments also induces hiding
298 in felids (leopard cats: Carlstead et al., 1993a; quarantined domestic cats: Rochlitz et al.,
299 1998). There is also pharmacological evidence to help infer the negative valence and high
300 arousal of the hiding response: in rats, anxiolytic administration (the benzodiazepine drug
301 midazolam) reverses rats' hiding response to a worn cat collar (Dielenberg and McGregor,
302 1999), and increases the proportion of time spent exploring in open arms in an elevated plus
303 maze, while anxiogenic substances (e.g. caffeine) increase the time spent hiding in the closed
304 arms of the maze (Pellow et al., 1985).

305

306 Freezing, TI and hiding are specific forms of inactivity expressed in response to a
307 (perceived) actual or potential threat, both in humans and in animals. In both, they are
308 reduced by anxiolytics and increased by anxiogenic drugs. Freezing, TI and hiding therefore
309 appear to be valid indicators of a negative, highly aroused affective state, and to date, our best
310 examples that specific forms of inactivity can be used as trustworthy indicators of specific
311 affective states (in this case, 'fear-like' states) in animals.

312

313 3.2. *Increased inactivity / decreased activity likely to be associated with negative*
314 *low-arousal affective states*

315 Increased inactivity expressed in situations where both threat levels and chances of getting
316 rewards are low (likely to be associated with low arousal negative affective states: Mendl et
317 al., 2010, see Introduction) will be discussed here, specifically targeting sickness,
318 depression-like, and boredom-like conditions.

319

320 3.2.1. Inactivity and ill-health

321 Lethargy (*i.e.* a state of decreased mental activity, characterised by sluggishness,
322 drowsiness, inactivity, and reduced alertness, APA, 2013) is a well-established component of
323 sickness behaviour, which is the ‘coordinate set of subjective, behavioural and physiological
324 changes that develop in sick individuals during the course of an infection’ (Dantzer, 2004).
325 ‘Sick individuals are somewhat depressed and lethargic’ and ‘show little interest in their
326 surroundings and stop eating and drinking’ (Dantzer, 2004). Reduced activity here is
327 considered a strategy of energy conservation in order to allow the full development of a fever
328 (which is associated with and plays a critical role in recovery from many pathogenic
329 infections), and so has an eventual benefit. However, this inactivity is very likely linked with
330 negative affective states, as it is ‘very often accompanied by pain’ (Dantzer, 2004), and in
331 humans, a transient depressive state has been reported to occur as an infectious episode
332 develops (Aubert, 1999). Sickness behaviour is common to many mammalian species (Hart,
333 1988; Maes et al., 2012): ‘lethargy’, ‘listlessness and disinterest in social interactions with the
334 environment’, ‘behavioural inhibition’, and ‘reduction of locomotor activity, exploration and
335 grooming’ have also been observed in sick animals. For instance, rats challenged with
336 bacterial and viral mimetics show decreased voluntary running wheel activity and, broadly,
337 less movement in their home cage (Hopwood et al., 2009). The general decrease in
338 behavioural activities in sick animals has been shown to reflect changes in motivational state
339 rather than a simple consequence of weakness: for example, if pups are removed from the

340 nest of lactating mice whose behavioural activity is depressed by LPS injection, the sick
341 mothers interrupt their sickness behaviour to bring the pups back to the nest, then return to
342 inactive recuperative behaviour (Aubert, 1999). As in humans, lethargy in sick animals is
343 likely to be associated with negative affect, such as pain (*e.g.* in dogs: Wiseman et al., 2001).

344 Perhaps more broadly, ill-health in humans (including not only infectious sickness but *e.g.*
345 injury, post-operative conditions, and chronic back disorders) reduces both voluntary (*e.g.*
346 work, recreational) and obligatory (*e.g.* self-care) activities (*e.g.* Tait et al., 1990). It seems to
347 have the same effect in animals: poor health conditions can increase the proportion of time
348 spent awake but lying down (*e.g.* postoperative pain in rabbits: Leach et al., 2009 and horses:
349 Pritchett et al., 2003; ear notching and tagging in piglets: Leslie et al., 2010; lameness in
350 dairy cattle: Chapinal et al., 2010; Calderon and Cook, 2011 and in broilers: Weeks et al.,
351 2000), whereas analgesia reduces time lying down in lame animals (*e.g.* dairy cattle: Schulz
352 et al., 2011; Offinger et al., 2013). Adult zebrafish (*Danio rerio*) injected with acetic acid (a
353 noxious chemical stimulus) display decreased swimming activity (Correia et al., 2011; but
354 see Steenbergen and Bardine, 2014 for an opposite effect on zebrafish larvae water-exposed
355 to acetic acid). High activity of a shoal could thus indicate that its members are healthy, and
356 joining it could be beneficial for fitness (*e.g.* active fish can be quicker to find food patches
357 and more confusing for predators), which might be part of the reason that, although shoaling
358 zebrafish usually prefer to join larger shoals, this preference can be shifted to a smaller shoal
359 if its members are comparatively more active than the fishes in the larger shoal (Pritchard et
360 al., 2001).

361 Poor health conditions associated with negative affective states such as pain, appear to
362 increase inactivity, both in humans and in animals, in each of which they are reduced by
363 analgesic drugs. Such inactivity is therefore likely to be associated with negative affective
364 states. Poor health-induced inactivity is, however, less specifically described (*i.e.* overall

365 increased inactivity / decreased activity) than, for example, those forms of inactivity
366 displayed in response to a perceived threat. The presence of signs of ill-health (*e.g.* fever,
367 injury) and/or knowledge of specific contexts in which inactivity increases (*e.g.* post-surgery)
368 therefore appears crucial to infer the affective state associated with such inactivity.

369

370 3.2.2. Inactivity and depression-like states

371 In humans, clinical depression -- by which we mean ‘major depressive disorder’ or
372 experiencing ‘depressive episodes’, to encompass DSM-V (Diagnostic Manual of Mental
373 Disorders fifth edition, American Psychiatric Association [APA], 2013) and ICD-10
374 (International Statistical Classification of Diseases and Related Health Problems, World
375 Health Organisation [WHO], 1994) terminologies -- is a common mental illness diagnosed by
376 the co-occurrence of several affective, cognitive and behavioural symptoms. These include a
377 ‘depressed (low, sad) mood most of the day, nearly every day, as indicated by either
378 subjective report (*e.g.* feels sad, empty, hopeless) or observation made by others (*e.g.* appears
379 tearful)’ (APA, 2013, P160). A common trigger is chronic stress, such as that arising from
380 aversive life events or chronic pain or illness (Blackburn-Munro and Blackburn-Munro,
381 2001; Siegrist, 2008; Hammen et al., 2009; APA, 2013). Cognitive changes can be associated
382 with depression and may act as mediators in some subjects, being hypothesised to contribute
383 to the onset and/or maintenance of the disease (Beck, 1967; Gotlib and Krasnoperova, 1998).
384 One such change, ‘learned helplessness’, is proposed to occur ‘when highly desired outcomes
385 are believed improbable or highly aversive outcomes are believed probable, and the
386 individual comes to expect that no response in his repertoire will change their likelihood’
387 (Abramson et al., 1978).

388 With respect to inactivity, a low, sad mood may induce increased inactivity even in
389 healthy people. For instance, Rucker and Petty (2004) showed that inducing sadness in

390 consumers in a laboratory setting yields a preference for an advertised product promoting
391 passivity (a vacation resort framed as a place to relax and rest), while inducing anger yields a
392 preference for a product promoting activity (a vacation resort framed as a place to enjoy
393 sports and activity). Accordingly, clinically depressed patients have been reported to be more
394 inactive -- by which we mean here a decrease in a variety of daily activities -- than their non-
395 depressed counterparts. This includes 'not doing fun activities or chores that need to be
396 accomplished' (Knowles, 1981), and reported difficulties initiating or completing social and
397 non-social activities (Baker et al., 1971; Schelde, 1998; APA, 2013). Reduced physical
398 activity (both mild, such as walking and gardening, and more vigorous, such as playing
399 sports) has been associated with clinical depression (Seime and Vickers, 2006; Lindwall et
400 al., 2011), while – cautiously³ - increased exercise has been reported in several reviews or
401 meta-analyses to improve depressed mood and/or anxiety (e.g. Byrne and Byrne, 1993; Dunn
402 et al., 2001; Seime and Vickers, 2006; Davis and Dimidjian, 2012).

403 Could inactive animals, or at least those displaying (certain forms of) inactivity (in certain
404 contexts), be experiencing 'depression-like' states?⁴ Presumably yes: dogs and cats (e.g. Fox,
405 1968, p. 357) and elephants (Mason and Veasey, 2010) have anecdotally been suggested to
406 become highly inactive when deprived of their owners or after the loss of a social companion,
407 as have apes housed long-term in barren environments in laboratories or zoos (e.g. Engel,
408 2002, p174; Brune et al., 2006), and socially deprived monkeys (e.g. Harlow and Harlow,
409 1962; Harlow and Suomi, 1974; Suomi et al., 1975). Because the aetiology corresponds to

³ Due to methodological biases present in one or more of the studies included in the review / meta-analysis, e.g. people are not systematically randomly assigned to treatment groups and/or there are potential confounds or no control groups and/or the amount of physical activity applied as a treatment is based on patients' self-reporting (no verification) and/or conclusions are expanded from normal subjects to clinical samples. These biases, however, are spread across individual studies, and a variety of biological and psychological mechanisms could explain the reported benefit of exercise on mood, cautiously suggesting that this commonly reported effect might be a 'trustable' phenomenon.

⁴ Discussing in detail whether or not non-humans can become *clinically depressed-like* - i.e. show states that share the same or most of the properties of those described in clinically depressed patients -- would go beyond the scope of this paper. However, even if the quality and quantity of current evidence are not yet sufficient to conclude this with certainty, both circumstantial and experimental evidence have led several authors (including us) to hypothesise that depression-like states occur in other animals as well (see e.g. Ferdowsian et al. 2011; Hennessy et al., 2014; Fureix et al., 2015).

410 theories of human depression emphasizing aversive life events and chronic stress as a
411 common trigger, such inactivity is likely to be associated with negative affect.

412 Moreover, the cognitive feature of learned helplessness has also been shown in animals,
413 and is a phenomenon typically accompanied by an overall decrease in activity (see *e.g.*
414 Mineka and Hendersen, 1985). Indeed, although the term learned helplessness referred
415 initially to a deficit in avoidance learning induced by repeated exposure to uncontrollable
416 shock (reviewed by *e.g.* Maier and Seligman, 1976), the meaning of the label has now been
417 expanded; it is sometimes applied to any ‘passive’ behaviour (*i.e.* quiescence or the absence
418 of active responses to stress, such as escape attempts; cf. Oxford English Dictionary, 2005)
419 that appears to result from exposure to uncontrollable stressors (Maier, 1984; see also
420 Wemelsfelder, 1990; Carlstead, 1996). For instance, sheep moved from pasture to
421 inescapable indoor crates (Fordham et al., 1991) and laboratory rodents placed in an
422 inescapable container filled with water (known as the Porsolt Test, reviewed in *e.g.* Deussing,
423 2006), both begin by reacting to the situation with agitation, but end up displaying inactivity
424 and unresponsiveness. According to the above-mentioned expanded definition, this eventual
425 response would reflect learned helplessness. Again, because the aetiology corresponds to
426 cognitive theories of human depression (Beck, 1967; Abramson et al., 1978; Gotlib and
427 Krasnoperova, 1998), this inactivity is believed to be a depression-like behaviour, and
428 therefore associated with a negative affective state. In mice and rats that ‘cease struggling and
429 remain floating motionless in the water, making only movements necessary to keep their head
430 above water’ (Porsolt et al., 1977) in the Porsolt test, additional support comes from the fact
431 that this specific form of inactivity is both amplified by stressors and alleviated by
432 antidepressants (Porsolt et al., 1977; Cryan et al., 2002; Matthews et al., 2005; Deussing,
433 2006; McArthur and Borsini, 2006). It also co-varies with other depression-like symptoms,
434 such as anhedonia (Strekalova et al., 2004), *i.e.* the loss of pleasure, a key feature of human

435 clinical depression (APA, 2013). The hypothesis that the term learned helplessness might also
436 be applicable to captive animals that seem very passive or inactive in their home environment
437 is also supported by findings that animals reared in socially isolated and/or barren cages are
438 more vulnerable to developing learned helplessness in avoidance learning paradigms than
439 those reared in more socially and physically complex, and presumably controllable,
440 environments are (Seligman, 1972; Chourbaji et al., 2005).

441 Finally, Fureix and colleagues (2012, 2015) recently described long-lasting inactive
442 ‘withdrawn’ states in certain riding horses, characterised by bouts of unresponsiveness,
443 remaining motionless with unblinking eyes with an apparently fixed gaze (reminiscent of the
444 reduced responsiveness and reduced interactivity of some depressed human patients) and
445 anhedonia. These states also correlate with stereotypic behaviour (a possible marker of
446 current, but also past exposure to stressors). While the aetiology of this specific form of
447 inactivity is currently unknown, its association with key features of human clinical depression
448 makes it likely to be associated with negative affect.

449 Do these findings demonstrate with certainty that these inactive animals are clinically
450 depressed, in the same way as depressed patients showing decreased variety in their daily
451 activities? The quality and quantity of current evidence are not yet sufficient to conclude this.
452 Moreover, while some forms of inactivity are highly specific (‘floating’ in rodents,
453 ‘withdrawn’ states in horses), others are not (*e.g.* passivity when exposed to inescapable,
454 uncontrollable stressors). However, that inactivity appears in contexts similar to those that
455 trigger the appearance of clinical depression in humans, or co-varies with key symptoms of
456 this pathology (*e.g.* anhedonia) is sufficiently consistent with the hypothesis to make
457 additional research into these topics, including how this inactivity would be modulated by
458 anti-depressant drug treatments, very worthwhile.

459

460 3.2.3. Inactivity and boredom

461 Boredom is a negative affective state induced by monotony or lower-than-optimal levels
462 of stimulation. In addition to self-report, this definitional link to negative affect is supported
463 by evidence of high motivation to avoid the state; for example, boredom-prone people show a
464 preference for activities that are perceived as risky and therefore frightening to most people,
465 but that increase stimulation levels, such as bungee-jumping (Michel et al., 1997). Self-
466 reports, however, are key to identifying boredom and situations that induce it (Harris, 2000).

467 In humans, lethargy is a common symptom (see *e.g.* Inglis, 1983), although this is often
468 seen following a period of sensation-seeking (Taylor and Cohen, 1972; Inglis, 1983; cf.
469 Berlyne, 1960 for an alternative possible time course) and thus in some cases, restlessness
470 may be seen rather than inactivity (reviewed by Kirkden, 2000). Imposed inactivity can also
471 be a cause of boredom (Berlyne, 1960; Heaman and Gupton, 1998). Most theoretical
472 discussion categorizes boredom as a state of under-arousal (*e.g.* Fiske and Maddi, 1961;
473 Stevenson, 1983; Mikulas and Vodanovich, 1993) given its association with low stimulation,
474 although Berlyne (1960) postulated that prolonged monotony can lead to increases in arousal;
475 others have similarly considered boredom simply as a state of ‘non-optimal’ arousal
476 (Eastwood et al., 2012). While there is some evidence from humans that arousal may
477 sometimes be elevated during boredom (*e.g.* EEG data from subjects exposed to sensory
478 deprivation after sleeping as much as possible: Berlyne, 1960), other studies have found
479 decreasing arousal over time when engaged in a boring task (*e.g.* Pattyn et al., 2008). Also
480 supporting the association with under-arousal, and thus supporting its inclusion in this section
481 of our discussion, methods of avoiding boredom are likely to increase arousal: these include
482 consumption of recreational drugs (Samuels and Samuels, 1974), which commonly include
483 stimulants (Boys et al., 2001), and participation in thrill-seeking activities, as previously
484 mentioned.

485 Due to the dependence on self-reported affect for identifying boredom in humans, this
486 state has been subject to little empirical investigation in animals, where self-report is
487 impossible and thus affect cannot be assessed directly. However, captive animals commonly
488 face monotonous environments, often less complex or lower in stimulation than those in
489 which their ancestors evolved (in some cases, even those they experienced themselves early
490 in life). For this reason, theory suggests that they would also find such situations aversive.
491 For example, McFarland (1989) proposed that when captive animals' immediate physical
492 needs are met but they cannot pursue other activities that would occupy their time in the wild
493 such as reproduction or mating, they are left in a state of 'limbo' and are likely to suffer
494 because most species will not have evolved methods of coping with such a situation. Veissier
495 et al. (2009) also argue that since sheep are sensitive to the same features of stimuli that
496 induce boredom in humans, they are potentially capable of experiencing it; the same
497 argument could be applied to many species. Inactivity is generally accepted as a common
498 consequence of housing in relatively barren cages or enclosures and interpreted as a sign of
499 poor welfare (DeMonte and LePape, 1997), which many people attribute to boredom (*e.g.*
500 Stevenson, 1983; Woodgush and Beilharz, 1983). Conversely, increasing activity or
501 behavioural diversity through provision of opportunities to interact with stimuli is assumed to
502 improve welfare (*e.g.* pigs: Woodgush and Beilharz, 1983; chimpanzees: Celli et al., 2003;
503 dogs: Wells, 2004). Sometimes this assumption has been supported by improvements in other
504 welfare indicators (*e.g.* Paquette and Prescott, 1988) or by animals' preference for the
505 enrichment (*e.g.* Rozek et al., 2010).

506 Both the use of the term 'boredom' in animals and its relationship to inactivity still need
507 validation, however. To provide a starting point for this work, Meagher and Mason (2012)
508 proposed an operational definition based on motivation to obtain stimulation, which should
509 be a universal symptom. The validity of this operational definition was supported by the fact

510 that this motivation was elevated in captive mink housed in non-enriched cages, predicted to
511 experience more boredom-like states. Thus, compared to mink housed in a preferred (Dallaire
512 et al., 2012) and more stimulus-rich environment, the mink behaved as bored humans would.
513 This method of assessment relied on measuring activity when given an opportunity to avoid
514 boredom rather than directly assessing inactivity in the hypothesized boredom-inducing
515 situation, because the latter might vary with time and between individuals (as in humans),
516 among other reasons. However, the study also identified a tentative link between the apparent
517 boredom and a specific subtype of inactivity when undisturbed in the home cage (lying down
518 with the eyes open). Future work could use self-administration of stimulants to further
519 validate the concept of boredom in barren-housed animals and its association with inactivity,
520 predicting that very inactive individuals in non-enriched cages would be most likely to self-
521 stimulate. At least until such work has been carried out for a given species, inactivity should
522 be used as an indicator of boredom with extreme caution: although high levels of inactivity in
523 monotonous environments may well be associated with boredom, the alternative response of
524 restlessness would make this indicator prone to false negatives (see also 5.1.), in which an
525 environment that is in fact boring does not increase group-level or even individual-level
526 inactivity levels.

527

528 **4. Increased inactivity / decreased activity as a sign of good affective states**

529 Increased inactivity or decreased activity likely to be associated with positive affective
530 states will now be discussed, again distinguishing inactivity likely to be associated with high
531 and low-arousal positive states.

532

533

534 4.1. *Increased inactivity / decreased activity likely to be associated with positive*
535 *highly-aroused affective states*

536 As stated in the Introduction, positive, highly-aroused affective states are likely to be
537 associated with appetitive motivational states, and function to facilitate seeking and obtaining
538 rewards (Mendl et al., 2010). Being *inactive* in order to *favour* reward *acquisition* sounds
539 intuitively unlikely to happen, and examples are rare even in humans, with perhaps the
540 exception of yogi meditation, which has been self-reported by meditators to be a highly-
541 aroused pleasant state (Cahn and Polich, 2006). Chess players close to winning a game and
542 focused on choosing the best strategy could also perhaps experience a highly-aroused and
543 pleasant motionless state; this is likely one example of what Csikszentmihalyi (1975; 1990)
544 termed a “flow” state. Flow states involve being concentrated on a task that is achievable but
545 sufficiently challenging to require focused attention and skill, and are self-reported as being
546 enjoyable, at least in retrospect (reviewed in Csikszentmihalyi 1990). However, although the
547 absence of evidence is not a proof of absence, one may reasonably doubt that animals
548 practice meditation or play chess. An animal example in this category might be cats
549 ‘stalking’: adults stalking prey (Wise, 1974) and kittens playing (Bateson and Young, 1981)
550 temporarily restrain any movement and stay perfectly motionless. Cats have been considered
551 to become ‘hypoactive’ while anticipating food rewards, displaying reduced behavioural
552 transitions between the offset of a conditioned stimulus and the onset of an unconditioned
553 stimulus in a Pavlovian conditioning paradigm (van den Bos et al., 2003). According to the
554 authors, this might be expected as ‘they [*cats*] normally employ a ‘sit-and-wait’ tactic while
555 close to their prey’. Bouts of immobility while stalking could therefore tentatively be seen as
556 a (cat-specific) form of inactivity that would favour reward acquisition, but the affective
557 state(s) associated with such a behaviour are clearly not validated yet (see *e.g.* Bassett and

558 Buchanan-Smith, 2007 for evidence that opposite affective states are sometimes associated
559 with anticipation).

560

561 4.2. *Increased inactivity / decreased activity likely to be associated with positive*
562 *low-arousal affective states*

563 Increased inactivity expressed in situations with low levels of experienced threat, and that
564 facilitates the expression of maintenance, consolidation and recovery (cf. Introduction) will
565 be discussed here, targeting more specifically ‘sun-basking’ and post-consummatory
566 inactivity. Note that resting will be discussed later (see part 5.4.).

567

568 4.2.1. ‘Sun-basking’ inactivity

569 In humans, UV exposure activates known reward centres in the brain (Harrington and
570 colleagues 2012, cited in Fell et al., 2014), and lying in the sun or, in other words, ‘sun-
571 basking’, has hedonic properties (Dhaenen, 1996; Loas et al., 2000); it might even turn into
572 an addictive behaviour (Fell et al., 2014). According to Balcombe (2009), ‘animals’ lives
573 afford them the opportunity to experience a wealth of other pleasures beyond the realms of
574 food, sex and touch, such as basking in the sun or seeking shade’. Supplying captive wombats
575 (*Lasiorninus latifrons*) with feed and olfactory items (so-called enrichments, but note that
576 such items did not reduce the time spent displaying stereotypic behaviours in this study) tends
577 to increase the time animals spent awake in lateral recumbency in direct sunlight, or in the
578 authors’ terms, ‘sun-basking’ (Hogan et al., 2010). Moreover, evolutionary perspectives
579 predict that behaviours that help maintain homeostasis and promote evolutionary fitness are
580 likely to often produce rewarding sensations (Cabanac, 1971; Fraser and Duncan, 1998).
581 Tawny frogmouths (*Padargus strigoides*; Kortner and Geiser, 1999) and diurnal striped mice
582 (*Rhabdomys pumilio*; Schradin et al., 2007) do chose to stand motionless or lie awake in

583 direct sunlight in cold conditions, a so-called ‘sun-basking’ behaviour that presumably helps
584 maintain homeostasis by facilitating passive thermoregulation and removes the aversive
585 feeling of coldness. Similarly, poikilothermic animals actively chose to sun-bask until their
586 body temperatures reach their preferred body levels (*e.g.* in turtle *Pseudemys Scripta*,
587 Crawford et al., 1983; in Nile crocodile *Crocodylus niloticus*, Downs et al., 2008; in blue
588 spiny lizard *Sceloporus cyanogeny*, Garrick, 1979). Interestingly, Fell et al. (2014) have
589 recently shown that chronic low doses of UV exposure elevate laboratory mice plasma levels
590 of β -endorphin, an endogenous opioid known to play a role in reinforcement. While one may
591 question the biological relevance of UV exposure in a nocturnal animal, these results
592 nevertheless suggest that sun-basking could have biologically relevant rewarding properties
593 in diurnal rodent species, such as the above-mentioned striped mouse (Schradin et al., 2007).
594 Thus, although the evidence is not yet conclusive, additional empirical tests of the hypothesis
595 that sun-basking is pleasurable in animals, as in humans, seem very worthwhile (*e.g.* in
596 domestic cats, anecdotally reported by their owners to lie down in certain areas at the time of
597 the day these areas are sunny: Fureix, personal observation).

598

599 4.2.2. Post-consummatory inactivity

600 Post-consummatory inactivity, such as inactivity immediately expressed post-copulation,
601 is likely to be associated with satisfaction and to be pleasurable. In humans, experiencing
602 sexual arousal to orgasm usually produces a pleasant calming effect of sexual satisfaction
603 (Graber et al., 1985; Levin, 2007), and partners frequently remain relatively inactive during
604 the post-coital time (*e.g.* remaining awake and cuddling with the partner, or falling asleep,
605 Hughes and Kruger, 2011). Remaining inactive close to their mates after copulation has also
606 been reported in animals. For instance, in horses, immediately following ejaculation, the
607 stallion’s body relaxes, and its head droops beside the mare’s neck for a few seconds, after

608 which the stallion dismounts and commonly stands quietly behind the mare, often relaxed and
609 inactive (Waring, 2003, P168). Rams similarly usually remain standing quietly beside the
610 female with their heads down slightly shortly after ejaculation and dismounting (Pepelko and
611 Clegg, 1965), while some mink remain motionless, as if sunk in deep stupor, for a period of
612 time after mating (Diez-Leon, 2014, personal communication). Mating mice generally fall
613 over onto their sides for 5-10 seconds immediately post-ejaculation whilst still coupled, with
614 open eyes and apparent unresponsiveness to sensory stimuli (*e.g.* being touched with a finger)
615 (Brennan, 2015, personal communication). Following evolutionary predictions (*e.g.* Cabanac,
616 1971; Fraser and Duncan, 1998) and by analogy with humans (Graber et al., 1985; Levin,
617 2007), sexual interaction and orgasm are typically likely to be pleasurable (see also Dixon,
618 2010, P392-393), at least in healthy male mammals (in which ejaculation can be observed).
619 Due to its very close temporal relationship with the sexual interaction, one may reasonably
620 hypothesize that this post-copulation inactivity in animals (or, at least, in male mammals) has,
621 just as in humans, a pleasant ‘calming’ affective component (see 4.2.3 and discussion for
622 further research suggestions).

623 Inactivity expressed in postprandial contexts could also be associated with positive
624 affective states. Postprandial inactivity is likely to be associated with satiety, *i.e.* in humans
625 the feeling of ‘fullness’ following a feeding episode (Benelam, 2009; Harrold et al., 2012),
626 and has been observed in a number of animal species (rats: *e.g.* Richter, 1922; Antin et al.,
627 1975; Willner et al., 1990; Rodgers et al., 2010; northern harriers *Circus cyaneus*: Temeles,
628 1989; sows: Zonderland et al., 2004; dogs: Bosch et al., 2009; cats: Fara and colleagues 1969,
629 cited in Orr et al., 1997). Further evidence that postprandial inactivity in animals is likely to
630 be associated with satiety comes from pharmacological studies: cholecystokinin⁵
631 administration, which in humans increases the feeling of fullness and reduces food

⁵ a group of peptides localized in the gut in mammals

632 consumption (*e.g.* Stacher et al., 1979; Crawley et al., 1982; Stacher et al., 1982; Sam et al.,
633 2012), also reduces food consumption in animals (rats, mice, sheep, pigs, monkeys, reviewed
634 in Crawley et al., 1982), and induces inactivity (rats: *e.g.* Antin et al., 1975; mice: Crawley et
635 al., 1981; rhesus monkeys: Falasco et al., 1979). In calves, being able to suck on a teat
636 increases the tendency to rest after milk consumption (Veissier et al., 2002), and this may be
637 mediated in part by cholecystinin, which increases in response to such sucking (De Passillé
638 et al., 1993).

639 Satiety *can* increase inactivity in humans as well (*e.g.* napping after lunch, Zammit et al.,
640 1992; Vela-Bueno et al., 2008), although the causal relationship remains debated (review in
641 Campbell, 1992), making it difficult to use evidence regarding affective states during satiety-
642 induced inactivity in humans. Nevertheless, because satiated humans self-report positive
643 affective states, such as satisfaction and relaxation (Panksepp, 2005; Boelsma et al., 2010;
644 Seehuus et al., 2013), one may reasonably hypothesize that postprandial inactivity in animals
645 has a positive affective component just as humans experience after eating. This suggestion is
646 supported by the finding that, in laying hen chicks, denying access to the part of a pen
647 designed to accommodate postprandial inactivity results in a more negative affective state
648 than in a baseline situation (where chicks have free access to that area), as evidenced by a
649 more ‘pessimistic-like’ response in a judgment bias paradigm (Seehuus et al., 2013).

650 With respect to *satiation*, *i.e.* the *processes* that bring episodes of eating behaviour to an
651 end (Benelam, 2009; Harrold et al., 2012), ingesting food is typically considered activity in
652 applied ethology research (see section 2); satiation therefore appears unlikely to involve
653 inactivity in most species, including humans. However, rumination, which has the primary
654 function of facilitating clearance of digesta from the rumen by reduction of particle size, is
655 most frequently expressed when the animals are motionless lying down (Wagnon, 1963;
656 Kilgour, 2012; Schirmann et al., 2012). As such, it could be seen as a (ruminant-specific)

657 satiation-induced specific form of inactivity. In humans, satiation is associated with positive
658 affective states, such as feelings of liking and satisfaction (*e.g.* Benelam, 2009; Seehuus et al.,
659 2013), and lying down ruminating has been suggested to be ‘a sign of relaxation in cattle’
660 (Phillips, 2002, from Espejo and Endres, 2007) and a sign that cows are ‘at ease’ (Bristow
661 and Holmes, 2007). Rumination also appears to decrease when animals are exposed to
662 aversive situations, such as social stressors (regrouping) and home-pen novelty (Schirmann et
663 al., 2011), disturbance by flies (presumably associated with discomfort: Wagnon, 1963, p47)
664 and ruminal acidosis (presumably associated with pain, lactating dairy cows: DeVries et al.,
665 2009).

666

667 4.2.3. Inactivity and positive affective states: further research suggestions

668 Being *inactive* in order to *favour* reward *acquisition* is likely rare, with perhaps the only
669 direct evidence coming from humans during yogi meditation, as discussed above. Our other
670 suggested example, bouts of immobility while stalking in cats, is clearly not validated as an
671 indicator of positive affective states in animals. Potentially more fruitful as affective state
672 indicators are specific forms of inactivity reported in humans and expressed in animals when
673 threat levels are low, such as sun-basking and post-consummatory inactivity. All of these still
674 need validation, however. Further work could investigate to what extent acute stressors or
675 chronically aversive environments would decrease such inactivity (and the opposite for
676 preferred environments), how these forms of inactivity would be modulated by
677 pharmacological manipulations inducing either negative or positive affective states, and,
678 more specifically, whether the putatively positive affective state associated with postprandial
679 inactivity would be lessened in force-fed animals (see Faure et al., 2001 for evidence that
680 force-feeding might be perceived as aversive in ducks). Further research is also warranted
681 into other forms of inactivity likely to be pleasurable in humans, such as being passively

682 rocked and breast-feeding, which could perhaps find equivalents in animals *choosing* to go
683 and float in the water and in lactating females.

684

685 **5. Misinterpreting inactivity as an indicator of affective state**

686 We will further discuss the relationship between increased inactivity and affective states
687 by presenting misleading situations prone to yield wrong conclusions. First, we will describe
688 some examples of ‘false negatives’ (*i.e.* those cases where the animal’s affective state is
689 likely to be either poor or good but the animal *is not* inactive), and ‘false positives’ (*i.e.* those
690 cases where the animal *is* inactive, eliciting interpretations about its affective state, while the
691 animal actually *does not* experience the presumed affective state). We will then discuss
692 specific forms of inactivity which appear to be not necessarily linked to an actual affective
693 state, but instead to a *lack* of emotion, and how the methodologies used to assess inactivity
694 could yield different interpretations with regards to its associated affective states, discussing
695 in detail the case of resting.

696

697 *5.1. The risk of wrong conclusions: some examples of ‘false negatives’*

698 As discussed above (sections 3 and 4), specific forms of inactivity and/or overall decreases
699 in activity in many contexts are likely to be associated with specific affective states; as such,
700 an inactive animal in a similar situation is believed to be in a more intense (negative or
701 positive) affective state than its comparatively more active counterparts. Assuming this
702 *systematically* would nevertheless sometimes yield incorrect conclusions; in some situations,
703 animals are likely to *experience the* specific (negative or positive) *affective states* of interest,
704 but *do not display* increased inactivity.

705 Inactivity can sometimes be one of two (or more) alternative responses – driven by
706 individual characteristics – to the same situation, which both indicate a similarly (in this

707 example) negative affective state. For instance, while individuals can respond to situations
708 involving a (perceived) threat by freezing or hiding, they can also display active reactions,
709 such as fleeing or even attacking (Boissy, 1995; Blanchard et al., 2011). In red deer, the
710 response strategies to a perceived threat differ according to age: juveniles employ a hiding
711 strategy, and freeze in response to threat, but as they age, they begin fleeing from some
712 threats instead (Espmark and Langvatn, 1985). This does not mean we should conclude that
713 adult red deer are not afraid of the perceived threat from which they are fleeing only because
714 they are not displaying inactive responses. More generally, personality can determine the
715 form of an individual's response, including whether they become inactive or not. For
716 example, speed of exploration of a novel environment is considered to reflect a personality
717 trait in birds, and individuals with different exploratory phenotypes also differ in the degree
718 to which they become inactive after social defeat (reviewed by Groothuis and Carere 2007).
719 Van Reenen et al. (2005) thus suggest that their failure to find a correlation between open
720 field locomotion and other measures of response to novelty might be explained by the
721 presence of different coping styles, such that some calves responded to the open field with
722 escape attempts, but others with immobility, novelty being nevertheless perceived as
723 frightening in both cases. Moreover, an individual's experience is likely to influence its stress
724 responses: for example, captive-born individuals may be more likely to respond actively to a
725 sub-optimal captive environment, developing stereotypic behaviour, while wild-caught
726 individuals may be more likely to respond by hiding (*e.g.* Jones et al., 2011; Camus et al.,
727 2013). Despite these differences, individuals displaying both response types are likely to
728 suffer from their sub-optimal life conditions.

729 Inactivity can also be one of two (or more) alternative responses – dependent this time on
730 situational characteristics - to different situations associated with a similar (in this example
731 negative) affective state. For instance, Cooper et al. (1996) showed that voles responded to an

732 unfamiliar sound by freezing if in an enriched environment where cover was available, but
733 otherwise responded actively, by running or digging; in such a case, there is no good reason
734 to conclude that running or digging animals are not afraid of the unfamiliar sound simply
735 because they do not freeze. Moreover, while ill-health (including painful) conditions increase
736 inactivity in a number of species, including humans (see 3.2.a.), both increased and decreased
737 sleep are used by caregivers as behavioural signs of pain in non-verbal cognitively impaired
738 children (McGrath et al., 1998), and animals sometimes also display active behaviours in
739 response to ill-health conditions. For instance, in mice experiencing scrotal approach
740 vasectomy, Leach et al. (2012) observed higher frequencies of pain behaviours (*e.g.* circle,
741 flinch, stagger, twitch and writhe) and higher Mouse Grimace Scale (MGS) scores in the
742 animals receiving a saline solution post-operatively, compared to pre-surgery periods and to
743 mice receiving post-operative analgesia (meloxicam, bupivacaine). Mice without post-
744 operative analgesia are likely to experience pain; however, none of the inactive behaviours
745 recorded in the study (*e.g.* ‘stand’ and ‘sleep’) differed pre- vs. post-surgery, nor between
746 treatment groups. One may hypothesize that at least some of the active pain-related
747 behaviours might allow animals to cope better with pain induced by the surgery than being
748 inactive. Although this hypothesis remains to be tested in the context of that study, focusing
749 only on the absence of increased inactivity here would lead to the conclusion that the mice
750 experiencing scrotal approach vasectomy without post-operative analgesia do not suffer,
751 which is contradicted by the displayed pain behaviours and MGS scores. Another example
752 comes from a study on Pekin ducks (*Anas platyrhynchos*), in which animals were provided
753 with environmental options allowing them to actively attempt to cope with the situation.
754 When injected either with saline solution or pathogen-associated molecular patterns, saline-
755 injected ducks exhibited pronounced anorexia strongly correlated with a fever response, but
756 none of the treatments significantly affected the level of animals’ activity, measured by

757 activity loggers surgically inserted into the abdominal cavity (Marais et al., 2013). According
758 to the authors, sick ducks might have actively attempted to lower their body temperature
759 during the defervescent phase of fever by getting in and out of the bathing tub provided. This
760 behaviour, which the authors had previously observed in ducks given pyrogens, would have
761 contributed to the amount of activity logged on the days when ducks were given pathogen-
762 associated molecular patterns.

763

764 5.2. *The risk of wrong conclusions: some examples of 'false positives'*

765 Erroneous interpretations might also come from those cases of 'false positives', where an
766 animal *is* inactive, raising interpretations about its affective state, while the animal's actual
767 affective state *does not differ, or even goes the opposite direction*, from the affective state of
768 its comparatively more active counterparts. For instance, if animals are afraid or motivated to
769 hide but unable to do so because no appropriate camouflaged hiding places are available,
770 their welfare is not likely to be better than if they were hiding (*e.g.* leopard cats: Carlstead et
771 al., 1993a; Wielebnowski et al., 2002; mink: Nimon and Broom, 1999; shelter cats: Kry and
772 Casey, 2007). Or, in other words, if animals are afraid or motivated to hide and able to do so
773 because the cage provides them with a hiding place, there is no good reason to conclude that
774 because they are inactive, their welfare is worse than the welfare of their counterparts who
775 are in the same situation but prevented from hiding. Similarly, successful environmental
776 enrichment often decreases inactivity in a wide range of species (*e.g.* Anna et al., 2002;
777 Koistinen et al., 2009; Rozek et al., 2010), with the exceptions to this rule being types of
778 physical enrichment that would primarily be expected to increase comfort or perceived
779 safety, such as shelters (Wurbel et al., 1998a; Tilly et al., 2010); it would be absurd to
780 conclude that providing animals with shelters decreases their welfare.

781 While the examples above highlight cases of false positives when inactivity is expected to
782 be associated with negative affective states, false positives can also happen when inactivity is
783 expected to be associated with positive affective states. For instance, Mason and Latham
784 (2004) found in a meta-analysis that stereotypic behaviours are more prevalent in populations
785 living in sub-optimal conditions than in populations kept under more welfare-friendly
786 conditions, but also that, more often than not, within populations where stereotypic behaviour
787 was prevalent, individuals that did not stereotype, or had relatively low levels of stereotypy,
788 had poorer welfare than those that with high levels, according to a variety of welfare
789 measures. Since non-stereotypic individuals are likely to be the most inactive individuals
790 within a population (*e.g.* Bildsoe et al., 1990; Wurbel et al., 1998b), this may indicate that at
791 an individual level, inactive responses to stressful conditions are actually more often
792 associated with poor welfare than with good welfare.

793

794 5.3. *The risk of wrong conclusions: cases where inactivity is linked to a lack of*
795 *emotion*

796 While the examples above discuss specific forms of inactivity which are likely to be
797 associated with (either negative or positive) affective states, some forms of inactivity appear
798 to be not necessarily linked to an actual affective state but instead a *lack* of emotion. For
799 instance, disorders of reduced motivation such as apathy, defined as ‘a state of diminished
800 motivation in the presence of normal consciousness, attention, cognitive capacity, and mood’
801 (Marin and Wilkosz, 2005)⁶ involve decreased activity. In Marin and Wilkozs’ words (our
802 emphasis), ‘patients with diminished motivation **all show diminished activity**’; however
803 they are also ‘**emotionally indifferent**... or display restricted responses to important life
804 events’. Another example is a ‘deconstructed state’ observed in the pre-suicidal phase and in

⁶ Apathy is not the only disorder of diminished motivation, but identifying the two other common disorders (abulia and akinetic mutism) relies on speech; therefore those states are not currently possible to operationalise in non-humans and of less interest here.

805 socially excluded individuals, defined as a ‘defensive state of cognitive deconstruction that
806 **avoids** meaningful thought, **emotions** and self-awareness, and **is characterized by lethargy**
807 **and passivity** and alerted time flow’ (cited from Twenge et al., 2003, emphasis ours). In
808 animals, Engel and Schmale (1972) described a broad category of stress-induced forms of
809 inactivity that include decreased responsiveness to the environment, can persist over a long
810 period of time, and are believed to be adaptive because they reduce predation risk and allow
811 the conservation of significant amounts of energy; they called this category conservation-
812 withdrawal (C-W). The actual valence of the affective state associated with C-W, if any, is
813 still debated, with some authors describing it as an ‘affectively neutral’ state (Weiner and
814 Lovitt, 1979).

815 While these forms of inactivity have (or, in the case of C-W, could have) no affective
816 component at the time they are displayed, it seems worth noting that they all appear in
817 negatively valenced contexts, and in humans, often yield situations from which individuals
818 are likely to suffer, such as conflicts with relatives due to family burden. Therefore, even
819 though these specific forms of inactivity cannot be considered as *indicators* of the
820 individual’s actual affective state, they should nevertheless be taken as a sign of exposure to
821 suboptimal environments, and potential poor welfare.

822

823 5.4. *Different methodologies, different conclusions?*

824 As previously highlighted (section 2), there is some variation in the literature in exactly
825 what the term ‘inactivity’ encompasses. While how inactivity is assessed depends on one’s
826 perspective and hypotheses under test, methodological variation in terms of how behaviour is
827 categorized as inactive *versus* active is likely to yield some diversity in the effects observed
828 in terms of welfare states associated to inactivity. For instance, relying only on pedometers,
829 radio-tracking or similar technology -- where any time not in locomotion is called inactivity –

830 would not discriminate *e.g.* a motionless healthy animal sun-basking (likely to experience
831 positive affective states, see 4.2.1) from an animal awake but inactive due to injury (likely to
832 experience negative affective states, see 3.2.1.).

833 A detailed example of how methodological variations in defining inactivity could
834 influence its interpretation in terms of associated affective states comes from resting. Resting
835 can be seen as a post-consummatory (of various activities) behaviour, and is often considered
836 to reflect positive affective states. Indeed, safe, comfortable contexts promote rest (*e.g.* larger
837 home stalls in horses: Raabymagle and Ladewig, 2006). Preferred situations often decrease
838 signs of poor welfare and increase time resting (enriched cages, in rats: Abou-Ismaïl and
839 Mahboub, 2011; and in mice: Tilly et al., 2010; bedding types that are preferred when the
840 animals are given a choice of stalls in horses: Hunter and Houpt, 1989; Mills et al., 2000;
841 Pedersen et al., 2004; Werhahn et al., 2010). So does providing a more naturalistic social
842 environment in horses by introducing adult conspecifics in groups of sub-adults (Bourjade et
843 al., 2008). Moreover, a variety of stressors, such as chronic exposure to mild unpredictable
844 stressors (rats: Cheeta et al., 1997), exposure to an aggressive dominant conspecific (male
845 tree shrews *Tupaia belangeri*: Fuchs and Flugge, 2002) and social isolation (rats: Hurst et al.,
846 1999), decrease the time the animals spend resting over hours or days. Rats exposed to sleep
847 disturbance (husbandry procedures performed during the non-active light phase) not
848 surprisingly sleep less, spending more time *awake non-active* and show higher indicators of
849 physiological stress and reduced welfare than do their conspecifics experiencing husbandry
850 procedures during their active dark phase (Abou-Ismaïl et al., 2008). Moreover, while
851 provoking sexual (positive) interactions during the inactive phase only briefly suppresses
852 sleep in male mice, aversive social conflict induces 12h long-lasting sleep disturbances
853 (Meerlo and Turek, 2001). Resting is therefore commonly interpreted as a sign that animals
854 are relaxed and experience positive affective states.

855 However, in a number of animal studies, resting and *sleeping* are merged together in the
856 behavioural repertoire, defined by the animal displaying a species-specific posture (usually
857 lying down, but sometimes also sitting or even standing still) *with eyes partially or fully*
858 *closed* (e.g. in rats: Hurst et al., 1999; Abou-Ismaïl et al., 2007; 2008; in rabbits: Zeidner et
859 al., 1983; in birds: Campbell and Tobler, 1984; in horses: Waring, 2003). This is because
860 measuring sleep, a restorative behaviour ‘not distinguished by movement’ (Carlson, 2012,
861 p289) and which ‘can be defined behaviourally by the normal suspension of consciousness
862 and electrophysiologically by specific brain wave criteria’ (Purves et al., 2007, p 707)
863 requires performing invasive and/or technically challenging (in animals) measurements, *i.e.*
864 electroencephalographic (EEG) measurement together with electromyographic (EMG)
865 signals. Following the rationale that the longer a bout of inactivity, the more likely it is to be
866 sleep, some authors have investigated duration of inactivity as a way to estimate sleep in mice
867 (Pack et al., 2007). While inactivity-defined sleep (in that study being motionless for ≥ 40 s)
868 and EEG-EMG defined sleep did show good convergence in mice (Pack et al., 2007), using
869 such a duration-of-inactivity-only criterion to estimate sleep appears however to be prone to
870 yield false positives. It would not discriminate, for instance, a healthy animal sleeping from
871 an animal awake but inactive due to pain (see part 3). While EEG-EMG therefore appear to
872 remain the ‘gold standard’ methods to measure sleep, using such techniques is however often
873 too challenging (practically) to perform in most of the farm, zoo and companion animal
874 species, and therefore cannot be applied in a vast number of studies in applied ethology
875 research.

876 Despite (realistically good) reasons to do so, merging sleep and rest in the animals’
877 behavioural repertoire could have significant implications with respect to the welfare states
878 associated to this inactivity. Indeed, in humans, neither sleep quantity nor its quality appear to

879 be trustworthy indicators of affective states. For instance, insomnia⁷ (APA, 2013) can be
880 caused either by negative feelings such as stress or pain (Purves et al., 2007, p728; Carlson,
881 2012, p298), or by ‘excited anticipation of a pleasurable event’ (Carlson, 2012, p298). Sleep
882 disturbance is also a prominent symptom of clinical depression (estimated to affect up to 90%
883 of those with depression, Paterson et al., 2009), but either insomnia or hypersomnia can be
884 observed (*e.g.* APA, 2013; WHO, 1994; Maurice-Tison et al., 1998; Henn and Vollmayr,
885 2005), with some depressed people even self-reporting mixed insomnia/hypersomnia
886 symptoms (Paterson et al., 2009). Similarly, both insomnia and hypersomnia are part of the
887 diagnostic symptoms under ICD-10 for withdrawal states from stimulants, with people
888 experiencing such states also self-reporting negative emotions such as ‘depressed mood’, and
889 ‘decreased contentedness / well-being’ (Juliano and Griffiths, 2004). It is also worth noting
890 that sleep manipulations yield quite erratic effects on people’s mood. In healthy people, acute
891 and short-term sleep deprivation usually worsens mood (*e.g.* Weinger and Ancoli-Israel,
892 2002; Drury et al., 2012), but extending sleep (*e.g.* by 2 or 3h per night beyond its habitual
893 duration) has been reported to worsen mood, to improve mood or to induce no mood change
894 (David et al., 1991; Ferrara and De Gennaro, 2001). Moreover, while sleep deprivation in
895 healthy people usually worsens mood, it is usually followed by a short-term mood
896 *improvement* in depressed patients (Benedetti and Colombo, 2011).

897 Thus, while a number of studies in animals do support the view that ‘resting’ is likely to
898 be associated with positive affective state (enhanced in preferred / positive contexts, reduced
899 in aversive conditions), it seems worth noting that, in the majority of these studies, the
900 relative proportion of the observed inactivity that is ‘simply’ resting cannot be disentangled
901 from that ‘purely’ sleeping due to methodological challenges. As human studies show that
902 sleep is clearly not a trustworthy indicator of the affective state (its duration and quality can

⁷ ‘subjective complaint of difficulty falling asleep or staying asleep, or poor sleep quality’, DSM-V p823

903 be modified in either direction under either positive or negative affective states), the
904 interpretation of the ‘resting + sleeping’ behaviour in animals in terms of its associated
905 affective state might not be so straightforward.

906

907

908 **6. Further research directions**

909 Can inactivity -- in its various forms – be a useful indicator of specific affective states in
910 animals? We think it can, based on analogies with humans self-reporting their feelings while
911 displaying specific forms of inactivity phenotypically similar to those displayed by animals in
912 similar situations (summarised in Table 1). Most of the specific forms we discussed in this
913 paper still need further refinement and validation before they could be used in this way,
914 however.

915 While some forms are unambiguously specific behaviours (*e.g.* freezing in rodents,
916 ‘withdrawn’ states in horses) or operationally definable (*e.g.* with regards to location or other
917 activities such as immediately post-mating) (see column 4 in Table 1), others are less
918 specifically described, such as overall increased inactivity / decreased activity in inactive ill
919 animals or individuals displaying signs of learned helplessness. Reassuringly, contextual
920 information probably favours correct recognition of the associated affective state: an
921 unmedicated animal being inactive post-surgery or displaying signs of ill-health (*e.g.* fever,
922 injury) is likely to experience the aversive affective component of ill-health conditions, while
923 exposure to inescapable, uncontrollable stressors is unlikely to induce positive feelings.
924 Given such contextual knowledge, inactivity may be useful as an indicator of intensity of the
925 affective state. Effort should nevertheless be made in the future to define these specific forms
926 of inactivity more precisely if relevant to hypothesis under test (*e.g.* by adding fine postural
927 descriptions) (cf. also 5.4.).

928 Further work could also investigate how those specific forms of inactivity that are
929 currently not pharmacologically validated (see Table 1, last column) would be modulated by
930 giving the animals drugs inducing either negative or positive affective states. This is provided
931 that such drugs have already been validated as inducing the affective state of interest for the
932 tested species, and are known *not* to induce sedative side effects (risk of circular reasoning
933 otherwise). Such validation would be of primary interest for any forms, but particularly for
934 those few forms observed in animals which are obviously not (food rumination) or not
935 systematically (satiety-induced inactivity) displayed by people, making it difficult in these
936 few cases to use humans-based evidence to infer the associated affective states in animals.

937 Beyond this, future validation work could investigate to what extent acute stressors and
938 chronically aversive environments increase those specific forms of inactivity believed to
939 reflect negative affective states (with the opposite being the case for preferred environments),
940 to provide a starting point for discriminating between forms of inactivity reflecting short-
941 and/or long-term affective states. It could also investigate the co-variation of a specific form
942 of inactivity with evolutionary fitness (following evolutionary perspectives that predict that
943 individuals are likely to avoid aversive sensations and pursue rewarding sensations that
944 respectively decrease and promote evolutionary fitness, Cabanac, 1971; Fraser and Duncan,
945 1998); and could investigate whether a specific form of inactivity co-varies with other
946 welfare indicators, provided these are previously-validated indicators of the specific affective
947 state under test (for instance excluding cortisol levels, reported to either increase or decrease
948 in chronically stressed individuals as well as to increase in some positive situations, *e.g.* in
949 humans: Miller et al., 2007, in animals: Rushen, 1991; Mormede et al., 2007).

950

951 **7. Conclusions**

952 Should more attention be paid to inactivity in behavioural and animal welfare studies?
953 Considering subtypes of inactivity, we think it should. First, as discussed in this paper, some
954 specific forms of inactivity (*e.g.* displayed in response to a perceived threat) are useful
955 indicators of poor welfare states. A number of others forms have, acknowledging that further
956 refinement and validation are still needed, the potential to indicate either negative or positive
957 affective states in animals. This makes additional research into this topic very worthwhile.
958 Moreover, even when inactivity does not result from poor welfare, levels of inactivity that are
959 too high or too low can directly or indirectly induce poorer affective states, raising welfare
960 concerns. For example, in group-housed hens, inactive hens are more likely to be victims of
961 feather pecking, and thus suffer due to high inactivity levels (Riber and Forkman, 2007).
962 Meanwhile, retaining adaptive forms of inactivity is still essential: in reintroduction
963 programmes for endangered species, individuals that have not been active enough to learn
964 appropriate skills before being reintroduced into the wild are likely to have poor welfare once
965 released, since they may be unable to attain sufficient food or find shelter, and may be at
966 higher risk of injury (McPhee, 2004).

967 Using inactivity as an indicator of affective states in animals does require a number of
968 changes in the way we often view inactivity in behavioural and animal welfare studies,
969 however. As discussed throughout this paper, inactivity is *not* a homogeneous category of
970 behaviour: there are many different, context- (and sometimes species-) specific forms.
971 Merging these specific forms into a single broad category certainly can yield erroneous
972 interpretations with regards to the associated affective states, by *e.g.* not discriminating a
973 healthy animals resting from an animal inactive due to ill-health conditions. Prior to data
974 collection, ethograms should include precise descriptions (*e.g.* by adding fine postural
975 descriptions) of any specific form(s) of inactivity relevant to hypotheses under test. A clear
976 description of which contexts trigger (or conversely, decrease) specific form(s) of inactivity

977 is also crucial, as it is the first, essential, step towards inferring its putatively associated
978 affective state(s). Additional justifications should be provided before inferring putative
979 affective states associated with inactivity in animals. Bringing human and animal studies
980 together to rely on analogies with humans self-reporting their feelings is one of the possible
981 justifications; so are pharmacological approaches, which strengthen construct validity.
982 Further research suggestions mentioned in this paper would certainly deepen our
983 understanding of what inactivity can reveal about affective states in non-human animals,
984 providing new ways of assessing treatment effects and a better understanding of the
985 implications of personality differences.

986

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996

997 **9. References**

998 Abou-Ismaïl, U.A., Burman, O.H.P., Nicol, C.J., Mendl, M., 2007. Can sleep behaviour be
999 used as an indicator of stress in group-housed rats (*Rattus norvegicus*)? *Anim. Welf.* 16,
1000 185-188.

1001 Abou-Ismaïl, U.A., Burman, O.H.P., Nicol, C.J., Mendl, M., 2008. Let sleeping rats lie: Does
1002 the timing of husbandry procedures affect laboratory rat behaviour, physiology and
1003 welfare? *Appl. Anim. Behav. Sci.* 111, 329-341.

1004 Abou-Ismaïl, U.A., Mahboub, H.D., 2011. The effects of enriching laboratory cages using
1005 various physical structures on multiple measures of welfare in singly-housed rats.
1006 *Laboratory Animals* 45, 145-153.

1007 Abrams, M.P., Carleton, R.N., Taylor, S., Asmundson, G.J.G., 2009. Human tonic
1008 immobility: measurement and correlates. *Depress. Anxiety.* 26, 550-556.

1009 Abramson, L.Y., Seligman, M.E.P., Teasdale, J.D., 1978. Learned helplessness in humans -
1010 critique and reformulation. *J. Abnorm. Psychol.* 87, 49-74.

1011 American Psychiatric Association, 2013. *Diagnostic and Statistical Manual of Mental*
1012 *Disorders*, fifth edition. American Psychiatric Association, Arlington, VA.

1013 Anna, I., Olsson, S., Dahlborn, K., 2002. Improving housing conditions for laboratory mice: a
1014 review of 'environmental enrichment. *Laboratory Animals* 36, 243-270.

1015 Anonymous, 2005. *Oxford English Dictionary*. Oxford University Press, Oxford, UK.

1016 Antin, J., Gibbs, J., Holt, J., Young, R.C., Smith, G.P., 1975. Cholecystokinin elicits the
1017 complete behavioral sequence of satiety in rats. *J. Comp. Physiol. Psychol.* 89, 784-790.

1018 Aubert, A., 1999. Sickness and behaviour in animals: a motivational perspective. *Neurosci.*
1019 *Biobehav. Rev.* 23, 1029-1036.

1020 Azevedo, T.M., Volchan, E., Imbiriba, L.A., Rodrigues, E.C., Oliveira, J.M., Oliveira, L.F.,
1021 Lutterbach, L.G., Vargas, C.D., 2005. A freezing-like posture to pictures of mutilation.
1022 *Psychophysiology* 42, 255-260.

1023 Baker, M., Dorzab, J., Winokur, G., Cadoret, R.J., 1971. Depressive disease - Classification
1024 and clinical characteristics. *Compr. Psychiatry.* 12, 354-365.

- 1025 Balcombe, J., 2009. Animal pleasure and its moral significance. *Appl. Anim. Behav. Sci.*
1026 118, 208-216.
- 1027 Barratt, E.S., 1965. EEG correlates of tonic immobility in the opossum (*Didelphis*
1028 *virginiana*). *Electroencephalogr. Clin. Neurophysiol.* 18, 709-711.
- 1029 Bassett, L., Buchanan-Smith, H.M., 2007. Effects of predictability on the welfare of captive
1030 animals. *Appl. Anim. Behav. Sci.* 102, 223-245.
- 1031 Bateson, P., Young, M., 1981. Separation from the mother and the development of play in
1032 cats. *Anim. Behav.* 29, 173-180.
- 1033 Beck, A.T., 1967. *Depression: Clinical, experimental and theoretical aspects.* Harper and
1034 Row, New York.
- 1035 Benedetti, F., Colombo, C., 2011. Sleep Deprivation in Mood Disorders.
1036 *Neuropsychobiology* 64, 141-151.
- 1037 Benelam, B., 2009. Satiation, satiety and their effects on eating behaviour. *Nutr. Bull.* 34,
1038 126-173.
- 1039 Benhajali, H., Richard-Yris, M.A., Leroux, M., Ezzaouia, M., Charfi, F., Hausberger, M.,
1040 2008. A note on the time budget and social behaviour of densely housed horses - A case
1041 study in Arab breeding mares. *Appl. Anim. Behav. Sci.* 112, 196-200.
- 1042 Berlyne, D.E., 1960. *Conflict, Arousal, and Curiosity.* McGraw-Hill, New York.
- 1043 Belzung, C., Lemoine, M., 2011. Criteria of validity for animal models of psychiatric
1044 disorders: focus on anxiety disorders and depression. *Biology of Mood & Anxiety*
1045 *Disorders* 2011, 1:9
- 1046 Bildsoe, M., Heller, K.E., Jeppesen, L.L., 1990. Stereotypies in female ranch: mink seasonal
1047 and diurnal variation. *Scientifur* 14, 243-248.

1048 Bildsoe, M., Heller, K.E., Jeppesen, L.L., 1991. Effects of immobility stress and food
1049 restriction on stereotypes in low and high stereotyping female ranch mink. *Behav.*
1050 *Processes* 25, 179-189.

1051 Blackburn-Munro, G., Blackburn-Munro, R.E., 2001. Chronic pain, chronic stress and
1052 depression: Coincidence or consequence? *J. Neuroendocrinol.* 13, 1009-1023.

1053 Blanchard, D.C., Griebel, G., Pobbe, R., Blanchard, R.J., 2011. Risk assessment as an
1054 evolved threat detection and analysis process. *Neurosci. Biobehav. Rev.* 35, 991-998.

1055 Blanchard, D.C., Hynd, A.L., Minke, K.A., Minemoto, T., Blanchard, R.J., 2001. Human
1056 defensive behaviors to threat scenarios show parallels to fear- and anxiety-related defense
1057 patterns of non-human mammals. *Neurosci. Biobehav. Rev.* 25, 761-770.

1058 Boelsma, E., Brink, E.J., Stafleu, A., Hendriks, H.F.J., 2010. Measures of postprandial
1059 wellness after single intake of two protein-carbohydrate meals. *Appetite* 54, 456-464.

1060 Boissy, A., 1995. Fear and fearfulness in animals. *Q. Rev. Biol.* 70, 165-191.

1061 Bosch, G., Beerda, B., van de Hoek, E., Hesta, M., van der Poel, A.F.B., Janssens, G.P.J.,
1062 Hendriks, W.H., 2009. Effect of dietary fibre type on physical activity and behaviour in
1063 kennelled dogs. *Appl. Anim. Behav. Sci.* 121, 32-41.

1064 Bourjade, M., Moulinot, M., Richard-Yris, M.A., Hausberger, M., 2008. Could adults be used
1065 to improve social skills of young horses, *Equus caballus*? *Dev. Psychobiol.* 50, 408-417.

1066 Bouton, M.E., Bolles, R.C., 1980. Conditioned fear assessed by freezing and by the
1067 suppression of 3 different baselines. *Anim. Learn. Behav.* 8, 429-434.

1068 Boys, A., Marsden, J., Strang, J., 2001. Understanding reasons for drug use amongst young
1069 people: a functional perspective. *Health Educ. Res.* 16, 457.

1070 Bracha, H.S., 2004. Freeze, flight, fight, fright, faint: Adaptationist perspectives on the acute
1071 stress response spectrum. *Cns Spectrums* 9, 679-685.

1072 Braud, W.G., Ginsburg, H.J., 1973. Effect of administration of adrenaline on immobility
1073 reaction in domestic fowl. *J. Comp. Physiol. Psychol.* 83, 124-127.

1074 Bristow, D.J., Holmes, D.S., 2007. Cortisol levels and anxiety-related behaviors in cattle.
1075 *Physiol. Behav.* 90, 626-628.

1076 Broom, D.M., 1988. The scientific assessment of animal-welfare. *Appl. Anim. Behav. Sci.*
1077 20, 5-19.

1078 Brune, M., Brune-Cohrs, U., McGrew, W.C., Preuschoft, S., 2006. Psychopathology in great
1079 apes: Concepts, treatment options and possible homologies to human psychiatric
1080 disorders. *Neurosci. Biobehav. Rev.* 30, 1246-1259.

1081 Burrell, A.M., Altman, J.D., 2006. The effect of the captive environment on activity of
1082 captive cotton-top tamarins (*Saguinus oedipus*). *J Appl. Anim. Welf. Sci.* 9(4), 269-276.

1083 Byrne, A., Byrne, D.G., 1993. The effect of exercise on depression, anxiety and other mood
1084 states - a review. *J. Psychosom. Res.* 37, 565-574.

1085 Cabanac, M., 1971. Physiological role of pleasure. *Science* 173, 1103-1107.

1086 Cahn, B.R., Polich, J., 2006. Meditation states and traits: EEG, ERP, and neuroimaging
1087 studies. *Psychol Bull.* 132, 180-211.

1088 Calderon, D.F., Cook, N.B., 2011. The effect of lameness on the resting behavior and
1089 metabolic status of dairy cattle during the transition period in a freestall-housed dairy herd.
1090 *J. Dairy Sci.* 94, 2883-2894.

1091 Campbell, S.S., 1992. The Timing and Structure of Spontaneous Naps, in: Stampi, C. (Ed.),
1092 Why we nap: evolution, chronobiology, and functions of polyphasic and ultrashort sleep,
1093 Birkhauser, Boston, USA, pp. 71-81.

1094 Campbell, S.S., Tobler, I., 1984. Animal sleep - A review of sleep duration across phylogeny.
1095 *Neurosci. Biobehav. Rev.* 8, 269-300.

1096 Camus, S.M.J., Rochais, C., Blois-Heulin, C., Li, Q., Hausberger, M., Bezard, E., 2013. Birth
1097 origin differentially affects depressive- like behaviours: are captive- born cynomolgus
1098 monkeys more vulnerable to depression than their wild- born counterparts? PloS one 8,
1099 e67711.

1100 Carlson, N.R., 2012. Physiology of Behavior 11th Edition. Pearson Education Inc., Boston,
1101 USA.

1102 Carlstead, K., 1996. Effects of captivity on the behavior of wild mammals in: Kleiman, D.G.,
1103 Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity,
1104 University of Chicago Press, Chicago,pp. 317-333.

1105 Carlstead, K., Brown, J.L., Seidensticker, J., 1993a. Behavioral and adrenocortical responses
1106 to environmental-changes in leopard cats (*Felis bengalensis*). Zoo Biol. 12, 321-331.

1107 Carlstead, K., Brown, J.L., Strawn, W., 1993b. Behavioral and physiological correlates of
1108 stress in laboratory cats. Appl. Anim. Behav. Sci. 38, 143-158.

1109 Celli, M.L., Tomonaga, M., Usono, T., Teramoto, M., Nagano, K., 2003. Tool use task as
1110 environmental enrichment for captive chimpanzees. Appl. Anim. Behav. Sci. 81, 171-182.

1111 Chapinal, N., de Passille, A.M., Rushen, J., Wagner, S., 2010. Automated methods for
1112 detecting lameness and measuring analgesia in dairy cattle. J. Dairy Sci. 93, 2007-2013.

1113 Cheeta, S., Ruigt, G., vanProosdij, J., Willner, P., 1997. Changes in sleep architecture
1114 following chronic mild stress. Biol. Psychiatry 41, 419-427.

1115 Chourbaji, S., Zacher, C., Sanchis-Segura, C., Spanagel, R., Gass, P., 2005. Social and
1116 structural housing conditions influence the development of a depressive-like phenotype in
1117 the learned helplessness paradigm in male mice. Behav. Brain Res. 164, 100-106.

1118 Clark, S.L.L., F.H.Cutler,J.T., 1939. A form of congenital myotonia in goats. J. Nerv. Ment.
1119 Dis. 90, 297-309.

1120 Cockram, M.S., 2004. A review of behavioural and physiological responses of sheep to
1121 stressors to identify potential behavioural signs of distress. *Anim. Welf.* 13, 283-291.

1122 Cronbach, L.J., Meehl, P.E., 1955. Construct validity in psychological tests. *Psychol. Bull.*
1123 52, 281–302.

1124 Cooper, J.J., Odberg, F., Nicol, C.J., 1996. Limitations on the effectiveness of environmental
1125 improvement in reducing stereotypic behaviour in bank voles (*Clethrionomys glareolus*).
1126 *Appl. Anim. Behav. Sci.* 48, 237-248.

1127 Correia, A.D., Cunha, S.R., Scholze, M., Stevens, E.D., 2011. A Novel Behavioral Fish
1128 Model of Nociception for Testing Analgesics. *Pharmaceuticals* 4, 665-680.

1129 Crawford, K.M., Spotila, J.R., Standora, E.A., 1983. Operative environmental temperatures
1130 and basking behavior of the turtle *Pseudemys scripta*. *Ecology* 64, 989-999.

1131 Crawley, J.N., Hays, S.E., Paul, S.M., Goodwin, F.K., 1981. Cholecystokinin reduces
1132 exploratory-behavior in mice. *Physiol. Behav.* 27, 407-411.

1133 Crawley, J.N., Rojasramirez, J.A., Mendelson, W.B., 1982. The role of central and peripheral
1134 cholecystokinin in mediating appetitive behaviors. *Peptides* 3, 535-538.

1135 Cryan, J.F., Markou, A., Lucki, I., 2002. Assessing antidepressant activity in rodents: recent
1136 developments and future needs. *Trends Pharmacol. Sci.* 23, 238-245.

1137 Csikszentmihalyi, M., 1975. *Beyond Boredom and Anxiety: Experiencing Flow in Work and*
1138 *Play*. Jossey-Bass, San Francisco.

1139 Csikszentmihalyi, M., 1990. *Flow: The psychology of optimal experience*. Harper & Row,
1140 New York.

1141 Dallaire, J.A., Meagher, R.K., Mason, G.J., 2012. Individual differences in stereotypic
1142 behaviour predict individual differences in the nature and degree of enrichment use in
1143 caged American mink. *Appl. Anim. Behav. Sci.* 142, 98-108.

1144 Dalm, S., de Visser, L., Spruijt, B.M., Oitzl, M.S., 2009. Repeated rat exposure inhibits the
1145 circadian activity patterns of C57BL/6J mice in the home cage. *Behav. Brain Res.* 196, 84-
1146 92.

1147 Dantzer, R., 2004. Cytokine-induced sickness behaviour: a neuroimmune response to
1148 activation of innate immunity. *Eur. J. Pharmacol.* 500, 399-411.

1149 David, M.M., Maclean, A.W., Knowles, J.B., Coulter, M.E., 1991. Rapid eye-movement
1150 latency and mood following a delay of bedtime in healthy-subjects: do the effects mimic
1151 changes in depressive-illness? *Acta Psychiatr. Scand.* 84, 33-39.

1152 Davis, K., Dimidjian, S., 2012. The Relationship Between Physical Activity and Mood
1153 Across the Perinatal Period: A Review of Naturalistic and Clinical Research to Guide
1154 Future Investigation of Physical Activity-Based Interventions for Perinatal Depression.
1155 *Clin. Psychol. Science and Practice* 19, 27-48.

1156 Dawkins, M.S., 1988. Behavioral deprivation - A central problem in animal-welfare. *Appl.*
1157 *Anim. Behav. Sci.* 20, 209-225.

1158 De Passillé, A.M.B., Christopherson, R., Rushen, J., 1993. Nonnutritive sucking by the calf
1159 and postprandial secretion of insulin, CCK, and gastrin. *Physiol. Behav.* 54, 1069-1073.

1160 DeMonte, M., LePape, G., 1997. Behavioural effects of cage enrichment in single-caged
1161 adult cats. *Anim. Welf.* 6, 53-66.

1162 Deussing, J.M., 2006. Animal models of depression. *Drug discovery today: disease models* 3,
1163 375-383.

1164 DeVries, T.J., Beauchemin, K.A., Dohme, F., Schwartzkopf-Genswein, K.S., 2009. Repeated
1165 ruminal acidosis challenges in lactating dairy cows at high and low risk for developing
1166 acidosis: Feeding, ruminating, and lying behavior. *J. Dairy Sci.* 92, 5067-5078.

1167 Dhaenen, H., 1996. Measurement of anhedonia. *Eur. Psychiatry* 11, 335-343.

1168 Dielenberg, R.A., McGregor, I.S., 1999. Habituation of the hiding response to cat odor in rats
1169 (*Rattus norvegicus*). J Comp. Psychol. 113, 376-387.

1170 Dixon, A., 2010. Homosexual behaviour in primates, in: Poiani, A. (Ed.), Animal
1171 homosexuality - a biosocial perspective, University Press, Cambridge, pp. 381-399.

1172 Downs, C.T., Greaver, C., Taylor, R., 2008. Body temperature and basking behaviour of Nile
1173 crocodiles (*Crocodylus niloticus*) during winter. J. Therm. Biol. 33, 185-192.

1174 Drury, D.A., Ferguson, S.A., Thomas, M.J.W., 2012. Restricted sleep and negative affective
1175 states in commercial pilots during short haul operations. Accid. Anal. Prev. 45, 80-84.

1176 Duncan, I.J.H. 2005. Science-based assessment of animal welfare: farm animals. Rev. Sci.
1177 Tech. Off. Int. Epiz. 24, 483-492.

1178 Duncan, I.J.H., 1970. Frustration in the fowl, in: Freeman, B.M., Gordon, R.F. (Eds.),
1179 Aspects of Poultry Behaviour, Edinburgh, UK, British Poultry Science Ltd., pp. 15-31.

1180 Dunn, A.L., Trivedi, M.H., O'Neal, H.A., 2001. Physical activity dose-response effects on
1181 outcomes of depression and anxiety. Med. Sci. Sports Exerc. 33, S587-S597.

1182 Eastwood, J.D., Frischen, A., Fenske, M.J., Smilek, D., 2012. The Unengaged Mind.
1183 Perspect. Psychol. Sci. 7, 482-495.

1184 Engel, C., 2002. Wild health - How animals keep themselves well and what we can learn
1185 from them. Weidenfeld and Nicolson, London.

1186 Engel, G.L., Schmale, A.H., 1972. Conservation-withdrawal: a primary regulatory process
1187 for organismic homeostasis, in: Elsevier (Ed.), Physiology, Emotion and Psychosomatic
1188 Illness, New York, pp. 57-75.

1189 Espejo, L.A., Endres, M.I., 2007. Herd-level risk factors for lameness in high-producing
1190 Holstein cows housed in freestall barns. J. Dairy Sci. 90, 306-314.

1191 Espmark, Y., Langvatn, R., 1985. Development and habituation of cardiac and behavioral-
1192 responses in young red deer calves (*cervus-elaphus*) exposed to alarm stimuli. J. Mammal.
1193 66, 702-711.

1194 Facchinetti, L.D., Imbiriba, L.A., Azevedo, T.M., Vargas, C.D., Volchan, E., 2006. Postural
1195 modulation induced by pictures depicting prosocial or dangerous contexts. Neurosci. Lett.
1196 410, 52-56.

1197 Falasco, J.D., Smith, G.P., Gibbs, J., 1979. Cholecystokinin suppresses sham feeding in the
1198 rhesus-monkey. Physiol. Behav.23, 887-890.

1199 Fanselow, M.S., 1982. The postshock activity burst. Anim. Learn. Behav. 10, 448-454.

1200 Fanselow, M.S., 1984. What is conditioned fear? Trends Neurosci. 7, 460-462.

1201 Fanselow, M.S., Helmstetter, F.J., 1988. Conditional analgesia, defensive freezing and
1202 benzodiazepines. Behav. Neurosci. 102, 233-243.

1203 Farook, J.M., McLachlan, C.S., Zhu, Y.Z., Lee, L., Moochhala, S.M., Wong, P.T.H., 2004.
1204 The CCK2 agonist BC264 reverses freezing behavior habituation in PVG hooded rats on
1205 repeated exposures to a cat. Neurosci. Lett. 355, 205-208.

1206 Faure, J.M., Guemene, D., Guy, G., 2001. Is there avoidance of the force feeding procedure
1207 in ducks and geese? Anim. Res. 50, 157-164.

1208 Fell, G.L., Robinson, K.C., Mao, J., Woolf, C.J., Fisher, D.E., 2014. Skin β -Endorphin
1209 Mediates Addiction to UV Light. Cell 157, 1527-1534.

1210 Ferdowsian, H.R., Durham, D.L., Kimwele, C., Kranendonk, G., Oтали, E., Akugizibwe, T.,
1211 Mulcahy, J.B., Ajarova, L., Johnson, C.M., 2011. Signs of Mood and Anxiety Disorders in
1212 Chimpanzees. Plos One 6, e19855.

1213 Ferrara, M., De Gennaro, L., 2001. How much sleep do we need? Sleep Med. Rev. 5, 155-
1214 179.

- 1215 Fiske, D.W., Maddi, S.R., 1961. Functions of varied experience / [edited by] Donald W.
1216 Fiske and Salvatore R. Maddi ; with contributions by James Bieri. Homewood, Ill. :
1217 Dorsey, Homewood, Ill.
- 1218 Fordham, D.P., Algahtani, S., Durotoye, L.A., Rodway, R.G., 1991. Changes in plasma-
1219 cortisol and beta-endorphin concentrations and behavior in sheep subjected to a change of
1220 environment. *Anim. Production* 52, 287-296.
- 1221 Forkman, B., Boissy, A., Meunier-Salauen, M.C., Canali, E., Jones, R.B., 2007. A critical
1222 review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.* 92,
1223 340-374.
- 1224 Fox, M.W., 1968. Abnormal behavior in animals. W.B. Saunders Company, Philadelphia.
- 1225 Fraser, D., 2008. Understanding animal welfare: the science in its cultural context. Wiley-
1226 Blackwell, Oxford. 324 pages
- 1227 Fraser, D., Duncan, I.J.H., 1998. 'Pleasures', 'pains' and animal welfare: Toward a natural
1228 history of affect. *Anim. Welf.* 7, 383-396.
- 1229 Fuchs, E., Flugge, G., 2002. Social stress in tree shrews: Effects on physiology, brain
1230 function, and behavior of subordinate individuals. *Pharmacol. Biochem. Behav.* 73, 247-
1231 258.
- 1232 Fureix, C., Beaulieu, C., Argaud, S., Rochais, C., Quinton, M., Henry, S., Hausberger, M.,
1233 Mason, G., 2015. Investigating anhedonia in a non-conventional species: do some riding
1234 horses *Equus caballus* display symptoms of depression? *Appl. Anim. Behav. Sci.* 162, 26-
1235 36.
- 1236 Fureix, C., Jegou, P., Henry, S., Lansade, L., Hausberger, M., 2012. Towards an Ethological
1237 Animal Model of Depression? A Study on Horses. *Plos One* 7, e39280.

1238 Galliano, G., Noble, L.M., Travis, L.A., Puechl, C., 1993. Victim reactions during
1239 rape/sexual assault - A preliminary study of the immobility response and its correlates. J.
1240 Interpers. Violence. 8, 109-114.

1241 Gallup, G.G., 1973. Tonic immobility in chickens - Is a stimulus that signals shock more
1242 aversive than receipt of shock. Anim. Learn. Behav. 1, 228-232.

1243 Gallup, G.G., 1974. Animal hypnosis: Factual status of a fictional concept. Psychol. Bull. 81,
1244 836-853.

1245 Gallup, G.G., Nash, R.F., Brown, C.W., 1971a. The effects of a tranquilizer on immobility
1246 reaction in chickens - Additional support for fear hypothesis. Psychon. Sci. 23, 127-128.

1247 Gallup, G.G., Nash, R.F., Potter, R.J., Donegan, N.H., 1970. Effect of varying conditions of
1248 fear on immobility reactions in domestic chickens (*Gallus gallus*). J. Comp. Physiol.
1249 Psychol. 73, 442-445.

1250 Gallup, G.G., Nash, R.F., Wagner, A.M., 1971b. Tonic immobility reaction in chickens -
1251 Response characteristics and methodology. Behavior Research Methods &
1252 Instrumentation 3, 237-239.

1253 Gallup, G.G., Williamson, G.T., 1972. Effect of food deprivation and a visual cliff on tonic
1254 immobility. Psychon. Sci. 29, 301-302.

1255 Garrick, L.D., 1979. Lizard Thermoregulation: Operant Responses for Heat at Different
1256 Thermal Intensities. Copeia 2, 258-266.

1257 Gilman, T.T., Marcuse, F.L., Moore, A.U., 1950. Animal hypnosis - A study in the induction
1258 of tonic immobility in chickens. J. Comp. Physiol. Psychol. 43, 99-111.

1259 Goats, G.C., 1994. Massage--the scientific basis of an ancient art: part 2. physiological and
1260 therapeutic effects. Br. J. Sports Med. 28, 153.

1261 Gotlib, I.H., Krasnoperova, E., 1998. Biased information processing as a vulnerability factor
1262 for depression. Behav. Ther. 29, 603-617.

1263 Graber, B., Rohrbaugh, J.W., Newlin, D.B., Varner, J.L., Ellingson, R.J., 1985. EEG during
1264 masturbation and ejaculation. Arch. Sex. Behav. 14, 491-503.

1265 Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis.
1266 Neuroscience and biobehavioral reviews, 29, 137-150.

1267 Hammen, C., Kim, E.Y., Eberhart, N.K., Brennan, P.A., 2009. Chronic and acute stress and
1268 the prediction of major depression in women. *Depress. Anxiety.* 26, 718-723.

1269 Hansen, S.W., Moller, S.H., 2008. Diurnal activity patterns of farm mink (*Mustela vison*)
1270 subjected to different feeding routines. *Appl. Anim. Behav. Sci.* 111, 146-157.

1271 Harlow, H., Suomi, S., 1974. Induced Depression in Monkeys. *Behav. Biol.* 12, 273-296.

1272 Harlow, H.F., Harlow, M.K., 1962. Social deprivation in monkeys. *Sci. Am.* 207, 136-146.

1273 Harris, M.B., 2000. Correlates and characteristics of boredom proneness and boredom. *J.*
1274 *Appl. Soc. Psychol.* 30, 576-598.

1275 Harrold, J.A., Doyey, T.M., Blundell, J.E., Halford, J.C.G., 2012. CNS regulation of appetite.
1276 *Neuropharmacology* 63, 3-17.

1277 Hart, B.L., 1988. Biological basis of the behavior of sick animals. *Neurosci. Biobehav. Rev.*
1278 12, 123-137.

1279 Heaman, M., Gupton, A., 1998. Perceptions of bed rest by women with high-risk
1280 pregnancies: A comparison between home and hospital. *Birth-Issues in Perinatal Care* 25,
1281 252-258.

1282 Heiderstadt, K.M., McLaughlin, R.M., Wright, D.C., Walker, S.E., Gomez-Sanchez, C.E.,
1283 2000. The effect of chronic food and water restriction on open-field behaviour and serum
1284 corticosterone levels in rats. *Lab. Anim.* 34, 20-28.

1285 Henn, F.A., Vollmayr, B., 2005. Stress models of depression: Forming genetically vulnerable
1286 strains. *Neurosci. Biobehav. Rev.* 29, 799-804.

- 1287 Hennessy, M.B., McCowan, B., Jiang, J., Capitanio, J.P., 2014. Depressive-like behavioral
1288 response of adult male rhesus monkeys during routine animal husbandry procedure.
1289 *Frontiers in Behav. Neurosci.* 8, 309.
- 1290 Hogan, L.A., Johnston, S.D., Lisle, A., Horsup, A.B., Janssen, T., Phillips, C.J.C., 2010.
1291 Stereotypies and environmental enrichment in captive southern hairy-nosed wombats,
1292 *Lasiorhinus latifrons*. *Appl. Anim. Behav. Sci.* 126, 85-95.
- 1293 Hopwood, N., Maswanganyi, T., Harden, L.M., 2009. Comparison of anorexia, lethargy, and
1294 fever induced by bacterial and viral mimetics in rats. *Can. J. Physiol. Pharmacol.* 87, 211-
1295 220.
- 1296 Hughes, S.M., Kruger, D.J., 2011. Sex Differences in Post-Coital Behaviors in Long- and
1297 Short-Term Mating: An Evolutionary Perspective. *J. Sex. Res.* 48, 496-505.
- 1298 Hunter, L., Houpt, K.A., 1989. Bedding material preferences of ponies. *J. Anim. Sci.* 67,
1299 1986-1991.
- 1300 Hurst, J.L., Barnard, C.J., Tolladay, U., Nevison, C.M., West, C.D., 1999. Housing and
1301 welfare in laboratory rats: effects of cage stocking density and behavioural predictors of
1302 welfare. *Anim. Behav.* 58, 563-586.
- 1303 Inglis, I.R., 1983. Towards a cognitive theory of exploratory behavior, in: Archer, J., Birke,
1304 L.I.A. (Eds.), *Exploration in animals and man*, Van Nostrand Reinhold, London, UK, pp.
1305 72-115.
- 1306 Jones, M.A., Mason, G.J., Pillay, N., 2011. Correlates of birth origin effects on the
1307 development of stereotypic behaviour in striped mice, *Rhabdomys*. *Anim. Behav.* 82, 149-
1308 159.
- 1309 Jones, R.B., 1992. The nature of handling immediately prior to test affects tonic immobility
1310 fear reactions in laying hens and broilers. *Appl. Anim. Behav. Sci.* 34, 247-254.

- 1311 Jones, R.B., Beuving, G., Blokhuis, H.J., 1988. Tonic immobility and heterophil lymphocyte
1312 responses of the domestic fowl to corticosterone infusion. *Physiol. Behav.* 42, 249-253.
- 1313 Juliano, L.M., Griffiths, R.R., 2004. A critical review of caffeine withdrawal: empirical
1314 validation of symptoms and signs, incidence, severity, and associated features.
1315 *Psychopharmacology* 176, 1-29.
- 1316 Kilgour, R.J., 2012. In pursuit of "normal": A review of the behaviour of cattle at pasture.
1317 *Appl. Anim. Behav. Sci.* 138, 1-11.
- 1318 Kirkden, R.D., 2000. Assessing motivational strength and studies of boredom and enrichment
1319 in pigs, University of Cambridge.
- 1320 Klemm, W.R., 1966. Electroencephalographic-behavioral dissociations during animal
1321 hypnosis. *Electroencephalogr. Clin. Neurophysiol.* 21, 365.
- 1322 Knowles, R.D., 1981. Coping with lethargy. *Am. J. Nurs.* 81, 1465-1465.
- 1323 Knox, D., Fitzpatrick, C.J., George, S.A., Abelson, J.L., Liberzon, I., 2012. Unconditioned
1324 freezing is enhanced in an appetitive context: Implications for the contextual dependency
1325 of unconditioned fear. *Neurobiol. Learn. Mem.* 97, 386-392.
- 1326 Koistinen, T., Turunen, A., Kiviniemi, V., Ahola, L., Mononen, J., 2009. Bones as
1327 enrichment for farmed blue foxes (*Vulpes lagopus*): Interaction with the bones and
1328 preference for a cage with the bones. *Appl. Anim. Behav. Sci.* 120, 108-116.
- 1329 Konrad, K., W., Bagshaw, M., 1970. Effect of novel stimuli on cats reared in a restricted
1330 environment. *J. Comp. Physiol. Psychol.* 70, 157-164.
- 1331 Kortner, G., Geiser, F., 1999. Roosting behaviour of the tawny frogmouth (*Padargus*
1332 *strigoides*). *J. Zool.* 248, 501-507.
- 1333 Kry, K., Casey, R., 2007. The effect of hiding enrichment on stress levels and behaviour of
1334 domestic cats (*Felis sylvestris catus*) in a shelter setting and the implications for adoption
1335 potential. *Anim. Welf.* 16, 375-383.

- 1336 Leach, M.C., Allweiler, S., Richardson, C., Roughan, J.V., Narbe, R., Flecknell, P.A., 2009.
1337 Behavioural effects of ovariohysterectomy and oral administration of meloxicam in
1338 laboratory housed rabbits. *Res. Vet. Sci.* 87, 336-347.
- 1339 Leach, M.C., Klaus, K., Miller, A.L., di Perrotolo, M.S., Sotocinal, S.G., Flecknell, P.A.,
1340 2012. The Assessment of Post-Vasectomy Pain in Mice Using Behaviour and the Mouse
1341 Grimace Scale. *Plos One* 7(4), e35656.
- 1342 Leaton, R.N., Borszcz, G.S., 1985. Potentiated startle - Its relation to freezing and shock
1343 intensity in rats. *J. Exp. Psychol. – Anim. Behav. Processes.* 11, 421-428.
- 1344 Leslie, E., Hernandez-Jover, M., Newman, R., Holyoake, P., 2010. Assessment of acute pain
1345 experienced by piglets from ear tagging, ear notching and intraperitoneal injectable
1346 transponders. *Appl. Anim. Behav. Sci.* 127, 86-95.
- 1347 Levin, R.J., 2007. Sexual activity, health and well-being: the beneficial roles of coitus and
1348 masturbation. *Sex. Relation. Ther.* 22, 135-148.
- 1349 Levitis, D.A., Lidicker, J.Z., Freund, G., 2009. Behavioural biologists do not agree on what
1350 constitutes behaviour. *Anim. Behav.* 78, 103-110.
- 1351 Lima, S.L., Rattenborg, N.C., Lesku, J.A., Amlaner, C.J., 2005. Sleeping under the risk of
1352 predation. *Anim. Behav.* 70, 723-736.
- 1353 Lindwall, M., Larsman, P., Hagger, M.S., 2011. The Reciprocal Relationship Between
1354 Physical Activity and Depression in Older European Adults: A Prospective Cross-Lagged
1355 Panel Design Using SHARE Data. *Health Psychol.* 30, 453-462.
- 1356 Loas, G., Noisette, C., Legrand, A., Boyer, P., 2000. Is anhedonia a specific dimension in
1357 chronic schizophrenia? *Schizophr. Bull.* 26, 495-506.
- 1358 Lopes, F.L., Azevedo, T.M., Imbiriba, L.A., Freire, R.C., Valenca, A.M., Caldirola, D.,
1359 Perna, G., Volchan, E., Nardi, A.E., 2009. Freezing reaction in panic disorder patients
1360 associated with anticipatory anxiety. *Depress. Anxiety.* 26, 917-921.

- 1361 Louvart, N., Maccari, S., Ducrocq, F., Thomas, P., Darnaudey, M., 2005. Long-term
1362 behavioural alterations in female rats after a single intense footshock followed by
1363 situational reminders. *Psychoneuroendocrinology* 30, 316-324.
- 1364 Lush, J.L., 1930. "Nervous" goats. *J. Hered.* 21, 243-247.
- 1365 Luyten, L., Vansteenwegen, D., van Kuyck, K., Nuttin, B., 2011. Towards chronic contextual
1366 conditioning in rats: The effects of different numbers of unpaired tone-shock presentations
1367 on freezing time and startle. *Acta Neurobiol. Exp.* 71, 331-338.
- 1368 Maes, M., Berk, M., Goehler, L., Song, C., Anderson, G., Galecki, P., Leonard, B., 2012.
1369 Depression and sickness behavior are Janus-faced responses to shared inflammatory
1370 pathways. *Bmc Med.* 10, 19.
- 1371 Maier, S.F., 1984. Learned helplessness and animal-models of depression. *Prog.*
1372 *Neuropsychopharmacol. Biol. Psychiatry.* 8, 435-446.
- 1373 Maier, S.F., Seligman, M.E.P., 1976. Learned helplessness - Theory and evidence. *J. Exp.*
1374 *Psychol. Gen.* 105, 3-46.
- 1375 Marais, M., Maloneya, S.K., Graya, D.A., 2013. Sickness behaviours in ducks include
1376 anorexia but not lethargy. *Appl. Anim. Behav. Sci.* 145, 102-108.
- 1377 Maren, S., Fanselow, M.S., 1998. Appetitive motivational states differ in their ability to
1378 augment aversive fear conditioning in rats (*Rattus norvegicus*). *J. Exp. Psychol. Anim.*
1379 *Behav. Processes.* 24, 369-373.
- 1380 Marin, R.S., Wilkosz, P.A., 2005. Disorders of diminished motivation. *J. Head. Trauma.*
1381 *Rehabil.* 20(4), 377-88.
- 1382 Maslach, C., Schaufeli, W.B., Leiter, M.P., 2001. Job burnout. *Annu. Rev. Psychol.* 52, 397-
1383 422.
- 1384 Mason, G.J., Latham, N.R., 2004. Can't stop, won't stop: is stereotypy a reliable animal
1385 welfare indicator? *Anim. Welf.* 13, 57-69.

1386 Mason, G.J., Veasey, J.S., 2010. How should the psychological well-being of zoo elephants
1387 be objectively investigated? *Zoo Biol.* 29, 237-255.

1388 Matthews, K., Christmas, D., Swan, J., Sorrell, E., 2005. Animal models of depression:
1389 navigating through the clinical fog. *Neurosci. Biobehav. Rev.* 29, 503-513.

1390 Maurice-Tison, S., Verdoux, H., Gay, B., Perez, P., Salamon, R., Bourgeois, M.L., 1998.
1391 How to improve recognition and diagnosis of depressive syndromes using international
1392 diagnostic criteria. *Br. J. Gen. Pract.* 48, 1245-1246.

1393 McArthur, R., Borsini, F., 2006. Animal models of depression in drug discovery: A historical
1394 perspective. *Pharmacol. Biochem. Behav.* 84, 436-452.

1395 McFarland, D., 1989. Longman Scientific & Technical, Wiley, Harlow Essex New York.

1396 McGrath, P.J., Rosmus, C., Canfield, C., Campbell, M.A., Hennigar, A., 1998. Behaviours
1397 caregivers use to determine pain in non-verbal, cognitively impaired individuals. *Dev.*
1398 *Med. Child. Neurol.* 40, 340-343.

1399 McPhee, M.E., 2004. Generations in captivity increases behavioral variance: considerations
1400 for captive breeding and reintroduction programs. *Biol. Conserv.* 115, 71-77.

1401 McPhee, M.E., Carlstead, K., 2010. The Importance of Maintaining Natural Behaviors in
1402 Captive Mammals, in: Kleiman, D.G., Thompson, K.V., Baer, C.K. (Eds.), *Wild*
1403 *Mammals in Captivity, Principles and techniques for zoo management*, second edition,
1404 University of Chicago Press, Chicago, pp. 303-313.

1405 Meagher, R.K., Campbell, D.L.M., Dallaire, J.A., Diez-Leon, M., Palme, R., Mason, G.J.,
1406 2013. Sleeping tight or hiding in fright? The welfare implications of different subtypes of
1407 inactivity in mink. *Appl. Anim. Behav. Sci.* 144, 138-146.

1408 Meagher, R.K., Mason, G.J., 2012. Environmental Enrichment Reduces Signs of Boredom in
1409 Caged Mink. *Plos One* 7(11), e49180.

1410 Meerlo, P., DeBoer, S.F., Koolhaas, J.M., Daan, S., VandenHoofdakker, R.H., 1996a.
1411 Changes in daily rhythms of body temperature and activity after a single social defeat in
1412 rats. *Physiol. Behav.* 59, 735-739.

1413 Meerlo, P., Overkamp, G.J.F., Benning, M.A., Koolhaas, J.M., vandenHoofdakker, R.H.,
1414 1996b. Long-term changes in open field behaviour following a single social defeat in rats
1415 can be reversed by sleep deprivation. *Physiol. Behav.* 60, 115-119.

1416 Meerlo, P., Turek, F.W., 2001. Effects of social stimuli on sleep in mice: non-rapid-eye-
1417 movement (NREM) sleep is promoted by aggressive interaction but not by sexual
1418 interaction. *Brain Res.* 907, 84-92.

1419 Mendl, M., Burman, O.H.P., Paul, E.S., 2010. An integrative and functional framework for
1420 the study of animal emotion and mood. *Proc. Biol. Sci. B.* 277, 2895-2904.

1421 Mewaldt, L.R., Rose, R.G., 1960. Orientation of migratory restlessness in the white-crowned
1422 sparrow. *Science* 131, 105-106.

1423 Michel, G., Carton, S., Jouvent, R., 1997. Sensation seeking and anhedonia in risk taking
1424 behaviors. Study in bungee jumpers. *Enceph.-Rev. Psychiatr. Clin. Biol. Ther.* 23, 403-
1425 411.

1426 Mikulas, W.L., Vodanovich, S.J., 1993. The essence of boredom. *Psychol. Rec.* 43, 3-12.

1427 Miller, G.E., Chen, E., Zhou, E.S., 2007. If it goes up, must it come down? Chronic stress and
1428 the hypothalamic-pituitary-adrenocortical axis in humans. *Psychol Bull.* 133, 25-45.

1429 Mills, D.S., Eckley, S., Cooper, J.J., 2000. Thoroughbred bedding preferences, associated
1430 behaviour differences and their implications for equine welfare. *Anim. Sci.* 70, 95-106.

1431 Mineka, S., Hendersen, R.W., 1985. Controllability and predictability in acquired motivation.
1432 *Annu. Rev. Psychol.* 36, 495-529.

1433 Mongeluzi, D.L., Rosellini, R.A., Ley, R., Caldarone, B.J., Stock, H.S., 2003. The
1434 conditioning of dyspneic suffocation fear - Effects of carbon dioxide concentration on
1435 behavioral freezing and analgesia. *Behav. Modif.* 27, 620-636.

1436 Mormede, P., Andanson, S., Auperin, B., Beerda, B., Guemene, D., Malnikvist, J., Manteca,
1437 X., Manteuffel, G., Prunet, P., van Reenen, C.G., Richard, S., Veissier, I., 2007.
1438 Exploration of the hypothalamic-pituitary-adrenal function as a tool to evaluate animal
1439 welfare. *Physiol. Behav.* 92, 317-339.

1440 Muhsen, K., Garty-Sandalon, N., Gross, R., Green, M.S., 2010. Psychological distress is
1441 independently associated with physical inactivity in Israeli adults. *Preventive Med.* 50,
1442 118-122.

1443 Nash, R.F., Gallup, G.G., Czech, D.A., 1976. Psychophysiological correlates of tonic
1444 immobility in domestic chicken (*Gallus gallus*). *Physiol. Behav.* 17, 413-418.

1445 Nimon, A.J., Broom, D.M., 1999. The welfare of farmed mink (*Mustela vison*) in relation to
1446 housing and management: A review. *Anim. Welf.* 8, 205-228.

1447 Nowak, R., 2006. Suckling, Milk, and the Development of Preferences Toward Maternal
1448 Cues by Neonates: From Early Learning to Filial Attachment? *Adv. Study. Behav.* 36, 1-
1449 58.

1450 O'Callaghan, K.A., Cripps, P.J., Downham, D.Y., Murray, R.D., 2003. Subjective and
1451 objective assessment of pain and discomfort due to lameness in dairy cattle. *Anim. Welf.*
1452 12, 605-610.

1453 Offinger, J., Herdtweck, S., Rizk, A., Starke, A., Heppelmann, M., Meyer, H., Janssen, S.,
1454 Beyerbach, M., Rehage, J., 2013. Postoperative analgesic efficacy of meloxicam in lame
1455 dairy cows undergoing resection of the distal interphalangeal joint. *J. Dairy Sci.* 96, 866-
1456 876.

1457 Orr, W.C., Shadid, G., Harnish, M.J., Elsenbruch, S., 1997. Meal composition and its effect
1458 on postprandial sleepiness. *Physiol. Behav.* 62, 709-712.

1459 Pack, A.I., Galante, R.J., Maislin, G., Cater, J., Metaxas, D., Lu, S., Zhang, L., Von Smith,
1460 R., Kay, T., Lian, J., Svenson, K., Peters, L.L., 2007. Novel method for high-throughput
1461 phenotyping of sleep in mice. *Physiol. Genomics* 28, 232-238.

1462 Panksepp, J., 2005. Affective consciousness: Core emotional feelings in animals and humans.
1463 *Conscious. Cogn.* 14, 30-80.

1464 Paquette, D., Prescott, J., 1988. Use of novel objects to enhance environments of captive
1465 chimpanzees. *Zoo Biol.* 7, 15-23.

1466 Paterson, L.M., Nutt, D.J., Wilson, S.J., 2009. NAPSAQ-1: National Patient Sleep
1467 Assessment Questionnaire in depression. *Int. J. Psychiatry Clin. Pract.* 13, 48-58.

1468 Pattyn, N., Neyt, X., Heridericlx, D., Soetens, E., 2008. Psychophysiological investigation
1469 of vigilance decrement: Boredom or cognitive fatigue? *Physiol. Behav.* 93, 369-378.

1470 Pedersen, G.R., Sondergaard, E., Ladewig, J., 2004. The influence of bedding on the time
1471 horses spend recumbent. *J. Equine Vet. Sci.* 24, 153-158.

1472 Pellow, S., Chopin, P., File, S.E., Briley, M., 1985. Validation of open-closed arm entries in
1473 an elevated plus-maze as a measure of anxiety in the rat. *J. Neurosci. Methods.* 14, 149-
1474 167.

1475 Pepelko, W.E., Clegg, M.T., 1965. Studies of mating behaviour and some factors influencing
1476 the sexual response in the male sheep *Ovis aries*. *Anim. Behav.* 13, 249-258.

1477 Porsolt, R.D., Bertin, A., Jalfre, M., 1977. Behavioral despair in mice - primary screening-test
1478 for antidepressants. *Archives Internationales De Pharmacodynamie Et De Therapie* 229,
1479 327-336.

1480 Prescott, R.G., 1970. Some behavioural effects of variables which influence general level of
1481 activity of rats. *Anim. Behav.* 18, 791-796.

1482 Pritchard, V.L., Lawrence, J., Butlin, R.K., Krause, J., 2001. Shoal choice in zebrafish, *Danio*
1483 *rerio*: the influence of shoal size and activity. *Anim. Behav.* 62, 1085-1088.

1484 Pritchett, L.C., Ulibarri, C., Roberts, M.C., Schneider, R.K., Sellon, D.C., 2003.
1485 Identification of potential physiological and behavioral indicators of postoperative pain in
1486 horses after exploratory celiotomy for colic. *Appl. Anim. Behav. Sci.* 80, 31-43.

1487 Purves, D., Augustine, G.J., Fitzpatrick, D., Hall, W.C., LaMantia, A.-S., McNamara, J.O.,
1488 White, L.E., 2007. *Neuroscience Fourth Edition*. Sinauer Associates, Inc., Sunderland,
1489 USA.

1490 Raabymagle, P., Ladewig, J., 2006. Lying behavior in horses in relation to box size. *J. Equine*
1491 *Vet. Sci.* 26, 11-17.

1492 Riber, A.B., Forkman, B., 2007. A note on the behaviour of the chicken that receives feather
1493 pecks. *Appl. Anim. Behav. Sci.* 108, 337-341.

1494 Richmond, M.A., Murphy, C.A., Pouzet, B., Schmid, P., Rawlins, J.N.P., Feldon, J., 1998. A
1495 computer controlled analysis of freezing behaviour. *J. Neurosci. Methods.* 86, 91-99.

1496 Richter, C.P.A., 1922. A behavioristic study of the activity of the rat. *Comp. Psychol.*
1497 *Monogr.* 1, 1-55.

1498 Rochlitz, I., Podberscek, A.L., Broom, D.M., 1998. Welfare of cats in a quarantine cattery.
1499 *Vet. Rec.* 143, 35-39.

1500 Rodgers, R.J., Holch, P., Tallett, A.J., 2010. Behavioural satiety sequence (BSS) Separating
1501 wheat from chaff in the behavioural pharmacology of appetite. *Pharmacol. Biochem.*
1502 *Behav.* 97, 3-14.

1503 Rozek, J.C., Danner, L.M., Stucky, P.A., Millam, J.R., 2010. Over-sized pellets naturalize
1504 foraging time of captive Orange-winged Amazon parrots (*Amazona amazonica*). *Appl.*
1505 *Anim. Behav. Sci.* 125, 80-87.

1506 Rucker, D.D., Petty, R.E., 2004. Emotion specificity and consumer behavior: Anger, sadness,
1507 and preference for activity. *Motiv. Emot.* 28, 3-21.

1508 Rushen, J., 1991. Problems associated with the interpretation of physiological data in the
1509 assessment of animal-welfare. *Appl. Anim. Behav. Sci.* 28, 381-386.

1510 Rushen, J., Munksgaard, L., Marnet, P.G., DePassille, A.M., 2001. Human contact and the
1511 effects of acute stress on cows at milking. *Appl. Anim. Behav. Sci.* 73, 1-14.

1512 Russell, J.A., Barrett, L.F., 1999. Core Affect, Prototypical Emotional Episodes, and Other
1513 Things Called Emotion : Dissecting the Elephant. *J. Pers. Soc. Psychol.* 76, 805-819.

1514 Sam, A.H., Troke, R.C., Tan, T.M., Bewick, G.A., 2012. The role of the gut/brain axis in
1515 modulating food intake. *Neuropharmacology* 63, 46-56.

1516 Samuels, D.J., Samuels, M., 1974. Low Self- Concept As A Cause of Drug Abuse. *J. Drug*
1517 *Educ.* 4, 421-436.

1518 Santos, J.M., Gargaro, A.C., Oliveira, A.R., Masson, S., Brandao, M.L., 2005.
1519 Pharmacological dissociation of moderate and high contextual fear as assessed by freezing
1520 behavior and fear-potentiated startle. *Eur. Neuropsychopharmacol.* 15, 239-246.

1521 Sargeant, A.B., Eberhardt, L.E., 1975. Death feigning by ducks in response to predation by
1522 red foxes (*Vulpes fulva*). *Am. Midl. Nat.* 94, 108-119.

1523 Schelde, J.T.M., 1998. Major depression: Behavioral markers of depression and recovery. *J.*
1524 *Nerv. Ment. Dis.* 186, 133-140.

1525 Schirmann, K., Chapinal, N., Weary, D.M., Heuwieser, W., von Keyserlingk, M.A.G., 2011.
1526 Short-term effects of regrouping on behavior of prepartum dairy cows. *J. Dairy Sci.* 94,
1527 2312-2319.

1528 Schirmann, K., Chapinal, N., Weary, D.M., Heuwieser, W., von Keyserlingk, M.A.G., 2012.
1529 Rumination and its relationship to feeding and lying behavior in Holstein dairy cows. *J.*
1530 *Dairy Sci.* 95, 3212-3217.

1531 Schradin, C., Krackow, S., Schubert, M., Keller, C., Schradin, B., Pillay, N., 2007.
1532 Regulation of activity in desert-living striped mice: The importance of basking. *Ethology*
1533 113, 606-614.

1534 Schulz, K.L., Anderson, D.E., Coetzee, J.F., White, B.J., Miesner, M.D., 2011. Effect of
1535 flunixin meglumine on the amelioration of lameness in dairy steers with amphotericin B-
1536 induced transient synovitis-arthritis. *Am. J. Vet. Res.* 72, 1431-1438.

1537 Seehuus, B., Mendl, M., Keeling, L.J., Blokhuis, H., 2013. Disrupting motivational
1538 sequences in chicks: Are there affective consequences? *Appl. Anim. Behav. Sci.* 148, 85-
1539 92.

1540 Seime, R.J., Vickers, K.S., 2006. The challenges of treating depression with exercise: From
1541 evidence to practice. *Clin. Psychol. Science and Practice* 13, 194-197.

1542 Seligman, M.E.P., 1972. Learned Helplessness. *Annu. Rev. Med.* 23, 407-412.

1543 Shuhama, R., Del-Ben, C.M., Loureiro, S.R., Graeff, F.G., 2008. Defensive responses to
1544 threat scenarios in Brazilians reproduce the pattern of Hawaiian Americans and non-
1545 human mammals. *Braz. J. Med. Biol. Res.* 41, 324-332.

1546 Siegrist, J., 2008. Chronic psychosocial stress at work and risk of depression: evidence from
1547 prospective studies. *Eur. Arch. Psychiatry Clin. Neurosci.* 258, 115-119.

1548 Stacher, G., Bauer, H., Steinringer, H., 1979. Cholecystokinin decreases appetite and
1549 activation evoked by stimuli arising from the preparation of a meal in man. *Physiol.*
1550 *Behav.* 23, 325-331.

1551 Stacher, G., Steinringer, H., Schmierer, G., Schneider, C., Winklehner, S., 1982.
1552 Cholecystokinin octapeptide decreases intake of solid food in man. *Peptides* 3, 133-136.

1553 Steenbergen, P.J., Bardine, N., 2014. Antinociceptive effects of buprenorphine in zebrafish
1554 larvae: An alternative for rodent models to study pain and nociception? *Appl. Anim.*
1555 *Behav. Sci.* 152, 92-99.

1556 Stevenson, M.F., 1983. The captive environment: its effect on exploratory and related
1557 behavioural responses in wild animals, in: Archer, J., Birke, L.I.A. (Eds.), *Exploration in*
1558 *Animals and Man*, Van Nostrand Reinhold, London, UK, pp. 176-197.

1559 Strekalova, T., Spanagel, R., Bartsch, D., Henn, F.A., Gass, P., 2004. Stress-induced
1560 anhedonia in mice is associated with deficits in forced swimming and exploration.
1561 *Neuropsychopharmacology* 29, 2007-2017.

1562 Suomi, S.J., Eisele, C.D., Grady, S.A., Harlow, H.F., 1975. Depressive behavior in adult
1563 monkeys following separation from family environment. *J. Abnorm. Psychol.* 84, 576-
1564 578.

1565 Tait, R.C., Chibnall, J.T., Krause, S., 1990. The pain disability index: psychometric
1566 properties. *Pain* 40, 171-182.

1567 Taylor, L., Cohen, S., 1972. *Psychological Survival: the Experience of Long Term*
1568 *Imprisonment*. Penguin Books Ltd, Harmondsworth, USA.

1569 Temeles, E.J., 1989. Effect of prey consumption on foraging activity of northern harriers.
1570 *Auk*. 106, 353-366.

1571 Thompson, R.K.R., Foltin, R.W., Boylan, R.J., Sweet, A., Graves, C.A., Lowitz, C.E., 1981.
1572 Tonic immobility in Japanese quail can reduce the probability of sustained attack by cats.
1573 *Anim. Learn. Behav.* 9, 145-149.

1574 Tilly, S.L.C., Dallaire, J., Mason, G.J., 2010. Middle-aged mice with enrichment-resistant
1575 stereotypic behaviour show reduced motivation for enrichment. *Anim. Behav.* 80, 363-373.

1576 Tripaldi, C., De Rosa, G., Grasso, F., Terzano, G.M., Napolitano, F., 2004. Housing system
1577 and welfare of buffalo (*Bubalus bubalis*) cows. *Anim. Sci.* 78, 477-483.

1578 Twenge, J.M., Catanese, K.R., Baumeister, R.F., 2003. Social exclusion and the
1579 deconstructed state: Time perception, meaninglessness, lethargy, lack of emotion, and
1580 self-awareness. *J. Pers. Soc. Psychol.* 85, 409-423.

1581 van den Bos, R., Meijer, M.K., van Renselaar, J.P., van der Harst, J.E., Spruijt, B.M., 2003.
1582 Anticipation is differently expressed in rats (*Rattus norvegicus*) and domestic cats (*Felis*
1583 *silvestris catus*) in the same Pavlovian conditioning paradigm. Behav. Brain Res. 141, 83-
1584 89.

1585 Van Reenen, C.G., O'Connell, N.E., Van der Werf, J.T.N., Korte, S.M., Hopster, H., Jones,
1586 R.B., Blokhuis, H.J., 2005. Responses of calves to acute stress: Individual consistency and
1587 relations between behavioral and physiological measures. Physiol. Behav.85, 557-570.

1588 Veissier, I., Boissy, A., Desire, L., Greiveldinger, L., 2009. Animals' emotions: studies in
1589 sheep using appraisal theories. Anim. Welf. 18, 347-354.

1590 Veissier, I., Després, A.M., Charpentier, G., Ramirez De La Fe, J., De Passillé, I., Rushen,
1591 A.R., Pradel, P., Ramirez De La Fe, P., 2002. Does nutritive and non- nutritive sucking
1592 reduce other oral behaviors and stimulate rest in calves? J. Anim. Sci. 80, 2574-2587.

1593 Vela-Bueno, A., Fernandez-Mendoza, J., Olavarrieta-Bernardino, S., Vgontzas, A.N., Bixler,
1594 E.O., de la Cruz-Troca, J.J., Rodriguez-Munoz, A., Oliván-Palacios, J., 2008. Sleep and
1595 behavioral correlates of napping among young adults: A survey of first-year university
1596 students in Madrid, Spain. J. Am. Coll. Health. 57, 150-158.

1597 Verleye, M., Gillardin, J.M., 2004. Effects of etifoxine on stress-induced hyperthermia,
1598 freezing behavior and colonic motor activation in rats. Physiol. Behav.82, 891-897.

1599 Vieira, A.D., Guesdon, V., De Passille, A.M., von Keyserlingk, M.A.G., Weary, D.M., 2008.
1600 Behavioural indicators of hunger in dairy calves. Appl. Anim. Behav. Sci. 109, 180-189.

1601 Vinke, C.M., van Leeuwen, J., Spruijt, B., 2005. Juvenile farmed mink (*Mustela vison*) with
1602 additional access to swimming water play more frequently than animals housed with a
1603 cylinder and platform, but without swimming water. Anim. Welf. 14, 53-60.

1604 Volchan, E., Souza, G.G., Franklin, C.M., Norte, C.E., Rocha-Rego, V., Oliveira, J.M.,
1605 David, I.A., Mendlowicz, M.V., Coutinho, E.S.F., Fiszman, A., Berger, W., Marques-

1606 Portella, C., Figueira, I., 2011. Is there tonic immobility in humans? Biological evidence
1607 from victims of traumatic stress. *Biol. Psychol.* 88, 13-19.

1608 Wagnon, K.A., 1963. Behavior of beef cows on a California range. *California Agricultural*
1609 *Experiment Station Bulletin* 799, 60.

1610 Wallace, K.J., Rosen, J.B., 2000. Predator odor as an unconditioned fear stimulus in rats:
1611 Elicitation of freezing by trimethylthiazoline, a component of fox feces. *Behav. Neurosci.*
1612 114, 912-922.

1613 Waring, G., 2003. *Horse Behavior*, second edition. Noyes Publications/William Andrew
1614 Publishing, Norwich, New York.

1615 Weeks, C.A., Danbury, T.D., Davies, H.C., Hunt, P., Kestin, S.C., 2000. The behaviour of
1616 broiler chickens and its modification by lameness. *Appl. Anim. Behav. Sci.* 67, 111-125.

1617 Weiner, M.F., Lovitt, R., 1979. Conservation-withdrawal versus depression. *Gen. Hosp.*
1618 *Psychiatry.* 1(4), 347-349.

1619 Weinger, M.B., Ancoli-Israel, S., 2002. Sleep deprivation and clinical performance. *Jama-*
1620 *JAMA* 287, 955-957.

1621 Wells, D.L., 2004. A review of environmental enrichment for kennelled dogs, *Canis*
1622 *familiaris*. *Appl. Anim. Behav. Sci.* 85, 307-317.

1623 Wells, D.L., 2005. A note on the influence of visitors on the behaviour and welfare of zoo-
1624 housed gorillas. *Appl. Anim. Behav. Sci.* 93, 13-17.

1625 Wemelsfelder, F., 1990. Boredom and Laboratory Animal Welfare, in: Rollin, B.E., Kesel,
1626 M.L. (Eds.), *The Experimental Animal in Biomedical Research*, CRC-Press, Boca Raton,
1627 Florida, pp. 243-272.

1628 Werhahn, H., Hessel, E.F., Bachhausen, I., Van den Weghe, H.F.A., 2010. Effects of
1629 Different Bedding Materials on the Behavior of Horses Housed in Single Stalls. *J. Equine*
1630 *Vet. Sci.* 30, 425-431.

1631 Whishaw, I.Q., Flannigan, K.P., Schallert, T., 1982. An assessment of the state hypothesis of
1632 animal 'hypnosis' through an analysis of neocortical and hippocampal EEG in
1633 spontaneously immobile and hypnotized rabbits. *Electroencephalogr. Clin. Neurophysiol.*
1634 54, 365-374.

1635 Wiedenmayer, C.P., Barr, G.A., 2001. Developmental changes in responsivity to threat are
1636 stimulus-specific in rats. *Dev. Psychobiol.* 39, 1-7.

1637 Wielebnowski, N.C., Fletchall, N., Carlstead, K., Busso, J.M., Brown, J.L., 2002.
1638 Noninvasive assessment of adrenal activity associated with husbandry and behavioral
1639 factors in the North American clouded leopard population. *Zoo Biol.* 21, 77-98.

1640 Willner, P., McGuirk, J., Phillips, G., Muscat, R., 1990. Behavioral-analysis of the anorectic
1641 effects of fluoxetine and fenfluramine. *Psychopharmacology* 102, 273-277.

1642 Wise, R.A., 1974. Lateral hypothalamic electrical stimulation: Does it make animals
1643 'hungry'? *Brain Res.* 67, 187-209.

1644 Wiseman, M.L., Nolan, A.M., Reid, J., Scott, E.M., 2001. Preliminary study on owner-
1645 reported behaviour changes associated with chronic pain in dogs. *Vet. Rec.* 149, 423-424.

1646 Woodgush, D.G.M., Beilharz, R.G., 1983. The enrichment of a bare environment for animals
1647 in confined conditions. *Appl. Anim. Ethol.* 10, 209-217.

1648 World Health Organisation, 1994. *International Statistical Classification of Diseases and*
1649 *Related Health Problems.* World Health Organisation, Geneva.

1650 Wurbel, H., Chapman, R., Rutland, C., 1998a. Effect of feed and environmental enrichment
1651 on development of stereotypic wire-gnawing in laboratory mice. *Appl. Anim. Behav. Sci.*
1652 60, 69-81.

1653 Wurbel, H., Freire, R., Nicol, C.J., 1998b. Prevention of stereotypic wire-gnawing in
1654 laboratory mice: Effects on behaviour and implications for stereotypy as a coping
1655 response. *Behav. Processes* 42, 61-72.

- 1656 Zammit, G.K., Ackerman, S.H., Shindledecker, R., Fauci, M., Smith, G.P., 1992.
1657 Postprandial sleep and thermogenesis in normal men. *Physiol. Behav.*52, 251-259.
- 1658 Zanella, A.J., Broom, D.M., Hunter, J.C., Mendl, M.T., 1996. Brain opioid receptors in
1659 relation to stereotypies, inactivity, and housing in sows. *Physiol. Behav.*59, 769-775.
- 1660 Zeidner, L.P., Denenberg, V.H., Thoman, E.B., Weyand, T., 1983. Comparisons of
1661 behavioral, motoric and electrical criteria for assessment of sleep-wake states in the rabbit.
1662 *Physiol. Behav.*31, 273-278.
- 1663 Zonderland, J.J., de Leeuw, J.A., Nolten, C., Spoolder, H.A.M., 2004. Assessing long-term
1664 behavioural effects of feeding motivation in group-housed pregnant sows; what, when and
1665 how to observe. *Appl. Anim. Behav. Sci.* 87, 15-30.

1666

1667 **10. Table legend**

1668 Table 1. Specific forms of inactivity and their association with specific affective states.

Table

Name	Valence	Arousal	Specific form of inactivity, defined operationally	Expressed in response to:	In humans this situation (or similar) has been reported to be:	Humans display a phenotypically similar inactivity:	Pharmacological evidence?
Freezing	Negative	High	Yes	(Perceived) actual or potential threat	Aversive	Yes	Yes (enhanced by anxiogenics, reduced by anxiolytics)
Tonic immobility	Negative	High	Yes	(Perceived) actual or potential threat	Aversive	Yes	Yes (enhanced by anxiogenics, reduced by anxiolytics)
Hiding	Negative	High	Yes (provided hiding opportunities)	(Perceived) actual or potential threat	Aversive	Yes	Yes (enhanced by anxiogenics, reduced by anxiolytics)
Ill-health inactivity	Negative	Low	No (decreased activity)	Illness, injury	Aversive	Yes	Yes (reduced by analgesics)
Learned helplessness related 'floating in despair' (laboratory rodents)	Negative	?	Yes	Porsolt (forced swim) test	Aversive	N/A (specific testing conditions in rodents are not transferable to humans)	Yes (reduced by antidepressants)
Learned helplessness related overall passivity	Negative	Low	No (decreased activity)	Inescapable / uncontrollable aversive environments	Aversive	Yes	?
Depression-like 'withdrawn' state (horses)	Negative	Low	Yes	?	N/A	No phenotypically exactly similar form	?
Boredom-like lying down with eyes open (mink)	Negative	Low (but debated)	Yes	Barren, impoverished environments	Aversive	Yes, but restlessness may also be seen	?
Standing/lying in the sun	Positive	Low	Yes (provided chose shaded / sunny areas)	Sunny area	Positive	Yes	Yes (induces a β -endorphin release)
Post-copulation inactivity	Positive	Low	Yes (timing mating)	Immediately after mating	Positive	Yes	?
Satiety-related inactivity	Positive	Low	Yes (timing eating)	Post-prandial	Positive	Unsure	?
Rumination (cattle)	Positive	Low	Yes	Post food consumption	N/A	N/A	?
Stillness when stalking (cats)	Positive	High	Yes	Predation, play	?	?	?