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

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Carole Fureix[a*], Rebecca K. Meagher[b]

[a] University of Bristol, School of Veterinary Sciences, Langford House, Langford, Bristol BS40 5DU, United Kingdom

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

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

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-heath, 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.

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

1. Introduction

Captive or domestic animals are often described as inactive, with the implicit (*e.g.* Broom, 1988), or explicit implication that this high level of inactivity is a welfare problem (*e.g.* Zanella et al., 1996; McPhee and Carlstead, 2010). Conversely, not being inactive *enough*, for instance when external demands require increased efforts to cope with challenges and when severely sleep deprived, may also indicate or cause poor welfare; it can have dramatic adverse consequences for organisms (*e.g.* Ferrara and De Gennaro, 2001; Maslach et al., 2001). However, the affective states -- our main focus with regards to welfare[1] -- associated with these elevated or suppressed levels of inactivity are still not well understood in non-human animals (henceforth 'animals'). This is in part because inactivity has rarely been the focus of behavioural studies and is often considered simply a default state rather than a true 'behaviour' (see *e.g.* Lima et al., 2005; Levitis et al., 2009).

In humans, too much inactivity can be associated with negative affective states (*e.g.* psychological distress, Muhsen et al., 2010). In animals, too, inactivity is elevated (and activity decreased) in a variety of situations where welfare is believed to be poor. In an extreme example, monkeys separated from their mothers after birth and raised alone in bare wire cages 'sit in their home cages and stare fixedly into space' (Harlow and Harlow, 1962). Juveniles raised in total isolation until 8 months of age needed as long as 12 to 27 weeks to begin to move at all, when placed with social companions in a room designed to trigger play (Harlow and Harlow, 1962; see Konrad and Bagshaw, 1970 for similar results in cats). Male rats exposed to social defeat become more inactive and less exploratory in novel environments than non-defeated controls (Meerlo et al., 1996a; Meerlo et al., 1996b), while 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,'s 3 circles 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

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

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

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

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

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

Freezing (sometimes also termed *attentive immobility*) is a common response in the face of an immediate (perceived) threat in various species, where an individual becomes abruptly motionless, monitoring a perceived source of danger (reviewed by Boissy, 1995). A 'freezing-like' state, characterised by increased immobility and rigidity (quantified using a force platform) and a reduced heart rate (also termed 'fear bradycardia'), has been described in humans. This state has been observed in healthy people viewing pictures of mutilation (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

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

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

In animals, hiding can be defined operationally using location (provided that there are 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 – cautiously[3] - 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 report 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).

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

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

3.2.3. Inactivity and boredom

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

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

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

Both the use of the term 'boredom' in animals and its relationship to inactivity still need validation, however. To provide a starting point for this work, Meagher and Mason (2012) proposed an operational definition based on motivation to obtain stimulation, which should 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

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

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

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

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

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

4.2.1. 'Sun-basking' inactivity

In humans, UV exposure activates known reward centres in the brain (Harrington and colleagues 2012, cited in Fell et al., 2014), and lying in the sun or, in other words, 'sun-basking', has hedonic properties (Dhaenen, 1996; Loas et al., 2000); it might even turn into an addictive behaviour (Fell et al., 2014). According to Balcombe (2009), 'animals' lives afford them the opportunity to experience a wealth of other pleasures beyond the realms of food, sex and touch, such as basking in the sun or seeking shade'. Supplying captive wombats (*Lasiorhinus latifrons*) with feed and olfactory items (so-called enrichments, but note that such items did not reduce the time spent displaying stereotypic behaviours in this study) tends to increase the time animals spent awake in lateral recumbency in direct sunlight, or in the authors' terms, 'sun-basking' (Hogan et al., 2010). Moreover, evolutionary perspectives predict that behaviours that help maintain homeostasis and promote evolutionary fitness are likely to often produce rewarding sensations (Cabanac, 1971; Fraser and Duncan, 1998). Tawny frogmouths (*Padargus strigoides;* Kortner and Geiser, 1999) and diurnal striped mice (*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 Dixson,
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: cholecystokinin[5]
631 administration, which in humans increases the feeling of fullness and reduces food

[5] a group of peptides localized in the gut in mammals

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

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

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

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

4.2.3. Inactivity and positive affective states: further research suggestions

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

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

Inactivity can also be one of two (or more) alternative responses – dependent this time on situational characteristics - to different situations associated with a similar (in this example 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

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

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

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

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

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

While the examples above discuss specific forms of inactivity which are likely to be associated with (either negative or positive) affective states, some forms of inactivity appear to be not necessarily linked to an actual affective state but instead a *lack* of emotion. For instance, disorders of reduced motivation such as apathy, defined as 'a state of diminished motivation in the presence of normal consciousness, attention, cognitive capacity, and mood' (Marin and Wilkosz, 2005)[6] involve decreased activity. In Marin and Wilkozs' words (our emphasis), 'patients with diminished motivation **all show diminished activity'**; however they are also '**emotionally indifferent**… or display restricted responses to important life 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 –

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

A detailed example of how methodological variations in defining inactivity could influence its interpretation in terms of associated affective states comes from resting. Resting can be seen as a post-consummatory (of various activities) behaviour, and is often considered to reflect positive affective states. Indeed, safe, comfortable contexts promote rest (*e.g.* larger home stalls in horses: Raabymagle and Ladewig, 2006). Preferred situations often decrease signs of poor welfare and increase time resting (enriched cages, in rats: Abou-Ismail and Mahboub, 2011; and in mice: Tilly et al., 2010; bedding types that are preferred when the animals are given a choice of stalls in horses: Hunter and Houpt, 1989; Mills et al., 2000; Pedersen et al., 2004; Werhahn et al., 2010). So does providing a more naturalistic social environment in horses by introducing adult conspecifics in groups of sub-adults (Bourjade et al., 2008). Moreover, a variety of stressors, such as chronic exposure to mild unpredictable stressors (rats: Cheeta et al., 1997), exposure to an aggressive dominant conspecific (male tree shrews *Tupaia belangeri*: Fuchs and Flugge, 2002) and social isolation (rats: Hurst et al., 1999), decrease the time the animals spend resting over hours or days. Rats exposed to sleep disturbance (husbandry procedures performed during the non-active light phase) not surprisingly sleep less, spending more time *awake non-active* and show higher indicators of physiological stress and reduced welfare than do their conspecifics experiencing husbandry procedures during their active dark phase (Abou-Ismail et al., 2008). Moreover, while provoking sexual (positive) interactions during the inactive phase only briefly suppresses sleep in male mice, aversive social conflict induces 12h long-lasting sleep disturbances (Meerlo and Turek, 2001). Resting is therefore commonly interpreted as a sign that animals 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-Ismail 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 ≥ 40s)
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, insomnia[7] (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 nothing 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 <u>not</u> 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 **Table 1.** Specific forms of inactivity and their association with specific affective states.

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	?	?	?

952 **Conclusions**

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

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

977 description of which contexts trigger (or conversely, decrease) specific form(s) of inactivity
978 is also crucial, as it is the first, essential, step towards inferring its putatively associated
979 affective state(s). Additional justifications should be provided before inferring putative
980 affective states associated with inactivity in animals. Bringing human and animal studies
981 together to rely on analogies with humans self-reporting their feelings is one of the possible
982 justifications; so are pharmacological approaches, which strengthen construct validity.
983 Further research suggestions mentioned in this paper would certainly deepen our
984 understanding of what inactivity can reveal about affective states in non-human animals,
985 providing new ways of assessing treatment effects and a better understanding of the
986 implications of personality differences.
987
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997
998 **8. References**
999 Abou-Ismail, U.A., Burman, O.H.P., Nicol, C.J., Mendl, M., 2007. Can sleep behaviour be
1000 used as an indicator of stress in group-housed rats (*Rattus norvegicus*)? Anim. Welf. 16,
1001 185-188.

1002 Abou-Ismail, U.A., Burman, O.H.P., Nicol, C.J., Mendl, M., 2008. Let sleeping rats lie: Does
1003 the timing of husbandry procedures affect laboratory rat behaviour, physiology and
1004 welfare? Appl. Anim. Behav. Sci. 111, 329-341.
1005 Abou-Ismail, U.A., Mahboub, H.D., 2011. The effects of enriching laboratory cages using
1006 various physical structures on multiple measures of welfare in singly-housed rats.
1007 Laboratory Animals 45, 145-153.
1008 Abrams, M.P., Carleton, R.N., Taylor, S., Asmundson, G.J.G., 2009. Human tonic
1009 immobility: measurement and correlates. Depress. Anxiety. 26, 550-556.
1010 Abramson, L.Y., Seligman, M.E.P., Teasdale, J.D., 1978. Learned helplessness in humans -
1011 critique and reformulation. J. Abnorm. Psychol. 87, 49-74.
1012 American Psychiatric Association, 2013. Diagnostic and Statistical Manual of Mental
1013 Disorders, fifth edition. American Psychiatric Association, Arlington, VA.
1014 Anna, I., Olsson, S., Dahlborn, K., 2002. Improving housing conditions for laboratory mice: a
1015 review of 'environmental enrichment. Laboratory Animals 36, 243-270.
1016 Anonymous, 2005. Oxford English Dictionary. Oxford University Press, Oxford, UK.
1017 Antin, J., Gibbs, J., Holt, J., Young, R.C., Smith, G.P., 1975. Cholecystokinin elicits the
1018 complete behavioral sequence of satiety in rats. J. Comp. Physiol. Psychol. 89, 784–790.
1019 Aubert, A., 1999. Sickness and behaviour in animals: a motivational perspective. Neurosci.
1020 Biobehav. Rev. 23, 1029-1036.
1021 Azevedo, T.M., Volchan, E., Imbiriba, L.A., Rodrigues, E.C., Oliveira, J.M., Oliveira, L.F.,
1022 Lutterbach, L.G., Vargas, C.D., 2005. A freezing-like posture to pictures of mutilation.
1023 Psychophysiology 42, 255-260.
1024 Baker, M., Dorzab, J., Winokur, G., Cadoret, R.J., 1971. Depressive disease - Classification
1025 and clinical characteristics. Compr. Psychiatry. 12, 354-365.

1026 Balcombe, J., 2009. Animal pleasure and its moral significance. Appl. Anim. Behav. Sci.
1027 118, 208-216.
1028 Barratt, E.S., 1965. EEG correlates of tonic immobility in the opossum *(Didelphis*
1029 *virginiana*). Electroencephalogr. Clin. Neurophysiol. 18, 709-711.
1030 Bassett, L., Buchanan-Smith, H.M., 2007. Effects of predictability on the welfare of captive
1031 animals. Appl. Anim. Behav. Sci. 102, 223-245.
1032 Bateson, P., Young, M., 1981. Separation from the mother and the development of play in
1033 cats. Anim. Behav.29, 173-180.
1034 Beck, A.T., 1967. Depression: Clinical, experimental and theoretical aspects. Harper and
1035 Row, New York.
1036 Benedetti, F., Colombo, C., 2011. Sleep Deprivation in Mood Disorders.
1037 Neuropsychobiology 64, 141-151.
1038 Benelam, B., 2009. Satiation, satiety and their effects on eating behaviour. Nutr. Bull. 34,
1039 126–173.
1040 Benhajali, H., Richard-Yris, M.A., Leroux, M., Ezzaouia, M., Charfi, F., Hausberger, M.,
1041 2008. A note on the time budget and social behaviour of densely housed horses - A case
1042 study in Arab breeding mares. Appl. Anim. Behav. Sci. 112, 196-200.
1043 Berlyne, D.E., 1960. Conflict, Arousal, and Curiosity. McGraw-Hill, New York.
1044 Belzung, C., Lemoine, M., 2011. Criteria of validity for animal models of psychiatric
1045 disorders: focus on anxiety disorders and depression. Biology of Mood & Anxiety
1046 Disorders 2011, 1:9
1047 Bildsoe, M., Heller, K.E., Jeppesen, L.L., 1990. Stereotypies in female ranch: mink seasonal
1048 and diurnal variation. Scientifur 14, 243-248.

1049 Bildsoe, M., Heller, K.E., Jeppesen, L.L., 1991. Effects of immobility stress and food
1050 restriction on stereotypes in low and high stereotyping female ranch mink. Behav.
1051 Processes 25, 179-189.
1052 Blackburn-Munro, G., Blackburn-Munro, R.E., 2001. Chronic pain, chronic stress and
1053 depression: Coincidence or consequence? J. Neuroendocrinol. 13, 1009-1023.
1054 Blanchard, D.C., Griebel, G., Pobbe, R., Blanchard, R.J., 2011. Risk assessment as an
1055 evolved threat detection and analysis process. Neurosci. Biobehav. Rev. 35, 991-998.
1056 Blanchard, D.C., Hynd, A.L., Minke, K.A., Minemoto, T., Blanchard, R.J., 2001. Human
1057 defensive behaviors to threat scenarios show parallels to fear- and anxiety-related defense
1058 patterns of non-human mammals. Neurosci. Biobehav. Rev. 25, 761-770.
1059 Boelsma, E., Brink, E.J., Stafleu, A., Hendriks, H.F.J., 2010. Measures of postprandial
1060 wellness after single intake of two protein-carbohydrate meals. Appetite 54, 456-464.
1061 Boissy, A., 1995. Fear and fearfulness in animals. Q. Rev. Biol. 70, 165-191.
1062 Bosch, G., Beerda, B., van de Hoek, E., Hesta, M., van der Poel, A.F.B., Janssens, G.P.J.,
1063 Hendriks, W.H., 2009. Effect of dietary fibre type on physical activity and behaviour in
1064 kennelled dogs. Appl. Anim. Behav. Sci. 121, 32-41.
1065 Bourjade, M., Moulinot, M., Richard-Yris, M.A., Hausberger, M., 2008. Could adults be used
1066 to improve social skills of young horses, *Equus caballus*? Dev. Psychobiol. 50, 408-417.
1067 Bouton, M.E., Bolles, R.C., 1980. Conditioned fear assessed by freezing and by the
1068 suppression of 3 different baselines. Anim. Learn. Behav. 8, 429-434.
1069 Boys, A., Marsden, J., Strang, J., 2001. Understanding reasons for drug use amongst young
1070 people: a functional perspective. Health Educ. Res. 16, 457.
1071 Bracha, H.S., 2004. Freeze, flight, fight, fright, faint: Adaptationist perspectives on the acute
1072 stress response spectrum. Cns Spectrums 9, 679-685.

1073 Braud, W.G., Ginsburg, H.J., 1973. Effect of administration of adrenaline on immobility
1074 reaction in domestic fowl. J. Comp. Physiol. Psychol. 83, 124-127.
1075 Bristow, D.J., Holmes, D.S., 2007. Cortisol levels and anxiety-related behaviors in cattle.
1076 Physiol. Behav.90, 626-628.
1077 Broom, D.M., 1988. The scientific assessment of animal-welfare. Appl. Anim. Behav. Sci.
1078 20, 5-19.
1079 Brune, M., Brune-Cohrs, U., McGrew, W.C., Preuschoft, S., 2006. Psychopathology in great
1080 apes: Concepts, treatment options and possible homologies to human psychiatric
1081 disorders. Neurosci. Biobehav. Rev. 30, 1246-1259.
1082 Burrell, A.M., Altman, J.D., 2006. The effect of the captive environment on activity of
1083 captive cotton-top tamarins (*Saguinus oedipus*). J Appl. Anim. Welf. Sci. 9(4), 269-276.
1084 Byrne, A., Byrne, D.G., 1993. The effect of exercise on depression, anxiety and other mood
1085 states - a review. J. Psychosom. Res. 37, 565-574.
1086 Cabanac, M., 1971. Physiological role of pleasure. Science 173, 1103-1107.
1087 Cahn, B.R., Polich, J., 2006. Meditation states and traits: EEG, ERP, and neuroimaging
1088 studies. Psychol Bull. 132, 180-211.
1089 Calderon, D.F., Cook, N.B., 2011. The effect of lameness on the resting behavior and
1090 metabolic status of dairy cattle during the transition period in a freestall-housed dairy herd.
1091 J. Dairy Sci. 94, 2883-2894.
1092 Campbell, S.S., 1992. The Timing and Structure of Spontaneaus Naps, in: Stampi, C. (Ed.),
1093 Why we nap: evolution, chronobiology, and functions of polyphasic and ultrashort sleep,
1094 Birkhauser, Boston, USA, pp. 71-81.
1095 Campbell, S.S., Tobler, I., 1984. Animal sleep - A review of sleep duration across phylogeny.
1096 Neurosci. Biobehav. Rev. 8, 269-300.

1097 Camus, S.M.J., Rochais, C., Blois-Heulin, C., Li, Q., Hausberger, M., Bezard, E., 2013. Birth
1098 origin differentially affects depressive- like behaviours: are captive- born cynomolgus
1099 monkeys more vulnerable to depression than their wild- born counterparts? PloS one 8,
1100 e67711.
1101 Carlson, N.R., 2012. Physiology of Behavior 11th Edition. Pearson Education Inc., Boston,
1102 USA.
1103 Carlstead, K., 1996. Effects of captivity on the behavior of wild mammals in: Kleiman, D.G.,
1104 Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity,
1105 University of Chicago Press, Chicago,pp. 317-333.
1106 Carlstead, K., Brown, J.L., Seidensticker, J., 1993a. Behavioral and adrenocortical responses
1107 to environmental-changes in leopard cats (Felis bengalensis). Zoo Biol. 12, 321-331.
1108 Carlstead, K., Brown, J.L., Strawn, W., 1993b. Behavioral and physiological correlates of
1109 stress in laboratory cats. Appl. Anim. Behav. Sci. 38, 143-158.
1110 Celli, M.L., Tomonaga, M., Udono, T., Teramoto, M., Nagano, K., 2003. Tool use task as
1111 environmental enrichment for captive chimpanzees. Appl. Anim. Behav. Sci. 81, 171-182.
1112 Chapinal, N., de Passille, A.M., Rushen, J., Wagner, S., 2010. Automated methods for
1113 detecting lameness and measuring analgesia in dairy cattle. J. Dairy Sci. 93, 2007-2013.
1114 Cheeta, S., Ruigt, G., vanProosdij, J., Willner, P., 1997. Changes in sleep architecture
1115 following chronic mild stress. Biol. Psychiatry 41, 419-427.
1116 Chourbaji, S., Zacher, C., Sanchis-Segura, C., Spanagel, R., Gass, P., 2005. Social and
1117 structural housing conditions influence the development of a depressive-like phenotype in
1118 the learned helplessness paradigm in male mice. Behav. Brain Res. 164, 100-106.
1119 Clark, S.L.L., F.H.Cutler,J.T., 1939. A form of congenital myotonia in goats. J. Nerv. Ment.
1120 Dis. 90, 297-309.

1121 Cockram, M.S., 2004. A review of behavioural and physiological responses of sheep to
1122 stressors to identify potential behavioural signs of distress. Anim. Welf. 13, 283-291.
1123 Cronbach, L.J., Meehl, P.E., 1955. Construct validity in psychological tests. Psychol. Bull.
1124 52, 281–302.
1125 Cooper, J.J., Odberg, F., Nicol, C.J., 1996. Limitations on the effectiveness of environmental
1126 improvement in reducing stereotypic behaviour in bank voles (*Clethrionomys glareolus*).
1127 Appl. Anim. Behav. Sci. 48, 237-248.
1128 Correia, A.D., Cunha, S.R., Scholze, M., Stevens, E.D., 2011. A Novel Behavioral Fish
1129 Model of Nociception for Testing Analgesics. Pharmaceuticals 4, 665-680.
1130 Crawford, K.M., Spotila, J.R., Standora, E.A., 1983. Operative environmental temperatures
1131 and basking behavior of the turtle *Pseudemys scripta*. Ecology 64, 989-999.
1132 Crawley, J.N., Hays, S.E., Paul, S.M., Goodwin, F.K., 1981. Cholecystokinin reduces
1133 exploratory-behavior in mice. Physiol. Behav.27, 407-411.
1134 Crawley, J.N., Rojasramirez, J.A., Mendelson, W.B., 1982. The role of central and peripheral
1135 cholecystokinin in mediating appetitive behaviors. Peptides 3, 535-538.
1136 Cryan, J.F., Markou, A., Lucki, I., 2002. Assessing antidepressant activity in rodents: recent
1137 developments and future needs. Trends Pharmacol. Sci. 23, 238-245.
1138 Csikszentmihalyi, M., 1975. Beyond Boredom and Anxiety: Experiencing Flow in Work and
1139 Play. Jossey-Bass, San Francisco.
1140 Csikszentmihalyi, M., 1990. Flow: The psychology of optimal experience. Harper & Row,
1141 New York.
1142 Dallaire, J.A., Meagher, R.K., Mason, G.J., 2012. Individual differences in stereotypic
1143 behaviour predict individual differences in the nature and degree of enrichment use in
1144 caged American mink. Appl. Anim. Behav. Sci. 142, 98-108.

1145 Dalm, S., de Visser, L., Spruijt, B.M., Oitzl, M.S., 2009. Repeated rat exposure inhibits the
1146 circadian activity patterns of C57BL/6J mice in the home cage. Behav. Brain Res. 196, 84-
1147 92.
1148 Dantzer, R., 2004. Cytokine-induced sickness behaviour: a neuroimmune response to
1149 activation of innate immunity. Eur. J. Pharmacol. 500, 399-411.
1150 David, M.M., Maclean, A.W., Knowles, J.B., Coulter, M.E., 1991. Rapid eye-movement
1151 latency and mood following a delay of bedtime in healthy-subjects: do the effects mimic
1152 changes in depressive-illness? Acta Psychiatr. Scand. 84, 33-39.
1153 Davis, K., Dimidjian, S., 2012. The Relationship Between Physical Activity and Mood
1154 Across the Perinatal Period: A Review of Naturalistic and Clinical Research to Guide
1155 Future Investigation of Physical Activity-Based Interventions for Perinatal Depression.
1156 Clin. Psychol. Science and Practice 19, 27-48.
1157 Dawkins, M.S., 1988. Behavioral deprivation - A central problem in animal-welfare. Appl.
1158 Anim. Behav. Sci. 20, 209-225.
1159 De Passillé, A.M.B., Christopherson, R., Rushen, J., 1993. Nonnutritive sucking by the calf
1160 and postprandial secretion of insulin, CCK, and gastrin. Physiol. Behav.54, 1069-1073.
1161 DeMonte, M., LePape, G., 1997. Behavioural effects of cage enrichment in single-caged
1162 adult cats. Anim. Welf. 6, 53-66.
1163 Deussing, J.M., 2006. Animal models of depression. Drug discovery today: disease models 3,
1164 375-383.
1165 DeVries, T.J., Beauchemin, K.A., Dohme, F., Schwartzkopf-Genswein, K.S., 2009. Repeated
1166 ruminal acidosis challenges in lactating dairy cows at high and low risk for developing
1167 acidosis: Feeding, ruminating, and lying behavior. J. Dairy Sci. 92, 5067-5078.
1168 Dhaenen, H., 1996. Measurement of anhedonia. Eur. Psychiatry 11, 335-343.

1169 Dielenberg, R.A., McGregor, I.S., 1999. Habituation of the hiding response to cat odor in rats
1170 (*Rattus norvegicus*). J Comp. Psychol.113, 376-387.
1171 Dixson, A., 2010. Homosexual behaviour in primates, in: Poiani, A. (Ed.), Animal
1172 homosexuality - a biosocial perspective, University Press, Cambridge, pp. 381-399.
1173 Downs, C.T., Greaver, C., Taylor, R., 2008. Body temperature and basking behaviour of Nile
1174 crocodiles (*Crocodylus niloticus*) during winter. J. Therm. Biol. 33, 185-192.
1175 Drury, D.A., Ferguson, S.A., Thomas, M.J.W., 2012. Restricted sleep and negative affective
1176 states in commercial pilots during short haul operations. Accid. Anal. Prev. 45, 80-84.
1177 Duncan, I.J.H. 2005. Science-based assessment of animal welfare: farm animals. Rev. Sci.
1178 Tech. Off. Int. Epiz. 24, 483-492.
1179 Duncan, I.J.H., 1970. Frustration in the fowl, in: Freeman, B.M., Gordon, R.F. (Eds.),
1180 Aspects of Poultry Behaviour, Edinburgh, UK, British Poultry Science Ltd., pp. 15–31.
1181 Dunn, A.L., Trivedi, M.H., O'Neal, H.A., 2001. Physical activity dose-response effects on
1182 outcomes of depression and anxiety. Med. Sci. Sports Exerc. 33, S587-S597.
1183 Eastwood, J.D., Frischen, A., Fenske, M.J., Smilek, D., 2012. The Unengaged Mind.
1184 Perspect. Psychol. Sci. 7, 482-495.
1185 Engel, C., 2002. Wild health - How animals keep themselves well and what we can learn
1186 from them. Weidenfeld and Nicolson, London.
1187 Engel, G.L., Schmale, A.H., 1972. Conservation-withdrawal: a primary regulatory process
1188 for organismic homeostasis, in: Elsevier (Ed.), Physiology, Emotion and Psychosomatic
1189 Illness, New York, pp. 57-75.
1190 Espejo, L.A., Endres, M.I., 2007. Herd-level risk factors for lameness in high-producing
1191 Holstein cows housed in freestall barns. J. Dairy Sci. 90, 306-314.

1192 Espmark, Y., Langvatn, R., 1985. Development and habituation of cardiac and behavioral-
1193 responses in young red deer calves (*cervus-elaphus*) exposed to alarm stimuli. J. Mammal.
1194 66, 702-711.
1195 Facchinetti, L.D., Imbiriba, L.A., Azevedo, T.M., Vargas, C.D., Volchan, E., 2006. Postural
1196 modulation induced by pictures depicting prosocial or dangerous contexts. Neurosci. Lett.
1197 410, 52-56.
1198 Falasco, J.D., Smith, G.P., Gibbs, J., 1979. Cholecystokinin suppresses sham feeding in the
1199 rhesus-monkey. Physiol. Behav.23, 887-890.
1200 Fanselow, M.S., 1982. The postshock activity burst. Anim. Learn. Behav. 10, 448-454.
1201 Fanselow, M.S., 1984. What is conditioned fear? Trends Neurosci. 7, 460-462.
1202 Fanselow, M.S., Helmstetter, F.J., 1988. Conditional analgesia, defensive freezing and
1203 benzodiazepines. Behav. Neurosci. 102, 233-243.
1204 Farook, J.M., McLachlan, C.S., Zhu, Y.Z., Lee, L., Moochhala, S.M., Wong, P.T.H., 2004.
1205 The CCK2 agonist BC264 reverses freezing behavior habituation in PVG hooded rats on
1206 repeated exposures to a cat. Neurosci. Lett. 355, 205-208.
1207 Faure, J.M., Guemene, D., Guy, G., 2001. Is there avoidance of the force feeding procedure
1208 in ducks and geese? Anim. Res. 50, 157-164.
1209 Fell, G.L., Robinson, K.C., Mao, J., Woolf, C.J., Fisher, D.E., 2014. Skin β-Endorphin
1210 Mediates Addiction to UV Light. Cell 157, 1527-1534.
1211 Ferdowsian, H.R., Durham, D.L., Kimwele, C., Kranendonk, G., Otali, E., Akugizibwe, T.,
1212 Mulcahy, J.B., Ajarova, L., Johnson, C.M., 2011. Signs of Mood and Anxiety Disorders in
1213 Chimpanzees. Plos One 6, e19855.
1214 Ferrara, M., De Gennaro, L., 2001. How much sleep do we need? Sleep Med. Rev. 5, 155-
1215 179.

1216 Fiske, D.W., Maddi, S.R., 1961. Functions of varied experience / [edited by] Donald W.
1217 Fiske and Salvatore R. Maddi ; with contributions by James Bieri. Homewood,Ill. :
1218 Dorsey, Homewood,Ill.
1219 Fordham, D.P., Algahtani, S., Durotoye, L.A., Rodway, R.G., 1991. Changes in plasma-
1220 cortisol and beta-endorphin concentrations and behavior in sheep subjected to a change of
1221 environment. Anim. Production 52, 287-296.
1222 Forkman, B., Boissy, A., Meunier-Salauen, M.C., Canali, E., Jones, R.B., 2007. A critical
1223 review of fear tests used on cattle, pigs, sheep, poultry and horses. Physiol. Behav. 92,
1224 340-374.
1225 Fox, M.W., 1968. Abnormal behavior in animals. W.B. Saunders Company, Philadelphia.
1226 Fraser, D., 2008. Understanding animal welfare: the science in its cultural context. Wiley-
1227 Blackwell, Oxford. 324 pages
1228 Fraser, D., Duncan, I.J.H., 1998. 'Pleasures','pains' and animal welfare: Toward a natural
1229 history of affect. Anim. Welf. 7, 383-396.
1230 Fuchs, E., Flugge, G., 2002. Social stress in tree shrews: Effects on physiology, brain
1231 function, and behavior of subordinate individuals. Pharmacol. Biochem. Behav. 73, 247-
1232 258.
1233 Fureix, C., Beaulieu, C., Argaud, S., Rochais, C., Quinton, M., Henry, S., Hausberger, M.,
1234 Mason, G., 2015. Investigating anhedonia in a non-conventional species: do some riding
1235 horses *Equus caballus* display symptoms of depression? Appl. Anim. Behav. Sci. 162, 26-
1236 36.
1237 Fureix, C., Jego, P., Henry, S., Lansade, L., Hausberger, M., 2012. Towards an Ethological
1238 Animal Model of Depression? A Study on Horses. Plos One 7, e39280.

1239 Galliano, G., Noble, L.M., Travis, L.A., Puechl, C., 1993. Victim reactions during
1240 rape/sexual assault - A preliminary study of the immobility response and its correlates. J.
1241 Interpers. Violence. 8, 109-114.
1242 Gallup, G.G., 1973. Tonic immobility in chickens - Is a stimulus that signals shock more
1243 aversive than receipt of shock. Anim. Learn. Behav. 1, 228-232.
1244 Gallup, G.G., 1974. Animal hypnosis: Factual status of a fictional concept. Psychol. Bull. 81,
1245 836-853.
1246 Gallup, G.G., Nash, R.F., Brown, C.W., 1971a. The effects of a tranquilizer on immobility
1247 reaction in chickens - Additional support for fear hypothesis. Psychon. Sci. 23, 127-128.
1248 Gallup, G.G., Nash, R.F., Potter, R.J., Donegan, N.H., 1970. Effect of varying conditions of
1249 fear on immobility reactions in domestic chickens (*Gallus gallus*). J. Comp. Physiol.
1250 Psychol. 73, 442-445.
1251 Gallup, G.G., Nash, R.F., Wagner, A.M., 1971b. Tonic immobility reaction in chickens -
1252 Response characteristics and methodology. Behavior Research Methods &
1253 Instrumentation 3, 237-239.
1254 Gallup, G.G., Williamson, G.T., 1972. Effect of food deprivation and a visual cliff on tonic
1255 immobility. Psychon. Sci. 29, 301-302.
1256 Garrick, L.D., 1979. Lizard Thermoregulation: Operant Responses for Heat at Different
1257 Thermal Intensities. Copeia 2, 258-266.
1258 Gilman, T.T., Marcuse, F.L., Moore, A.U., 1950. Animal hypnosis - A study in the induction
1259 of tonic immobility in chickens. J. Comp. Physiol. Psychol. 43, 99-111.
1260 Goats, G.C., 1994. Massage--the scientific basis of an ancient art: part 2. physiological and
1261 therapeutic effects. Br. J. Sports Med. 28, 153.
1262 Gotlib, I.H., Krasnoperova, E., 1998. Biased information processing as a vulnerability factor
1263 for depression. Behav. Ther. 29, 603-617.

1264 Graber, B., Rohrbaugh, J.W., Newlin, D.B., Varner, J.L., Ellingson, R.J., 1985. EEG during
1265 masturbation and ejaculation. Arch. Sex. Behav. 14, 491-503.
1266 Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis.
1267 Neuroscience and biobehavioral reviews, 29, 137-150.
1268 Hammen, C., Kim, E.Y., Eberhart, N.K., Brennan, P.A., 2009. Chronic and acute stress and
1269 the prediction of major depression in women. Depress. Anxiety. 26, 718-723.
1270 Hansen, S.W., Moller, S.H., 2008. Diurnal activity patterns of farm mink (*Mustela vison*)
1271 subjected to different feeding routines. Appl. Anim. Behav. Sci. 111, 146-157.
1272 Harlow, H., Suomi, S., 1974. Induced Depression in Monkeys. Behav. Biol. 12, 273–296.
1273 Harlow, H.F., Harlow, M.K., 1962. Social deprivation in monkeys. Sci. Am. 207, 136-146.
1274 Harris, M.B., 2000. Correlates and characteristics of boredom proneness and boredom. J.
1275 Appl. Soc. Psychol. 30, 576-598.
1276 Harrold, J.A., Doyey, T.M., Blundell, J.E., Halford, J.C.G., 2012. CNS regulation of appetite.
1277 Neuropharmacology 63, 3-17.
1278 Hart, B.L., 1988. Biological basis of the behavior of sick animals. Neurosci. Biobehav. Rev.
1279 12, 123-137.
1280 Heaman, M., Gupton, A., 1998. Perceptions of bed rest by women with high-risk
1281 pregnancies: A comparison between home and hospital. Birth-Issues in Perinatal Care 25,
1282 252-258.
1283 Heiderstadt, K.M., McLaughiin, R.M., Wright, D.C., Walker, S.E., Gomez-Sanchez, C.E.,
1284 2000. The effect of chronic food and water restriction on open-field behaviour and serum
1285 corticosterone levels in rats. Lab. Anim. 34, 20-28.
1286 Henn, F.A., Vollmayr, B., 2005. Stress models of depression: Forming genetically vulnerable
1287 strains. Neurosci. Biobehav. Rev. 29, 799-804.

1288 Hennessy, M.B., McCowan, B., Jiang, J., Capitanio, J.P., 2014. Depressive-like behavioral
1289 response of adult male rhesus monkeys during routine animal husbandry procedure.
1290 Frontiers in Behav. Neurosci. 8, 309.
1291 Hogan, L.A., Johnston, S.D., Lisle, A., Horsup, A.B., Janssen, T., Phillips, C.J.C., 2010.
1292 Stereotypies and environmental enrichment in captive southern hairy-nosed wombats,
1293 Lasiorhinus latifrons. Appl. Anim. Behav. Sci. 126, 85-95.
1294 Hopwood, N., Maswanganyi, T., Harden, L.M., 2009. Comparison of anorexia, lethargy, and
1295 fever induced by bacterial and viral mimetics in rats. Can. J. Physiol. Pharmacol. 87, 211-
1296 220.
1297 Hughes, S.M., Kruger, D.J., 2011. Sex Differences in Post-Coital Behaviors in Long- and
1298 Short-Term Mating: An Evolutionary Perspective. J. Sex. Res. 48, 496-505.
1299 Hunter, L., Houpt, K.A., 1989. Bedding material preferences of ponies. J. Anim. Sci. 67,
1300 1986-1991.
1301 Hurst, J.L., Barnard, C.J., Tolladay, U., Nevison, C.M., West, C.D., 1999. Housing and
1302 welfare in laboratory rats: effects of cage stocking density and behavioural predictors of
1303 welfare. Anim. Behav.58, 563-586.
1304 Inglis, I.R., 1983. Towards a cognitive theory of exploratory behavior, in: Archer, J., Birke,
1305 L.I.A. (Eds.), Exploration in animals and man, Van Nostrand Reinhold, London, UK, pp.
1306 72-115.
1307 Jones, M.A., Mason, G.J., Pillay, N., 2011. Correlates of birth origin effects on the
1308 development of stereotypic behaviour in striped mice, Rhabdomys. Anim. Behav.82, 149-
1309 159.
1310 Jones, R.B., 1992. The nature of handling immediately prior to test affects tonic immobility
1311 fear reactions in laying hens and broilers. Appl. Anim. Behav. Sci. 34, 247-254.

1312 Jones, R.B., Beuving, G., Blokhuis, H.J., 1988. Tonic immobility and heterophil lymphocyte
1313 responses of the domestic fowl to corticosterone infusion. Physiol. Behav.42, 249-253.
1314 Juliano, L.M., Griffiths, R.R., 2004. A critical review of caffeine withdrawal: empirical
1315 validation of symptoms and signs, incidence, severity, and associated features.
1316 Psychopharmacology 176, 1-29.
1317 Kilgour, R.J., 2012. In pursuit of "normal": A review of the behaviour of cattle at pasture.
1318 Appl. Anim. Behav. Sci. 138, 1-11.
1319 Kirkden, R.D., 2000. Assessing motivational strength and studies of boredom and enrichment
1320 in pigs, University of Cambridge.
1321 Klemm, W.R., 1966. Electroencephalographic-behavioral dissociations during animal
1322 hypnosis. Electroencephalogr. Clin. Neurophysiol. 21, 365.
1323 Knowles, R.D., 1981. Coping with lethargy. Am. J. Nurs. 81, 1465-1465.
1324 Knox, D., Fitzpatrick, C.J., George, S.A., Abelson, J.L., Liberzon, I., 2012. Unconditioned
1325 freezing is enhanced in an appetitive context: Implications for the contextual dependency
1326 of unconditioned fear. Neurobiol. Learn. Mem. 97, 386-392.
1327 Koistinen, T., Turunen, A., Kiviniemi, V., Ahola, L., Mononen, J., 2009. Bones as
1328 enrichment for farmed blue foxes (*Vulpes lagopus*): Interaction with the bones and
1329 preference for a cage with the bones. Appl. Anim. Behav. Sci. 120, 108-116.
1330 Konrad, K., W., Bagshaw, M., 1970. Effect of novel stimuli on cats reared in a restricted
1331 environment. J. Comp. Physiol. Psychol. 70, 157-164.
1332 Kortner, G., Geiser, F., 1999. Roosting behaviour of the tawny frogmouth (*Padargus*
1333 *strigoides*). J. Zool. 248, 501-507.
1334 Kry, K., Casey, R., 2007. The effect of hiding enrichment on stress levels and behaviour of
1335 domestic cats (*Felis sylvestris catus*) in a shelter setting and the implications for adoption
1336 potential. Anim. Welf. 16, 375-383.

1337 Leach, M.C., Allweiler, S., Richardson, C., Roughan, J.V., Narbe, R., Flecknell, P.A., 2009.
1338 Behavioural effects of ovariohysterectomy and oral administration of meloxicam in
1339 laboratory housed rabbits. Res. Vet. Sci. 87, 336-347.
1340 Leach, M.C., Klaus, K., Miller, A.L., di Perrotolo, M.S., Sotocinal, S.G., Flecknell, P.A.,
1341 2012. The Assessment of Post-Vasectomy Pain in Mice Using Behaviour and the Mouse
1342 Grimace Scale. Plos One 7(4), e35656.
1343 Leaton, R.N., Borszcz, G.S., 1985. Potentiated startle - Its relation to freezing and shock
1344 intensity in rats. J. Exp. Psychol. – Anim. Behav. Processes. 11, 421-428.
1345 Leslie, E., Hernandez-Jover, M., Newman, R., Holyoake, P., 2010. Assessment of acute pain
1346 experienced by piglets from ear tagging, ear notching and intraperitoneal injectable
1347 transponders. Appl. Anim. Behav. Sci. 127, 86-95.
1348 Levin, R.J., 2007. Sexual activity, health and well-being: the beneficial roles of coitus and
1349 masturbation. Sex. Relation. Ther. 22, 135-148.
1350 Levitis, D.A., Lidicker, J.Z., Freund, G., 2009. Behavioural biologists do not agree on what
1351 constitutes behaviour. Anim. Behav.78, 103-110.
1352 Lima, S.L., Rattenborg, N.C., Lesku, J.A., Amlaner, C.J., 2005. Sleeping under the risk of
1353 predation. Anim. Behav.70, 723-736.
1354 Lindwall, M., Larsman, P., Hagger, M.S., 2011. The Reciprocal Relationship Between
1355 Physical Activity and Depression in Older European Adults: A Prospective Cross-Lagged
1356 Panel Design Using SHARE Data. Health Psychol. 30, 453-462.
1357 Loas, G., Noisette, C., Legrand, A., Boyer, P., 2000. Is anhedonia a specific dimension in
1358 chronic schizophrenia? Schizophr. Bull. 26, 495-506.
1359 Lopes, F.L., Azevedo, T.M., Imbiriba, L.A., Freire, R.C., Valenca, A.M., Caldirola, D.,
1360 Perna, G., Volchan, E., Nardi, A.E., 2009. Freezing reaction in panic disorder patients
1361 associated with anticipatory anxiety. Depress. Anxiety. 26, 917-921.

1362 Louvart, N., Maccari, S., Ducrocq, F., Thomas, P., Darnaudery, M., 2005. Long-term
1363 behavioural alterations in female rats after a single intense footshock followed by
1364 situational reminders. Psychoneuroendocrinology 30, 316-324.
1365 Lush, J.L., 1930. "Nervous" goats. J. Hered. 21, 243-247.
1366 Luyten, L., Vansteenwegen, D., van Kuyck, K., Nuttin, B., 2011. Towards chronic contextual
1367 conditioning in rats: The effects of different numbers of unpaired tone-shock presentations
1368 on freezing time and startle. Acta Neurobiol. Exp. 71, 331-338.
1369 Maes, M., Berk, M., Goehler, L., Song, C., Anderson, G., Galecki, P., Leonard, B., 2012.
1370 Depression and sickness behavior are Janus-faced responses to shared inflammatory
1371 pathways. Bmc Med. 10, 19.
1372 Maier, S.F., 1984. Learned helplessness and animal-models of depression. Prog.
1373 Neuropsychopharmacol. Biol. Psychiatry. 8, 435-446.
1374 Maier, S.F., Seligman, M.E.P., 1976. Learned helplessness - Theory and evidence. J. Exp.
1375 Psychol. Gen. 105, 3-46.
1376 Marais, M., Maloneya, S.K., Graya, D.A., 2013. Sickness behaviours in ducks include
1377 anorexia but not lethargy. Appl. Anim. Behav. Sci. 145, 102-108.
1378 Maren, S., Fanselow, M.S., 1998. Appetitive motivational states differ in their ability to
1379 augment aversive fear conditioning in rats (*Rattus norvegicus*). J. Exp. Psychol. Anim.
1380 Behav. Processes. 24, 369-373.
1381 Marin, R.S., Wilkosz, P.A., 2005. Disorders of diminished motivation. J. Head. Trauma.
1382 Rehabil. 20(4), 377-88.
1383 Maslach, C., Schaufeli, W.B., Leiter, M.P., 2001. Job burnout. Annu. Rev. Psychol. 52, 397-
1384 422.
1385 Mason, G.J., Latham, N.R., 2004. Can't stop, won't stop: is stereotypy a reliable animal
1386 welfare indicator? Anim. Welf. 13, 57-69.

1387 Mason, G.J., Veasey, J.S., 2010. How should the psychological well- being of zoo elephants
1388 be objectively investigated? Zoo Biol. 29, 237-255.
1389 Matthews, K., Christmas, D., Swan, J., Sorrell, E., 2005. Animal models of depression:
1390 navigating through the clinical fog. Neurosci. Biobehav. Rev. 29, 503-513.
1391 Maurice-Tison, S., Verdoux, H., Gay, B., Perez, P., Salamon, R., Bourgeois, M.L., 1998.
1392 How to improve recognition and diagnosis of depressive syndromes using international
1393 diagnostic criteria. Br. J. Gen. Pract. 48, 1245-1246.
1394 McArthur, R., Borsini, F., 2006. Animal models of depression in drug discovery: A historical
1395 perspective. Pharmacol. Biochem. Behav. 84, 436-452.
1396 McFarland, D., 1989. Longman Scientific & Technical, Wiley, Harlow Essex New York.
1397 McGrath, P.J., Rosmus, C., Canfield, C., Campbell, M.A., Hennigar, A., 1998. Behaviours
1398 caregivers use to determine pain in non-verbal, cognitively impaired individuals. Dev.
1399 Med. Child. Neurol. 40, 340-343.
1400 McPhee, M.E., 2004. Generations in captivity increases behavioral variance: considerations
1401 for captive breeding and reintroduction programs. Biol. Conserv. 115, 71-77.
1402 McPhee, M.E., Carlstead, K., 2010. The Importance of Maintaining Natural Behaviors in
1403 Captive Mammals, in: Kleiman, D.G., Thompson, K.V., Baer, C.K. (Eds.), Wild
1404 Mammals in Captivity, Principles and techniques for zoo management, second edition,
1405 University of Chicago Press, Chicago, pp. 303-313.
1406 Meagher, R.K., Campbell, D.L.M., Dallaire, J.A., Diez-Leon, M., Palme, R., Mason, G.J.,
1407 2013. Sleeping tight or hiding in fright? The welfare implications of different subtypes of
1408 inactivity in mink. Appl. Anim. Behav. Sci. 144, 138-146.
1409 Meagher, R.K., Mason, G.J., 2012. Environmental Enrichment Reduces Signs of Boredom in
1410 Caged Mink. Plos One 7(11), e49180.

1411 Meerlo, P., DeBoer, S.F., Koolhaas, J.M., Daan, S., VandenHoofdakker, R.H., 1996a.
1412 Changes in daily rhythms of body temperature and activity after a single social defeat in
1413 rats. Physiol. Behav.59, 735-739.
1414 Meerlo, P., Overkamp, G.J.F., Benning, M.A., Koolhaas, J.M., vandenHoofdakker, R.H.,
1415 1996b. Long-term changes in open field behaviour following a single social defeat in rats
1416 can be reversed by sleep deprivation. Physiol. Behav.60, 115-119.
1417 Meerlo, P., Turek, F.W., 2001. Effects of social stimuli on sleep in mice: non-rapid-eye-
1418 movement (NREM) sleep is promoted by aggressive interaction but not by sexual
1419 interaction. Brain Res. 907, 84-92.
1420 Mendl, M., Burman, O.H.P., Paul, E.S., 2010. An integrative and functional framework for
1421 the study of animal emotion and mood. Proc. Biol. Sci. B. 277, 2895-2904.
1422 Mewaldt, L.R., Rose, R.G., 1960. Orientation of migratory restlessness in the white-crowned
1423 sparrow. Science 131, 105-106.
1424 Michel, G., Carton, S., Jouvent, R., 1997. Sensation seeking and anhedonia in risk taking
1425 behaviors. Study in bungee jumpers. Enceph.-Rev. Psychiatr. Clin. Biol. Ther. 23, 403-
1426 411.
1427 Mikulas, W.L., Vodanovich, S.J., 1993. The essence of boredom. Psychol. Rec. 43, 3-12.
1428 Miller, G.E., Chen, E., Zhou, E.S., 2007. If it goes up, must it come down? Chronic stress and
1429 the hypothalamic-pituitary-adrenocortical axis in humans. Psychol Bull. 133, 25-45.
1430 Mills, D.S., Eckley, S., Cooper, J.J., 2000. Thoroughbred bedding preferences, associated
1431 behaviour differences and their implications for equine welfare. Anim. Sci. 70, 95-106.
1432 Mineka, S., Hendersen, R.W., 1985. Controllability and predictability in acquired motivation.
1433 Annu. Rev. Psychol. 36, 495-529.

1434 Mongeluzi, D.L., Rosellini, R.A., Ley, R., Caldarone, B.J., Stock, H.S., 2003. The
1435 conditioning of dyspneic suffocation fear - Effects of carbon dioxide concentration on
1436 behavioral freezing and analgesia. Behav. Modif. 27, 620-636.
1437 Mormede, P., Andanson, S., Auperin, B., Beerda, B., Guemene, D., Malnikvist, J., Manteca,
1438 X., Manteuffel, G., Prunet, P., van Reenen, C.G., Richard, S., Veissier, I., 2007.
1439 Exploration of the hypothalamic-pituitary-adrenal function as a tool to evaluate animal
1440 welfare. Physiol. Behav.92, 317-339.
1441 Muhsen, K., Garty-Sandalon, N., Gross, R., Green, M.S., 2010. Psychological distress is
1442 independently associated with physical inactivity in Israeli adults. Preventive Med. 50,
1443 118-122.
1444 Nash, R.F., Gallup, G.G., Czech, D.A., 1976. Psychophysiological correlates of tonic
1445 immobility in domestic chicken (*Gallus gallus*). Physiol. Behav.17, 413-418.
1446 Nimon, A.J., Broom, D.M., 1999. The welfare of farmed mink (*Mustela vison*) in relation to
1447 housing and management: A review. Anim. Welf. 8, 205-228.
1448 Nowak, R., 2006. Suckling, Milk, and the Development of Preferences Toward Maternal
1449 Cues by Neonates: From Early Learning to Filial Attachment? Adv. Study. Behav. 36, 1-
1450 58.
1451 O'Callaghan, K.A., Cripps, P.J., Downham, D.Y., Murray, R.D., 2003. Subjective and
1452 objective assessment of pain and discomfort due to lameness in dairy cattle. Anim. Welf.
1453 12, 605-610.
1454 Offinger, J., Herdtweck, S., Rizk, A., Starke, A., Heppelmann, M., Meyer, H., Janssen, S.,
1455 Beyerbach, M., Rehage, J., 2013. Postoperative analgesic efficacy of meloxicam in lame
1456 dairy cows undergoing resection of the distal interphalangeal joint. J. Dairy Sci. 96, 866-
1457 876.

1458 Orr, W.C., Shadid, G., Harnish, M.J., Elsenbruch, S., 1997. Meal composition and its effect
1459 on postprandial sleepiness. Physiol. Behav.62, 709-712.
1460 Pack, A.I., Galante, R.J., Maislin, G., Cater, J., Metaxas, D., Lu, S., Zhang, L., Von Smith,
1461 R., Kay, T., Lian, J., Svenson, K., Peters, L.L., 2007. Novel method for high-throughput
1462 phenotyping of sleep in mice. Physiol. Genomics 28, 232-238.
1463 Panksepp, J., 2005. Affective consciousness: Core emotional feelings in animals and humans.
1464 Conscious. Cogn. 14, 30-80.
1465 Paquette, D., Prescott, J., 1988. Use of novel objects to enhance environments of captive
1466 chimpanzees. Zoo Biol. 7, 15-23.
1467 Paterson, L.M., Nutt, D.J., Wilson, S.J., 2009. NAPSAQ-1: National Patient Sleep
1468 Assessment Questionnaire in depression. Int. J. Psychiatry Clin. Pract. 13, 48-58.
1469 Pattyn, N., Neyt, X., Heridericlcx, D., Soetens, E., 2008. Psychophysiological investigation
1470 of vigilance decrement: Boredom or cognitive fatigue? Physiol. Behav. 93, 369-378.
1471 Pedersen, G.R., Sondergaard, E., Ladewig, J., 2004. The influence of bedding on the time
1472 horses spend recumbent. J. Equine Vet. Sci. 24, 153-158.
1473 Pellow, S., Chopin, P., File, S.E., Briley, M., 1985. Validation of open-closed arm entries in
1474 an elevated plus-maze as a measure of anxiety in the rat. J. Neurosci. Methods. 14, 149-
1475 167.
1476 Pepelko, W.E., Clegg, M.T., 1965. Studies of mating behaviour and some factors influencing
1477 the sexual response in the male sheep Ovis aries. Anim. Behav.13, 249-258.
1478 Porsolt, R.D., Bertin, A., Jalfre, M., 1977. Behavioral despair in mice - primary screening-test
1479 for antidepressants. Archives Internationales De Pharmacodynamie Et De Therapie 229,
1480 327-336.
1481 Prescott, R.G., 1970. Some behavioural effects of variables which influence general level of
1482 activity of rats. Anim. Behav.18, 791-796.

1483 Pritchard, V.L., Lawrence, J., Butlin, R.K., Krause, J., 2001. Shoal choice in zebrafish, Danio
1484 rerio: the influence of shoal size and activity. Anim. Behav.62, 1085-1088.
1485 Pritchett, L.C., Ulibarri, C., Roberts, M.C., Schneider, R.K., Sellon, D.C., 2003.
1486 Identification of potential physiological and behavioral indicators of postoperative pain in
1487 horses after exploratory celiotomy for colic. Appl. Anim. Behav. Sci. 80, 31-43.
1488 Purves, D., Augustine, G.J., Fitzpatrick, D., Hall, W.C., LaMantia, A.-S., McNamara, J.O.,
1489 White, L.E., 2007. Neuroscience Fourth Edition. Sinauer Associates, Inc., Sunderland,
1490 USA.
1491 Raabymagle, P., Ladewig, J., 2006. Lying behavior in horses in relation to box size. J. Equine
1492 Vet. Sci. 26, 11-17.
1493 Riber, A.B., Forkman, B., 2007. A note on the behaviour of the chicken that receives feather
1494 pecks. Appl. Anim. Behav. Sci. 108, 337-341.
1495 Richmond, M.A., Murphy, C.A., Pouzet, B., Schmid, P., Rawlins, J.N.P., Feldon, J., 1998. A
1496 computer controlled analysis of freezing behaviour. J. Neurosci. Methods. 86, 91-99.
1497 Richter, C.P.A., 1922. A behavioristic study of the activity of the rat. Comp. Psychol.
1498 Monogr. 1, 1-55.
1499 Rochlitz, I., Podberscek, A.L., Broom, D.M., 1998. Welfare of cats in a quarantine cattery.
1500 Vet. Rec. 143, 35-39.
1501 Rodgers, R.J., Holch, P., Tallett, A.J., 2010. Behavioural satiety sequence (BSS) Separating
1502 wheat from chaff in the behavioural pharmacology of appetite. Pharmacol. Biochem.
1503 Behav. 97, 3-14.
1504 Rozek, J.C., Danner, L.M., Stucky, P.A., Millam, J.R., 2010. Over-sized pellets naturalize
1505 foraging time of captive Orange-winged Amazon parrots (*Amazona amazonica*). Appl.
1506 Anim. Behav. Sci. 125, 80-87.

1507 Rucker, D.D., Petty, R.E., 2004. Emotion specificity and consumer behavior: Anger, sadness,
1508 and preference for activity. Motiv. Emot. 28, 3-21.
1509 Rushen, J., 1991. Problems associated with the interpretation of physiological data in the
1510 assessment of animal-welfare. Appl. Anim. Behav. Sci. 28, 381-386.
1511 Rushen, J., Munksgaard, L., Marnet, P.G., DePassille, A.M., 2001. Human contact and the
1512 effects of acute stress on cows at milking. Appl. Anim. Behav. Sci. 73, 1-14.
1513 Russell, J.A., Barrett, L.F., 1999. Core Affect, Prototypical Emotional Episodes, and Other
1514 Things Called Emotion : Dissecting the Elephant. J. Pers. Soc. Psychol. 76, 805-819.
1515 Sam, A.H., Troke, R.C., Tan, T.M., Bewick, G.A., 2012. The role of the gut/brain axis in
1516 modulating food intake. Neuropharmacology 63, 46-56.
1517 Samuels, D.J., Samuels, M., 1974. Low Self- Concept As A Cause of Drug Abuse. J. Drug
1518 Educ. 4, 421-436.
1519 Santos, J.M., Gargaro, A.C., Oliveira, A.R., Masson, S., Brandao, M.L., 2005.
1520 Pharmacological dissociation of moderate and high contextual fear as assessed by freezing
1521 behavior and fear-potentiated startle. Eur. Neuropsychopharmacol. 15, 239-246.
1522 Sargeant, A.B., Eberhardt, L.E., 1975. Death feigning by ducks in response to predation by
1523 red foxes (*Vulpes fulva*). Am. Midl. Nat. 94, 108-119.
1524 Schelde, J.T.M., 1998. Major depression: Behavioral markers of depression and recovery. J.
1525 Nerv. Ment. Dis. 186, 133-140.
1526 Schirmann, K., Chapinal, N., Weary, D.M., Heuwieser, W., von Keyserlingk, M.A.G., 2011.
1527 Short-term effects of regrouping on behavior of prepartum dairy cows. J. Dairy Sci. 94,
1528 2312-2319.
1529 Schirmann, K., Chapinal, N., Weary, D.M., Heuwieser, W., von Keyserlingk, M.A.G., 2012.
1530 Rumination and its relationship to feeding and lying behavior in Holstein dairy cows. J.
1531 Dairy Sci. 95, 3212-3217.

1532 Schradin, C., Krackow, S., Schubert, M., Keller, C., Schradin, B., Pillay, N., 2007.
1533 Regulation of activity in desert-living striped mice: The importance of basking. Ethology
1534 113, 606-614.
1535 Schulz, K.L., Anderson, D.E., Coetzee, J.F., White, B.J., Miesner, M.D., 2011. Effect of
1536 flunixin meglumine on the amelioration of lameness in dairy steers with amphotericin B-
1537 induced transient synovitis-arthritis. Am. J. Vet. Res. 72, 1431-1438.
1538 Seehuus, B., Mendl, M., Keeling, L.J., Blokhuis, H., 2013. Disrupting motivational
1539 sequences in chicks: Are there affective consequences? Appl. Anim. Behav. Sci. 148, 85-
1540 92.
1541 Seime, R.J., Vickers, K.S., 2006. The challenges of treating depression with exercise: From
1542 evidence to practice. Clin. Psychol. Science and Practice 13, 194-197.
1543 Seligman, M.E.P., 1972. Learned Helplessness. Annu. Rev. Med. 23, 407-412.
1544 Shuhama, R., Del-Ben, C.M., Loureiro, S.R., Graeff, F.G., 2008. Defensive responses to
1545 threat scenarios in Brazilians reproduce the pattern of Hawaiian Americans and non-
1546 human mammals. Braz. J. Med. Biol. Res. 41, 324-332.
1547 Siegrist, J., 2008. Chronic psychosocial stress at work and risk of depression: evidence from
1548 prospective studies. Eur. Arch. Psychiatry Clin. Neurosci. 258, 115-119.
1549 Stacher, G., Bauer, H., Steinringer, H., 1979. Cholecystokinin decreases appetite and
1550 activation evoked by stimuli arising from the preparation of a meal in man. Physiol.
1551 Behav.23, 325-331.
1552 Stacher, G., Steinringer, H., Schmierer, G., Schneider, C., Winklehner, S., 1982.
1553 Cholecystokinin octapeptide decreases intake of solid food in man. Peptides 3, 133-136.
1554 Steenbergen, P.J., Bardine, N., 2014. Antinociceptive effects of buprenorphine in zebrafish
1555 larvae: An alternative for rodent models to study pain and nociception? Appl. Anim.
1556 Behav. Sci. 152, 92-99.

1557 Stevenson, M.F., 1983. The captive environment: its effect on exploratory and related
1558 behavioural responses in wild animals, in: Archer, J., Birke, L.I.A. (Eds.), Exploration in
1559 Animals and Man, Van Nostrand Reinhold, London, UK, pp. 176-197.
1560 Strekalova, T., Spanagel, R., Bartsch, D., Henn, F.A., Gass, P., 2004. Stress-induced
1561 anhedonia in mice is associated with deficits in forced swimming and exploration.
1562 Neuropsychopharmacology 29, 2007-2017.
1563 Suomi, S.J., Eisele, C.D., Grady, S.A., Harlow, H.F., 1975. Depressive behavior in adult
1564 monkeys following separation from family environment. J. Abnorm. Psychol. 84, 576-
1565 578.
1566 Tait, R.C., Chibnall, J.T., Krause, S., 1990. The pain disability index: psychometric
1567 properties. Pain 40, 171-182.
1568 Taylor, L., Cohen, S., 1972. Psychological Survival: the Experience of Long Term
1569 Imprisonment. Penguin Books Ltd, Harmondsworth, USA.
1570 Temeles, E.J., 1989. Effect of prey consumption on foraging activity of northern harriers.
1571 Auk. 106, 353-366.
1572 Thompson, R.K.R., Foltin, R.W., Boylan, R.J., Sweet, A., Graves, C.A., Lowitz, C.E., 1981.
1573 Tonic immobility in Japanese quail can reduce the probability of sustained attack by cats.
1574 Anim. Learn. Behav. 9, 145-149.
1575 Tilly, S.L.C., Dallaire, J., Mason, G.J., 2010. Middle-aged mice with enrichment-resistant
1576 stereotypic behaviour show reduced motivation for enrichment. Anim. Behav.80, 363-373.
1577 Tripaldi, C., De Rosa, G., Grasso, F., Terzano, G.M., Napolitano, F., 2004. Housing system
1578 and welfare of buffalo (*Bubalus bubalis*) cows. Anim. Sci. 78, 477-483.
1579 Twenge, J.M., Catanese, K.R., Baumeister, R.F., 2003. Social exclusion and the
1580 deconstructed state: Time perception, meaninglessness, lethargy, lack of emotion, and
1581 self-awareness. J. Pers. Soc. Psychol. 85, 409-423.

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

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

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

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

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

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

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

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

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

1607 Portella, C., Figueira, I., 2011. Is there tonic immobility in humans? Biological evidence
1608 from victims of traumatic stress. Biol. Psychol. 88, 13-19.
1609 Wagnon, K.A., 1963. Behavior of beef cows on a California range. California Agricultural
1610 Experiment Station Bulletin 799, 60.
1611 Wallace, K.J., Rosen, J.B., 2000. Predator odor as an unconditioned fear stimulus in rats:
1612 Elicitation of freezing by trimethylthiazoline, a component of fox feces. Behav. Neurosci.
1613 114, 912-922.
1614 Waring, G., 2003. Horse Behavior, second edition. Noyes Publications/William Andrew
1615 Publishing, Norwich, New York.
1616 Weeks, C.A., Danbury, T.D., Davies, H.C., Hunt, P., Kestin, S.C., 2000. The behaviour of
1617 broiler chickens and its modification by lameness. Appl. Anim. Behav. Sci. 67, 111-125.
1618 Weiner, M.F., Lovitt, R., 1979. Conservation-withdrawal versus depression. Gen. Hosp.
1619 Psychiatry. 1(4), 347-349.
1620 Weinger, M.B., Ancoli-Israel, S., 2002. Sleep deprivation and clinical performance. Jama-
1621 JAMA 287, 955-957.
1622 Wells, D.L., 2004. A review of environmental enrichment for kennelled dogs, Canis
1623 familiaris. Appl. Anim. Behav. Sci. 85, 307-317.
1624 Wells, D.L., 2005. A note on the influence of visitors on the behaviour and welfare of zoo-
1625 housed gorillas. Appl. Anim. Behav. Sci. 93, 13-17.
1626 Wemelsfelder, F., 1990. Boredom and Laboratory Animal Welfare, in: Rollin, B.E., Kesel,
1627 M.L. (Eds.), The Experimental Animal in Biomedical Research, CRC-Press, Boca Raton,
1628 Florida, pp. 243-272.
1629 Werhahn, H., Hessel, E.F., Bachhausen, I., Van den Weghe, H.F.A., 2010. Effects of
1630 Different Bedding Materials on the Behavior of Horses Housed in Single Stalls. J. Equine
1631 Vet. Sci. 30, 425-431.

1632 Whishaw, I.Q., Flannigan, K.P., Schallert, T., 1982. An assessment of the state hypothesis of
1633 animal 'hypnosis' through an analysis of neocortical and hippocampal EEG in
1634 spontaneously immobile and hypnotized rabbits. Electroencephalogr. Clin. Neurophysiol.
1635 54, 365-374.
1636 Wiedenmayer, C.P., Barr, G.A., 2001. Developmental changes in responsivity to threat are
1637 stimulus-specific in rats. Dev. Psychobiol. 39, 1-7.
1638 Wielebnowski, N.C., Fletchall, N., Carlstead, K., Busso, J.M., Brown, J.L., 2002.
1639 Noninvasive assessment of adrenal activity associated with husbandry and behavioral
1640 factors in the North American clouded leopard population. Zoo Biol. 21, 77-98.
1641 Willner, P., McGuirk, J., Phillips, G., Muscat, R., 1990. Behavioral-analysis of the anorectic
1642 effects of fluoxetine and fenfluramine. Psychopharmacology 102, 273-277.
1643 Wise, R.A., 1974. Lateral hypothalamic electrical stimulation: Does it make animals
1644 'hungry'? Brain Res. 67, 187-209.
1645 Wiseman, M.L., Nolan, A.M., Reid, J., Scott, E.M., 2001. Preliminary study on owner-
1646 reported behaviour changes associated with chronic pain in dogs. Vet. Rec. 149, 423-424.
1647 Woodgush, D.G.M., Beilharz, R.G., 1983. The enrichment of a bare environment for animals
1648 in confined conditions. Appl. Anim. Ethol. 10, 209-217.
1649 World Health Organisation, 1994. International Statistical Classification of Diseases and
1650 Related Health Problems. World Health Organisation, Geneva.
1651 Wurbel, H., Chapman, R., Rutland, C., 1998a. Effect of feed and environmental enrichment
1652 on development of stereotypic wire-gnawing in laboratory mice. Appl. Anim. Behav. Sci.
1653 60, 69-81.
1654 Wurbel, H., Freire, R., Nicol, C.J., 1998b. Prevention of stereotypic wire-gnawing in
1655 laboratory mice: Effects on behaviour and implications for stereotypy as a coping
1656 response. Behav. Processes 42, 61-72.

1657 Zammit, G.K., Ackerman, S.H., Shindledecker, R., Fauci, M., Smith, G.P., 1992.
1658 Postprandial sleep and thermogenesis in normal men. Physiol. Behav.52, 251-259.
1659 Zanella, A.J., Broom, D.M., Hunter, J.C., Mendl, M.T., 1996. Brain opioid receptors in
1660 relation to stereotypies, inactivity, and housing in sows. Physiol. Behav.59, 769-775.
1661 Zeidner, L.P., Denenberg, V.H., Thoman, E.B., Weyand, T., 1983. Comparisons of
1662 behavioral, motoric and electrical criteria for assessment of sleep-wake states in the rabbit.
1663 Physiol. Behav.31, 273-278.
1664 Zonderland, J.J., de Leeuw, J.A., Nolten, C., Spoolder, H.A.M., 2004. Assessing long-term
1665 behavioural effects of feeding motivation in group-housed pregnant sows; what, when and
1666 how to observe. Appl. Anim. Behav. Sci. 87, 15-30.
1667
1668