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

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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

40   welfare studies: specific forms of inactivity identified in this paper are, or have the potential

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

42

43   **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

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[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

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

2. How is inactivity defined and measured?

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

167 hyperactivity or decreases in activity during anticipation, but actually measures the number of

168 behavioural transitions rather than total amount of time spent moving or stationary (*e.g.* van

169 den Bos et al., 2003). Studies using any of these definitions of inactivity will be discussed

170 here.

171

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

173 Increased inactivity likely to be associated with negative affective states will be

174 considered here, distinguishing specific forms of inactivity expressed in response to a

175 perceived threat (likely to be associated with negative high-arousal affective states, Mendl et

176 al., 2010, cf. Introduction) from those expressed in situations where threat levels but also

177 chances of getting rewards are low (likely to be associated with negative low-arousal

178 affective states).

179

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

181 Inactivity that may occur in response to a perceived (frightening) threat stimulus will be

182 presented here, targeting more specifically the freezing, tonic immobility and hiding

183 responses.

184

185 **Freezing** (sometimes also termed *attentive immobility*) is a common response in the face

186 of an immediate (perceived) threat in various species, where an individual becomes abruptly

187 motionless, monitoring a perceived source of danger (reviewed by Boissy, 1995). A

188 'freezing-like' state, characterised by increased immobility and rigidity (quantified using a

189 force platform) and a reduced heart rate (also termed 'fear bradycardia'), has been described

190 in humans. This state has been observed in healthy people viewing pictures of mutilation

191 (that they self-rated as negative in valence and high in arousal) compared to neutral or

192   positively rated pictures (Azevedo et al., 2005; Facchinetti et al., 2006), as well as in patients

193   diagnosed with panic disorders when seeing either pictures of mutilation or images that were

194   anxiogenic due to their pathologies (*e.g.* crowded areas for agoraphobic patients), compared

195   to neutral pictures (Lopes et al., 2009).

196   In animals, freezing is used to quantify fearfulness in many behavioural tests (see *e.g.*

197   Bouton and Bolles, 1980; Forkman et al., 2007). It has been particularly well-described in

198   rodents, on which we will focus here, and can be operationally defined as 'the absence of all

199   visible movement of the body and vibrissae, except for movements necessitated by

200   respiration' (Fanselow, 1982). The description can also include (species-specific) postural

201   elements, such as a 'characteristic immobile, crouching posture' in rats, and autonomic

202   changes, *i.e.* a decreased heart rate (similarly to the 'fear bradychardia' recorded in freezing

203   humans) and an increased respiratory rate (Fanselow, 1984). Freezing can be induced by

204   exposing rats to a predator odour (*e.g.* Wallace and Rosen, 2000; Knox et al., 2012), as well

205   as to conditioned stimuli or contexts paired with aversive experiences (electric shocks: *e.g.*

206   Fanselow, 1984; Richmond et al., 1998; Luyten et al., 2011; carbon dioxide inducing

207   dyspnoeic suffocation: Mongeluzi et al., 2003). The more intense the aversive stimuli are, the

208   longer the rats remain frozen (Fanselow and Helmstetter, 1988; Wallace and Rosen, 2000;

209   Mongeluzi et al., 2003; Santos et al., 2005, but see Leaton and Borszcz, 1985 for non-

210   monotonic effects). Freezing is 'not a simple suppression of activity' (Fanselow, 1984) but a

211   highly aroused state (Bracha, 2004): rats' percentage of time spent freezing when exposed to

212   a conditioned stimulus previously paired with electric shock was positively correlated with

213   the amplitude of their acoustic startle response in the presence of that conditioned stimulus

214   (Leaton and Borszcz, 1985). Interestingly, neither food deprivation (an aversive experience

215   but not assumed to induce 'fear', Maren and Fanselow, 1998; Heiderstadt et al., 2000), nor

216   exposure to smells unrelated to predation (*e.g.* butyric acid, banana and pear odours, Wallace

217 and Rosen, 2000; Knox et al., 2012) induce freezing responses. Moreover, in rats where the

218 risk of infanticide by unrelated adult males ends around weaning, exposure to a sexually

219 experienced, unrelated male rat induces freezing in young rats only before they reach a

220 natural weaning age (around 26 d), whereas exposure to a cat odour (a predation risk relevant

221 during all life stages) induces the freezing response in rats before and after weaning age

222 (Wiedenmayer and Barr, 2001). Additional evidence that the freezing response is associated

223 with negative valence in rodents comes from pharmacological corroboration: in rats, while

224 freezing in response to a cat exposure was gradually suppressed over repeated daily exposure

225 (Farook et al., 2004), administration of anxiogenic drugs restores the freezing behaviour.

226 Conversely, the administration of anxiolytic drugs (*e.g.* midazolam, diazepam) reduces the

227 duration of rats' place-conditioned freezing response (Fanselow and Helmstetter, 1988;

228 Verleye and Gillardin, 2004; Santos et al., 2005).

229

230 Another specific form of inactivity also displayed in response to a threat in various species

231 is **tonic immobility (TI)** (*e.g.* Gallup et al., 1971b). In humans, 'TI-like' states are

232 characterised by a temporary behavioural state of motor inhibition, associated with tremors,

233 eye closure, increased breathing, and coldness, and have been reported to occur in response to

234 situations involving intense fear and physical restraint such as interpersonal trauma (sexual

235 assault, torture, armed robbery)[2] (Galliano et al., 1993; Abrams et al., 2009). Although such

236 studies are non-experimental in nature (and therefore results may not be generalised to any

237 human population), TI-like responses appear to be far from uncommon. For example, across

238 several studies reviewed in Galliano et al. (1993), from 12% to 50% of the studied victims of

239 rape/sexual assaults were 'paralyzed' motionless and did not resist their attackers in any way.

240 Displaying TI-like responses during traumatic episodes has also been reported to positively

---

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

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

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

266 (Gallup et al., 1970; Gallup, 1973), rough handling (bird inverted for 30s: laying hens and

267 broilers, Jones, 1992), and exposure to loud noise (Gallup et al., 1970). While freezing in

268 rodents appears to be a risk-assessment behaviour to a (perceived) distant threat (Blanchard et

269 al., 2011), TI happens *following physical restraint*, and has been suggested to be an anti-

270 predation response even after the animal has been captured. Such 'death-feigning' might

271 induce the predator to loosen its hold (Gilman et al., 1950; Engel and Schmale, 1972;

272 Sargeant and Eberhardt, 1975; see Thompson et al., 1981 for evidence TI can deter

273 predators). This response seems specific to fear-inducing situations: food-depriving chickens,

274 which is aversive but not likely frightening, does not increase these animals' TI duration

275 (Gallup and Williamson, 1972). Additional evidence supporting the negative valence and

276 high arousal of the TI response in birds comes from pharmacological validation: in chicks,

277 pre-TI-induction administration of adrenaline (Braud and Ginsburg, 1973) and corticosterone

278 (Jones et al., 1988) increases the TI duration and/or the propensity of birds to display TI,

279 while a pre-TI-induction tranquilizer injection reduces the duration of the TI response (Gallup

280 et al., 1971a).

281

282 Another -- perhaps less species-specific -- form of inactivity that can be displayed in

283 response to a perceived threat is **hiding.** In humans, hiding (protecting oneself behind

284 something) is one of the defensive strategies chosen by subjects in laboratory studies in

285 response to fearful threat scenarios such as *'Late at night… you are sleeping alone in your*

286 *bed. You suddenly wake up feeling that you heard a suspicious noise'*. Not surprisingly, the

287 presence of a place of concealment or protection in the scenario promoted the hiding choice;

288 so did distant (rather than close) threat stimuli (Blanchard et al., 2001; Shuhama et al., 2008).

289 In animals, hiding can be defined operationally using location (provided that there are

290 locations suitable for hiding in the environment): hiding animals are 'remaining stationary

291 and out of sight or camouflaged using any kind of shelter or visual barrier' (Meagher et al.,

292 2013). In rodents, exposure to a predator or to its odour initially induces a hiding response

293 (*e.g.* rats exposed to a worn cat collar: Dielenberg and McGregor, 1999; mice repeatedly

294 exposed to a rat moving around on top of their cages: Dalm et al., 2009). In laboratory cats,

295 exposure to complex stressors (involving unpredictable mildly aversive procedures) increases

296 time spent awake/alert and attempting to hide, and suppresses active exploratory and play

297 behaviour (Carlstead et al., 1993b). Translocation to novel environments also induces hiding

298 in felids (leopard cats: Carlstead et al., 1993a; quarantine 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

consumers in a laboratory setting yields a preference for an advertised product promoting passivity (a vacation resort framed as a place to relax and rest), while inducing anger yields a preference for a product promoting activity (a vacation resort framed as a place to enjoy sports and activity). Accordingly, clinically depressed patients have been reported to be more inactive -- by which we mean here a decrease in a variety of daily activities -- than their non-depressed counterparts. This includes 'not doing fun activities or chores that need to be accomplished' (Knowles, 1981), and reported difficulties initiating or completing social and non-social activities (Baker et al., 1971; Schelde, 1998; APA, 2013). Reduced physical activity (both mild, such as walking and gardening, and more vigorous, such as playing sports) has been associated with clinical depression (Seime and Vickers, 2006; Lindwall et al., 2011), while – cautiously[3] - increased exercise has been reported in several reviews or meta-analyses to improve depressed mood and/or anxiety (*e.g.* Byrne and Byrne, 1993; Dunn et al., 2001; Seime and Vickers, 2006; Davis and Dimidjian, 2012).

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

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[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).

410 theories of human depression emphasizing aversive life events and chronic stress as a

411 common trigger, such inactivity is likely to be associated with negative affect.

412   Moreover, the cognitive feature of learned helplessness has also been shown in animals,

413 and is a phenomenon typically accompanied by an overall decrease in activity (see *e.g.*

414 Mineka and Hendersen, 1985). Indeed, although the term learned helplessness referred

415 initially to a deficit in avoidance learning induced by repeated exposure to uncontrollable

416 shock (reviewed by *e.g.* Maier and Seligman, 1976), the meaning of the label has now been

417 expanded; it is sometimes applied to any 'passive' behaviour (*i.e.* quiescence or the absence

418 of active responses to stress, such as escape attempts; cf. Oxford English Dictionary, 2005)

419 that appears to result from exposure to uncontrollable stressors (Maier, 1984; see also

420 Wemelsfelder, 1990; Carlstead, 1996). For instance, sheep moved from pasture to

421 inescapable indoor crates (Fordham et al., 1991) and laboratory rodents placed in an

422 inescapable container filled with water (known as the Porsolt Test, reviewed in *e.g.* Deussing,

423 2006), both begin by reacting to the situation with agitation, but end up displaying inactivity

424 and unresponsiveness. According to the above-mentioned expanded definition, this eventual

425 response would reflect learned helplessness. Again, because the aetiology corresponds to

426 cognitive theories of human depression (Beck, 1967; Abramson et al., 1978; Gotlib and

427 Krasnoperova, 1998), this inactivity is believed to be a depression-like behaviour, and

428 therefore associated with a negative affective state. In mice and rats that 'cease struggling and

429 remain floating motionless in the water, making only movements necessary to keep their head

430 above water' (Porsolt et al., 1977) in the Porsolt test, additional support comes from the fact

431 that this specific form of inactivity is both amplified by stressors and alleviated by

432 antidepressants (Porsolt et al., 1977; Cryan et al., 2002; Matthews et al., 2005; Deussing,

433 2006; McArthur and Borsini, 2006). It also co-varies with other depression-like symptoms,

434 such as anhedonia (Strekalova et al., 2004), *i.e.* the loss of pleasure, a key feature of human

435   clinical depression (APA, 2013). The hypothesis that the term learned helplessness might also

436   be applicable to captive animals that seem very passive or inactive in their home environment

437   is also supported by findings that animals reared in socially isolated and/or barren cages are

438   more vulnerable to developing learned helplessness in avoidance learning paradigms than

439   those reared in more socially and physically complex, and presumably controllable,

440   environments are (Seligman, 1972; Chourbaji et al., 2005).

441   Finally, Fureix and colleagues (2012, 2015) recently described long-lasting inactive

442   'withdrawn' states in certain riding horses, characterised by bouts of unresponsiveness,

443   remaining motionless with unblinking eyes with an apparently fixed gaze (reminiscent of the

444   reduced responsiveness and reduced interactivity of some depressed human patients) and

445   anhedonia. These states also correlate with stereotypic behaviour (a possible marker of

446   current, but also past exposure to stressors). While the aetiology of this specific form of

447   inactivity is currently unknown, its association with key features of human clinical depression

448   makes it likely to be associated with negative affect.

449   Do these findings demonstrate with certainty that these inactive animals are clinically

450   depressed, in the same way as depressed patients showing decreased variety in their daily

451   activities? The quality and quantity of current evidence are not yet sufficient to conclude this.

452   Moreover, while some forms of inactivity are highly specific ('floating' in rodents,

453   'withdrawn' states in horses), others are not (*e.g.* passivity when exposed to inescapable,

454   uncontrollable stressors). However, that inactivity appears in contexts similar to those that

455   trigger the appearance of clinical depression in humans, or co-varies with key symptoms of

456   this pathology (*e.g.* anhedonia) is sufficiently consistent with the hypothesis to make

457   additional research into these topics, including how this inactivity would be modulated by

458   anti-depressant drug treatments, very worthwhile.

459

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.

485   Due to the dependence on self-reported affect for identifying boredom in humans, this

486   state has been subject to little empirical investigation in animals, where self-report is

487   impossible and thus affect cannot be assessed directly. However, captive animals commonly

488   face monotonous environments, often less complex or lower in stimulation than those in

489   which their ancestors evolved (in some cases, even those they experienced themselves early

490   in life). For this reason, theory suggests that they would also find such situations aversive.

491   For example, McFarland (1989) proposed that when captive animals' immediate physical

492   needs are met but they cannot pursue other activities that would occupy their time in the wild

493   such as reproduction or mating, they are left in a state of 'limbo' and are likely to suffer

494   because most species will not have evolved methods of coping with such a situation. Veissier

495   et al. (2009) also argue that since sheep are sensitive to the same features of stimuli that

496   induce boredom in humans, they are potentially capable of experiencing it; the same

497   argument could be applied to many species. Inactivity is generally accepted as a common

498   consequence of housing in relatively barren cages or enclosures and interpreted as a sign of

499   poor welfare (DeMonte and LePape, 1997), which many people attribute to boredom (*e.g.*

500   Stevenson, 1983; Woodgush and Beilharz, 1983). Conversely, increasing activity or

501   behavioural diversity through provision of opportunities to interact with stimuli is assumed to

502   improve welfare (*e.g.* pigs: Woodgush and Beilharz, 1983; chimpanzees: Celli et al., 2003;

503   dogs: Wells, 2004). Sometimes this assumption has been supported by improvements in other

504   welfare indicators (*e.g.* Paquette and Prescott, 1988) or by animals' preference for the

505   enrichment (*e.g.* Rozek et al., 2010).

506   Both the use of the term 'boredom' in animals and its relationship to inactivity still need

507   validation, however. To provide a starting point for this work, Meagher and Mason (2012)

508   proposed an operational definition based on motivation to obtain stimulation, which should

509   be a universal symptom. The validity of this operational definition was supported by the fact

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

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

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

4.1.   Increased inactivity / decreased activity likely to be associated with positive

highly-aroused affective states

536   As stated in the Introduction, positive, highly-aroused affective states are likely to be

537   associated with appetitive motivational states, and function to facilitate seeking and obtaining

538   rewards (Mendl et al., 2010). Being *inactive* in order to *favour* reward *acquisition* sounds

539   intuitively unlikely to happen, and examples are rare even in humans, with perhaps the

540   exception of yogi meditation, which has been self-reported by meditators to be a highly-

541   aroused pleasant state (Cahn and Polich, 2006). Chess players close to winning a game and

542   focused on choosing the best strategy could also perhaps experience a highly-aroused and

543   pleasant motionless state; this is likely one example of what Csikszentmihalyi (1975; 1990)

544   termed a "flow" state. Flow states involve being concentrated on a task that is achievable but

545   sufficiently challenging to require focused attention and skill, and are self-reported as being

546   enjoyable, at least in retrospect (reviewed in Csikszentmihalyi 1990). However, although the

547   absence of evidence is not a proof of absence, one may reasonably doubt that animals

548   practice meditation or play chess. An animal example in this category might be cats

549   'stalking': adults stalking prey (Wise, 1974) and kittens playing (Bateson and Young, 1981)

550   temporarily restrain any movement and stay perfectly motionless. Cats have been considered

551   to become 'hypoactive' while anticipating food rewards, displaying reduced behavioural

552   transitions between the offset of a conditioned stimulus and the onset of an unconditioned

553   stimulus in a Pavlovian conditioning paradigm (van den Bos et al., 2003). According to the

554   authors, this might be expected as 'they [*cats*] normally employ a 'sit-and-wait' tactic while

555   close to their prey'. Bouts of immobility while stalking could therefore tentatively be seen as

556   a (cat-specific) form of inactivity that would favour reward acquisition, but the affective

557   state(s) associated with such a behaviour are clearly not validated yet (see *e.g.* Bassett and

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

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

Inactivity expressed in postprandial contexts could also be associated with positive affective states. Postprandial inactivity is likely to be associated with satiety, *i.e.* in humans the feeling of 'fullness' following a feeding episode (Benelam, 2009; Harrold et al., 2012), and has been observed in a number of animal species (rats: *e.g.* Richter, 1922; Antin et al., 1975; Willner et al., 1990; Rodgers et al., 2010; northern harriers *Circus cyaneus*: Temeles, 1989; sows: Zonderland et al., 2004; dogs: Bosch et al., 2009; cats: Fara and colleagues 1969, cited in Orr et al., 1997). Further evidence that postprandial inactivity in animals is likely to be associated with satiety comes from pharmacological studies: cholecystokinin[5] administration, which in humans increases the feeling of fullness and reduces food

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

632 consumption (*e.g.* Stacher et al., 1979; Crawley et al., 1982; Stacher et al., 1982; Sam et al.,

633 2012), also reduces food consumption in animals (rats, mice, sheep, pigs, monkeys, reviewed

634 in Crawley et al., 1982), and induces inactivity (rats: *e.g.* Antin et al., 1975; mice: Crawley et

635 al., 1981; rhesus monkeys: Falasco et al., 1979). In calves, being able to suck on a teat

636 increases the tendency to rest after milk consumption (Veissier et al., 2002), and this may be

637 mediated in part by cholecystokinin, which increases in response to such sucking (De Passillé

638 et al., 1993).

639 Satiety *can* increase inactivity in humans as well (*e.g.* napping after lunch, Zammit et al.,

640 1992; Vela-Bueno et al., 2008), although the causal relationship remains debated (review in

641 Campbell, 1992), making it difficult to use evidence regarding affective states during satiety-

642 induced inactivity in humans. Nevertheless, because satiated humans self-report positive

643 affective states, such as satisfaction and relaxation (Panksepp, 2005; Boelsma et al., 2010;

644 Seehuus et al., 2013), one may reasonably hypothesize that postprandial inactivity in animals

645 has a positive affective component just as humans experience after eating. This suggestion is

646 supported by the finding that, in laying hen chicks, denying access to the part of a pen

647 designed to accommodate postprandial inactivity results in a more negative affective state

648 than in a baseline situation (where chicks have free access to that area), as evidenced by a

649 more 'pessimistic-like' response in a judgment bias paradigm (Seehuus et al., 2013).

650 With respect to *satiation*, *i.e.* the *processes* that bring episodes of eating behaviour to an

651 end (Benelam, 2009; Harrold et al., 2012), ingesting food is typically considered activity in

652 applied ethology research (see section 2); satiation therefore appears unlikely to involve

653 inactivity in most species, including humans. However, rumination, which has the primary

654 function of facilitating clearance of digesta from the rumen by reduction of particle size, is

655 most frequently expressed when the animals are motionless lying down (Wagnon, 1963;

656 Kilgour, 2012; Schirmann et al., 2012). As such, it could be seen as a (ruminant-specific)

657 satiation-induced specific form of inactivity. In humans, satiation is associated with positive

658 affective states, such as feelings of liking and satisfaction (*e.g.* Benelam, 2009; Seehuus et al.,

659 2013), and lying down ruminating has been suggested to be 'a sign of relaxation in cattle'

660 (Phillips, 2002, from Espejo and Endres, 2007) and a sign that cows are 'at ease' (Bristow

661 and Holmes, 2007). Rumination also appears to decrease when animals are exposed to

662 aversive situations, such as social stressors (regrouping) and home-pen novelty (Schirmann et

663 al., 2011), disturbance by flies (presumably associated with discomfort: Wagnon, 1963, p47)

664 and ruminal acidosis (presumably associated with pain, lactating dairy cows: DeVries et al.,

665 2009).

666

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

668   Being *inactive* in order to *favour* reward *acquisition* is likely rare, with perhaps the only

669 direct evidence coming from humans during yogi meditation, as discussed above. Our other

670 suggested example, bouts of immobility while stalking in cats, is clearly not validated as an

671 indicator of positive affective states in animals. Potentially more fruitful as affective state

672 indicators are specific forms of inactivity reported in humans and expressed in animals when

673 threat levels are low, such as sun-basking and post-consummatory inactivity. All of these still

674 need validation, however. Further work could investigate to what extent acute stressors or

675 chronically aversive environments would decrease such inactivity (and the opposite for

676 preferred environments), how these forms of inactivity would be modulated by

677 pharmacological manipulations inducing either negative or positive affective states, and,

678 more specifically, whether the putatively positive affective state associated with postprandial

679 inactivity would be lessened in force-fed animals (see Faure et al., 2001 for evidence that

680 force-feeding might be perceived as aversive in ducks). Further research is also warranted

681 into other forms of inactivity likely to be pleasurable in humans, such as being passively

682   rocked and breast-feeding, which could perhaps find equivalents in animals *choosing* to go

683   and float in the water and in lactating females.

684

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

686   We will further discuss the relationship between increased inactivity and affective states

687   by presenting misleading situations prone to yield wrong conclusions. First, we will describe

688   some examples of 'false negatives' (*i.e.* those cases where the animal's affective state is

689   likely to be either poor or good but the animal <u>is not</u> inactive), and 'false positives' (*i.e.* those

690   cases where the animal <u>is</u> 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 <u>lack</u> 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 <u>*do not*</u> *display* increased inactivity.

705   Inactivity can sometimes be one of two (or more) alternative responses – driven by

706   individual characteristics – to the same situation, which both indicate a similarly (in this

707 example) negative affective state. For instance, while individuals can respond to situations

708 involving a (perceived) threat by freezing or hiding, they can also display active reactions,

709 such as fleeing or even attacking (Boissy, 1995; Blanchard et al., 2011). In red deer, the

710 response strategies to a perceived threat differ according to age: juveniles employ a hiding

711 strategy, and freeze in response to threat, but as they age, they begin fleeing from some

712 threats instead (Espmark and Langvatn, 1985). This does not mean we should conclude that

713 adult red deer are not afraid of the perceived threat from which they are fleeing only because

714 they are not displaying inactive responses. More generally, personality can determine the

715 form of an individual's response, including whether they become inactive or not. For

716 example, speed of exploration of a novel environment is considered to reflect a personality

717 trait in birds, and individuals with different exploratory phenotypes also differ in the degree

718 to which they become inactive after social defeat (reviewed by Groothuis and Carere 2007).

719 Van Reenen et al. (2005) thus suggest that their failure to find a correlation between open

720 field locomotion and other measures of response to novelty might be explained by the

721 presence of different coping styles, such that some calves responded to the open field with

722 escape attempts, but others with immobility, novelty being nevertheless perceived as

723 frightening in both cases. Moreover, an individual's experience is likely to influence its stress

724 responses: for example, captive-born individuals may be more likely to respond actively to a

725 sub-optimal captive environment, developing stereotypic behaviour, while wild-caught

726 individuals may be more likely to respond by hiding (*e.g.* Jones et al., 2011; Camus et al.,

727 2013). Despite these differences, individuals displaying both response types are likely to

728 suffer from their sub-optimal life conditions.

729 Inactivity can also be one of two (or more) alternative responses – dependent this time on

730 situational characteristics - to different situations associated with a similar (in this example

731 negative) affective state. For instance, Cooper et al. (1996) showed that voles responded to an

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

781   While the examples above highlight cases of false positives when inactivity is expected to

782   be associated with negative affective states, false positives can also happen when inactivity is

783   expected to be associated with positive affective states. For instance, Mason and Latham

784   (2004) found in a meta-analysis that stereotypic behaviours are more prevalent in populations

785   living in sub-optimal conditions than in populations kept under more welfare-friendly

786   conditions, but also that, more often than not, within populations where stereotypic behaviour

787   was prevalent, individuals that did not stereotype, or had relatively low levels of stereotypy,

788   had poorer welfare than those that with high levels, according to a variety of welfare

789   measures. Since non-stereotypic individuals are likely to be the most inactive individuals

790   within a population (*e.g.* Bildsoe et al., 1990; Wurbel et al., 1998b), this may indicate that at

791   an individual level, inactive responses to stressful conditions are actually more often

792   associated with poor welfare than with good welfare.

793

794   *5.3.   The risk of wrong conclusions: cases where inactivity is linked to <u>a lack of</u>*

795   *emotion*

796   While the examples above discuss specific forms of inactivity which are likely to be

797   associated with (either negative or positive) affective states, some forms of inactivity appear

798   to be not necessarily linked to an actual affective state but instead a *lack* of emotion. For

799   instance, disorders of reduced motivation such as apathy, defined as 'a state of diminished

800   motivation in the presence of normal consciousness, attention, cognitive capacity, and mood'

801   (Marin and Wilkosz, 2005)[6] involve decreased activity. In Marin and Wilkozs' words (our

802   emphasis), 'patients with diminished motivation **all show diminished activity'**; however

803   they are also '**emotionally indifferent**… or display restricted responses to important life

804   events'. Another example is a 'deconstructed state' observed in the pre-suicidal phase and in

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[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.

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

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

5.4.   Different methodologies, different conclusions?

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

830 would not discriminate *e.g.* a motionless healthy animal sun-basking (likely to experience

831 positive affective states, see 4.2.1) from an animal awake but inactive due to injury (likely to

832 experience negative affective states, see 3.2.1.).

833   A detailed example of how methodological variations in defining inactivity could

834 influence its interpretation in terms of associated affective states comes from resting. Resting

835 can be seen as a post-consummatory (of various activities) behaviour, and is often considered

836 to reflect positive affective states. Indeed, safe, comfortable contexts promote rest (*e.g.* larger

837 home stalls in horses: Raabymagle and Ladewig, 2006). Preferred situations often decrease

838 signs of poor welfare and increase time resting (enriched cages, in rats: Abou-Ismail and

839 Mahboub, 2011; and in mice: Tilly et al., 2010; bedding types that are preferred when the

840 animals are given a choice of stalls in horses: Hunter and Houpt, 1989; Mills et al., 2000;

841 Pedersen et al., 2004; Werhahn et al., 2010). So does providing a more naturalistic social

842 environment in horses by introducing adult conspecifics in groups of sub-adults (Bourjade et

843 al., 2008). Moreover, a variety of stressors, such as chronic exposure to mild unpredictable

844 stressors (rats: Cheeta et al., 1997), exposure to an aggressive dominant conspecific (male

845 tree shrews *Tupaia belangeri*: Fuchs and Flugge, 2002) and social isolation (rats: Hurst et al.,

846 1999), decrease the time the animals spend resting over hours or days. Rats exposed to sleep

847 disturbance (husbandry procedures performed during the non-active light phase) not

848 surprisingly sleep less, spending more time *awake non-active* and show higher indicators of

849 physiological stress and reduced welfare than do their conspecifics experiencing husbandry

850 procedures during their active dark phase (Abou-Ismail et al., 2008). Moreover, while

851 provoking sexual (positive) interactions during the inactive phase only briefly suppresses

852 sleep in male mice, aversive social conflict induces 12h long-lasting sleep disturbances

853 (Meerlo and Turek, 2001). Resting is therefore commonly interpreted as a sign that animals

854 are relaxed and experience positive affective states.

855   However, in a number of animal studies, resting and *sleeping* are merged together in the

856   behavioural repertoire, defined by the animal displaying a species-specific posture (usually

857   lying down, but sometimes also sitting or even standing still) *with eyes partially or fully*

858   *closed* (*e.g.* in rats: Hurst et al., 1999; Abou-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 $\geq$ 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

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[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	?	?	?

Conclusions

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

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

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

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