

1 **Heart rate as a measure of emotional arousal in evolutionary biology**

2 Claudia A.F. Wascher

3

4 Behavioural Ecology Research Group, School of Life Sciences, Anglia Ruskin University,

5 United Kingdom

6

7 *Corresponding author: Claudia A.F. Wascher: School of Life Sciences, Anglia Ruskin

8 University, East Road, Cambridge, CB1 1PT United Kingdom; Phone: +4369912381419; e-

9 mail: claudia.wascher@gmail.com

10 **Abstract**

11 How individuals interact with their environment and respond to changes is a key
12 area of research in evolutionary biology. A physiological parameter that provides an instant
13 proxy for the activation of the automatic nervous system, and can be measured relatively
14 easily, is modulation of heart rate. Over the past four decades, heart rate has been used to
15 assess emotional arousal in non-human animals in a variety of contexts, including social
16 behaviour, animal cognition, animal welfare, and animal personality. In this review, I
17 summarise how measuring heart rate has provided new insights to how social animals cope
18 with challenges in their environment. I assess the advantages and limitations of different
19 technologies used to measure heart rate in this context, including wearable heart rate belts
20 and implantable transmitters, and provide an overview of prospective research avenues
21 using established and new technologies, with special focus on implications for applied
22 research on animal welfare.

23

24

25 **Key words:** animal welfare, cognition, emotional arousal, heart rate, individual differences,
26 social behaviour

27

28 **1. Introduction**

29 Since the mid 1970s, starting with a seminal book by Hans Selye, investigating
30 individual responses to challenges in the environment, *i.e.* stressors, is an important area of
31 research in evolutionary biology [1]. Physiological activation helps organisms to adapt to
32 environmental changes and maintain homeostasis [2]. Activation of the sympathetic branch
33 of the automatic nervous system can be captured by an increase in heart rate, defined as
34 the number of contractions of the heart per minute (beats per minute, bpm) [3], which
35 indicates the initiation of a physiological stress response, defined as coping response to
36 external and internal stimuli [1] and emotional arousal, a state of heightened psychological
37 activity [4]. These concepts are closely related, where the physiological stress response is
38 often seen as a general response to all stimuli, whereas emotional arousal takes the
39 animal's perception of the situation into consideration [5]. Measures of heart rate
40 variability, *i.e.* variation in the time interval between heartbeats, have been suggested to
41 reflect the balance between the regulation of the sympathetic and parasympathetic branch
42 of the automatic nervous system [6,7]. As these responses are plastic and context
43 dependent [8], heart rate measures can provide important insight into how animals
44 perceive and respond to their environment [9]. Further, heart rate is positively correlated to
45 metabolic rate and thus can be used as reliable proxy of energy expenditure [10].
46 Ultimately, stress related increases in heart rate can increase the overall energy expenditure
47 of individuals [11], which is constrained by physical and/or physiological conditions [10].
48 Heart rate response to stress can be considerable, for example in Yellow-eyed penguins,
49 *Megadyptes antipodes*, heart rate was more than two times higher during partner reunion
50 with mutual calling (174 bpm) compared to heart rate during resting (77 bpm) and heart
51 rate returned to baseline levels within seconds after the stimulus ended [12]. In greater

52 white-fronted geese, *Anser albifrons*, maximum heart rate during agonistic encounters
53 increased four times in comparison to mean heart rate during resting (110 bpm), whereas
54 mean heart rates during walking, feeding and preening was similar to resting heart rate (98
55 – 118 bpm). Mean heart rate during flight was similar to maximum heart rates during
56 agonistic encounters (413 bpm) and heart rate returned to baseline values in less than 10
57 seconds [13]. In mammals, heart rate during exercise (running) increased linearly with
58 running speed and depended on body size (resting heart rates: 63 – 581 bpm; maximum
59 heart rate during running: 183 – 679 bpm) [14]. In domestic pigs, *Sus scrofa*, mean heart
60 rate increased from 52 bpm during resting to 79 bpm during walking and a maximum heart
61 rate of 157 bpm when losing a physical encounter [15].

62

63 Here, I review studies that used heart rate as a measure of emotional arousal in the
64 fields of social behaviour, animal cognition, animal welfare, and personality research (Table
65 1). A first study, published in the late 1970s used heart rate as a measure of anthropogenic
66 disturbance, measured by custom designed wearable transmitter harnesses in bighorn
67 sheep, *Ovis canadensis* [16]. After this early study in free-ranging animals, only ten years
68 later, first laboratory studies in primates measured heart rate responses to social
69 interactions and different social stimuli via electrodes attached to the skin surface or
70 implanted transmitters [17–19]. It took another ten years, until heart rate in the late 90s
71 became a more broadly used measure of emotional arousal in different context, with
72 researchers also starting to use different technologies (implanted radio-transmitter,
73 wearable heart rate belts, artificial eggs; Table 1). I further provide an outlook into future
74 research avenues which could be potentially be explored with new technologies allowing for

75 heart rate measurements to be more broadly applied in different contexts, freely moving
76 animals, and a wider variety of species.

77

78 **2. Social modulation of heart rate**

79 Heart rate has been shown to be strongly affected by social interactions in a wide
80 range of species. Responses of individuals during social interactions can be quantified using
81 mean or maximum heart rate during the encounter [20], heart rate increase, calculated as
82 the difference between the momentary baseline heart rate value a couple of seconds (2-3)
83 before the interaction and either the mean heart rate value during the interaction or the
84 instantaneous maximum heart rate [20,21], recovery period until heart rate returns to
85 baseline [22] or excess heart rate, calculated as the mean heart rate increase over baseline
86 heart rate times the duration of that increase [21]. Heart rate during and after agonistic
87 encounters usually increases (blind cave crayfish, *Orconectes australis packardi*: [23];
88 bighorn sheep, *Ovis canadensis canadensis*: [16]; domestic pigs: [15]; greylag geese, *Anser*
89 *anser*: [24]; Figure 1(A) in comparison to heart rate during take-off Figure 1(B); greater
90 white-fronted geese: [13]; king penguins, *Aptenodytes patagonicus*: [21]; pigtail macaque,
91 *Macaca nemestrina*: [17]; Table 2). In greylag geese, mean heart rate during aggressive
92 encounters (157 bpm) is significantly higher compared to mean heart rate other behaviours
93 for example resting (84 bpm), head up (131 bpm), preening (117 bpm) or feeding (118
94 bpm). Heart rate in greylag geese increased from 134 bpm during standing and walking, to
95 159 bpm during swimming and 368 bpm when flying [25]. Heart rate increases after
96 agonistic encounters in greylag geese on average lasted for 8 seconds (range: 1 – 261
97 seconds; C.A.F. Wascher, unpublished data). Affiliative behaviours generally reduce heart

98 rate (cattle, *Bos taurus*: [26]; pigtail macaque [17]; rhesus macaques, *Macaca mulatta*: [27])
99 and being paired with a long-term social partner was shown to buffer an increase in heart
100 rate during aggressive encounters in male greylag geese [28]. Responses often differ
101 depending on an individual's role as initiator or receiver in the interaction, or whether the
102 individual is dominant or subordinate to its interaction partner. For example, in rats, *Rattus*
103 *norvegicus*, and greylag geese, individuals winning agonistic encounters had significantly
104 higher levels of emotional arousal compared to the defeated individuals [20,29]. Already the
105 approach by a dominant group member and the associated risk of aggression was found to
106 significantly increase heart rate in rhesus macaques [27], and even indirect social
107 interactions can affect heart rate, for example observing aggressive interactions as a
108 bystander [21,30], or visual and olfactory presentation of dominant or aggressive individuals
109 [18,31]. The relationship between social status and heart rate can manifest itself in rank-
110 dependent differences in resting heart rates, as described in red deer, *Cervus elaphus*,
111 where subordinate individuals have lower resting heart rates compared to dominant
112 individuals, which might result in a better capacity to minimize energy requirements [32].

113

114 Current research shows that heart rate provides a suitable proxy for estimating
115 individual investment into the social domain, and that measuring heart rate in a variety of
116 social contexts facilitates investigating the adaptive benefits of social relationships across
117 different time frames. However, presently, only few studies report detailed individual
118 physiological responses to social interactions and often these studies describe short-term
119 effects only instead of investigating any long-term impacts of emotional arousal on energy
120 expenditure, health, reproductive output, or longevity.

121

122

123 **3. Measuring heart rate in the context of animal cognition research**

124 Generally, the study of animal cognition investigates mechanisms by which animals
125 acquire, process, store, and act upon information in the environment [33]. A major
126 constraint in understanding these processes is that cognition can only be indirectly
127 assessed, for example by observing behaviours in response to experimental manipulation,
128 and that behavioural responses to stimuli can be difficult to interpret if individuals differ in
129 the expression of emotional arousal - or do not show any notable behavioural change in
130 response to stimuli [30]. However, given that physiological changes to an external stimulus
131 strongly depends on an individual's perception and evaluation of the event [5], measuring
132 physiological parameters such as heart rate can be a promising quantitative tool to assess
133 cognitive processes and arousal in response to stimuli in the environment. Lambs, *Ovis*
134 *aries*, and rats responded with a heart rate increase to novel, sudden, and unpredictable
135 stimuli [34,35]. When engaging in learning tasks, heart rate increased in goats, *Capra hircus*
136 [36], horses, *Equus caballus* [37], and cattle [38] but decreased in European starlings,
137 *Sturnus vulgaris* [39]. In future, improved biologging technology to measure heart rate in
138 different contexts, could allow to more objectively quantify cognitive function in a wide
139 range of species, as already shown by the use of neurologgers to measure
140 electroencephalograms in order to quantify sleep patterns in free-living animals [40–43].

141

142 Heart rate allows to gain insights into the perceived level of difficulty of a cognitive
143 challenge or whether individuals can differentiate between specific stimuli. Studies
144 measuring heart rate during presentation of conspecific and heterospecific photographs

145 showed that chimpanzees, *Pan troglodytes*, respond differently to familiar humans and
146 strangers [19], and their different heart rate response to aggressive, friendly, or unfamiliar
147 conspecifics suggests that chimpanzees can also discriminate between those categories
148 [18]. Similarly, heart rate measured in response to auditory stimuli indicated that dogs,
149 *Canis familiaris*, can differentiate between conspecific barks given in different contexts [44],
150 and blue penguin chicks, *Eudyptula minor*, had a higher heart rate during playbacks of calls
151 from familiar individuals (siblings and neighbours) compared to calls of unfamiliar
152 individuals [45]. Interestingly, penguin chicks did not express observable behavioural
153 differences between the treatments, highlighting again that heart rate can reveal
154 individuals' ability to discriminate between stimuli where it could not have been inferred
155 from behavioural observations.

156

157 Heart rate can also reveal whether and to what degree animals respond to emotions of
158 other individuals, *i.e.*, emotional contagion. When watching conspecifics experiencing
159 stimuli of a negative emotional valence, dogs and horses responded with a higher heart rate
160 compared to seeing others experiencing a positive treatment [46,47], and hens, *Gallus*
161 *gallus domesticus*, significantly increased heart rate when their young was exposed to a mild
162 stressor [48]. Similarly, greylag geese responded with a higher increase in heart rate when
163 observing interactions involving closely affiliated individuals (pair-partner and family
164 members) instead of non-affiliated individuals, even in the apparent absence of a
165 behavioural response to these interactions (Figure 1(C)) [30].

166

167 Although heart rate presents a good means for quantifying the level of emotional
168 arousal, and does so more accurately compared to behavioural measures, it does not

169 provide information about the valence of emotional arousal, because heart rate increases in
170 response to both positive and negative experiences [49,50]. Potentially, different
171 parameters of heart rate variability may allow to better disentangle effects of positive
172 versus negative valence [51,52]. Future research investigating heart rate during cognitive
173 experiments could provide not only insights into cognitive abilities of individuals and
174 advance the field of animal cognition, but also improve our understanding of heart rate
175 modulation in response to a variety of carefully chosen stimuli.

176

177 **4. Individual differences in heart rate**

178 Consistent inter-individual variation in phenotypic traits, including behavioural and
179 physiological traits, have been described in a wide variety of species. With regards to
180 physiology, individuals differ in both different reactivity to challenges in the environment as
181 well as baseline levels [53]. In some species, individuals with more aggressive behavioural
182 traits have been shown to increase heart rate more during aggressive interactions
183 compared to less aggressive individuals [54,55]. Heart rate of chickens from different
184 pedigrees (low and high feather pecking lines) did not significantly differ during baseline
185 conditions or during restraint stress, but heart rates in high feather pecking lines tended to
186 be elevated for longer [56]. In Yellow-eyed penguins individuals differed in their responses
187 and habituation to anthropogenic disturbances [57]. Domestication is also assumed to
188 affect physiological traits. Wild animals had higher average heart rates compared to farmed
189 individuals in Atlantic salmon, *Salmo salar*: [58], and dogs have higher resting heart rate
190 compared to wolves, *Canis lupus*: [59].

191

192 While most studies reported in this review focus on heart rate or heart rate variability,
193 research on individual responses to challenges could also include more detailed
194 investigations into individual recovery periods [60]. Also, repeatability of physiological
195 responses over time and across contexts has hardly been investigated but would provide
196 insights into the development and maintenance of consistent phenotypes, *i.e.*, ‘animal
197 personality’. In summary, a better understanding of individual differences in physiological
198 responses across different contexts could reveal links between behaviour and physiology,
199 which affect behavioural decision making and the evolution of different life-history
200 strategies [53,61]. For example, individual stress responses can be linked to the energy
201 demands of various reproductive stages [62,63], season [11,64,65], moulting [66,67], length
202 of light-dark cycle [68], predation risk [69], parasite load [70].

203

204 **5. Implications for animal welfare**

205 Good animal welfare is generally assumed when animals are not experiencing
206 unnecessary stress. Since heart rate can be used to quantify the activation of the
207 physiological stress response, monitoring heart rate can ultimately be considered a useful
208 tool when attempting to improve animal welfare in a variety of contexts. The benefit of
209 using heart rate as a measure of the physiological stress response, in contrast to, for
210 example, glucocorticoid levels, is that heart rate can reflect individual levels of arousal
211 accurately and at a high temporal resolution, and even small physiological responses to
212 specific stimuli, in the absence of visible behavioural reactions, can be isolated [71].

213

214 Heart rate can be used to monitor arousal levels of individuals when evaluating the
215 effectiveness of measures intended to reduce stress, for example, when enrichment or
216 other changes are introduced in animal shelters or laboratories. In kennelled dogs, the
217 presentation of auditory and olfactory enrichment decreased heart rate and changed heart
218 rate variability, indicating stress reduction [72,73], and mice, *Mus musculus*, that were
219 housed in enriched conditions had a significantly lower heart rate compared to individuals
220 housed under minimal husbandry conditions without enrichment and periods of individual
221 housing [74]. Generally, social isolation can cause significant increases in heart rate (alpaca,
222 *Vicugna pacos*: [75]; dogs: [59]; cattle, *Bos taurus*: [76]; cynomolgus monkeys, *Macaca*
223 *fascicularis*: [77]; goats: [49]; wolves [59]). However, affiliative behaviours, even if
224 performed by heterospecifics, can have a stress-reducing effect; grooming carried out by a
225 familiar human decreased heart rate in laboratory-kept rhesus monkeys [78], dairy cows
226 [79] and lambs [80]. Measuring heart rate can also reveal ineffective enrichment designs or
227 unsuccessful attempts of stress reduction in animal housing. For example, individually
228 housed rhesus monkeys in a laboratory environment did not show any changes in heart rate
229 in response to increasing cage sizes [81] and auditory enrichment did not result in the
230 expected reduction in heart rate in African green monkeys, *Chlorocebus aethiops* [82].

231

232 Biologging technologies to measure heart rate could be widely used to assess effects
233 of anthropogenic disturbance onto wildlife. This is especially relevant as previous studies
234 have shown that individuals can show pronounced emotional arousal, as measured by heart
235 rate, in the absence of obvious behavioural changes. For example, American black bears,
236 *Ursus americanus*, and bighorn sheep, *Ovis canadensis*, showed no behavioural responses
237 but significantly increased heart rate in response to anthropogenic disturbances, such as

238 drone overflights and vehicle traffic [16,83]. Anthropogenic sounds alone were identified as
239 stressor that led to elevated heart rate in farm animals [84], and fish [85]. Also, direct
240 human contact can increase heart rate in wild animals; for example Brown bears, *Ursus*
241 *arctos*, significantly increased heart rate in response to dog hunts and human encounters
242 [86] (Figure 1(D)) and in captive koalas, *Phascolarctos cinereus*, heart rate increased in the
243 presence of tourists compared to situations without humans [87]. Human approach towards
244 nesting birds may not always lead to females leaving the nest, but elevated heart rate for
245 extended periods can increase energy expenditure (Adelie penguins, *Pygoscelis adeliae*:
246 [88]; Humboldt penguin, *Spheniscus humboldti*: [12]; Yellow-eyed penguin [89]; wandering
247 albatrosses, *Diomedea exulans*: [90]). In contrast, other populations might be found to be
248 more resilient; for example, nesting American oystercatchers, *Haematopus palliatus*, did not
249 significantly increase heart rate in response to a variety of human disturbances, including
250 human approach, off-road vehicles, and aircraft overflights [91], and greylag geese did not
251 significantly increase heart rate in response to familiar humans approaching [92]. Responses
252 to human approach can also be affected by previous experience with humans and wild
253 animals can habituate to the presence of humans [60,93]. Knowledge about physiological
254 responses of wild animals to human disturbances can be used to develop guidelines and
255 recommendations to minimise impact of human activities [94].

256

257 A core application for using heart rate measurements to assess animal welfare is in the
258 context of livestock management, given the large numbers of animals kept for food
259 production and increasing demands for improved ethical production of animal products.
260 Decisions on transport and husbandry routines should aim to minimise arousal levels, and
261 heart rate monitoring can provide important evidence for approaches that aim to improve

262 animal welfare. For example, when transporting sheep, heart rate revealed differences in
263 the perceived stress depending on the methods of driving and loading sheep [95,96], and
264 cognitively enriched pigs have a lower heart rate during feeding announcement compared
265 to a control group [97]. Recently, heart rate measures are also implemented in precision
266 livestock farming, defined as the use of advanced technologies for continuous automated
267 real-time animal monitoring to optimize the contribution of each animal [98–102]. In future,
268 heart rate could be used on a large-scale to identify early signs of decreased welfare or poor
269 health in groups of farmed animals, pets or critically endangered animals in a conservation
270 context (Table 1).

271

272 **6. Summary and future research directions**

273 Heart rate provides an accurate and comprehensive measure of activation of the
274 emotional arousal in non-human animals [9]. Here, I propose that research on heart rate
275 modulation in a wide variety of species and different contexts could be of interdisciplinary
276 interest and would provide important insights for basic research, animal welfare, and
277 conservation.

278

279 One of the biggest advantages of heart rate measures is that it allows relatively
280 accessible measuring of short-term levels of emotional arousal in response to single events
281 (*e.g.*, vocalisations, social interactions, human disturbance), but heart rate can also assess
282 impact of long-term stressors on individuals' physiology (*e.g.*, seasonal effects, noise
283 pollution) and reveal chronic stress. Assessment of heart rate can be cheaper compared to

284 other measures of activation of the physiological stress response, for example non-invasive
285 measures of glucocorticoid metabolites in faeces [103].

286

287 A major methodological challenge in evolutionary biology research is that, when
288 quantifying activation of the physiological stress response, studies often compare absolute
289 levels of arousal or stress, with little consideration about the adaptive benefit or cost
290 associated with the response [104]. Activation of the physiological stress response has been
291 proposed to have both adaptive and maladaptive aspects [104]. Short-term increases in
292 heart rate are considered adaptative to help individuals to cope with a given stimulus in the
293 environment. However, increases in heart rate result in an increase in energy expenditure
294 and long-term maintenance of an elevated physiological stress response might be costly and
295 have negative effects on an individual's health and fitness [*e.g.*, 72]. For example, stress
296 through group instability caused increased coronary artery atherosclerosis in dominant male
297 cynomolgus monkeys compared to subordinate individuals [107]. A better understanding of
298 potential fitness consequences of activation of the physiological stress response in
299 behavioural biology is important for interpreting findings about heart rate responses in
300 different contexts. Recording multiple physiological parameters simultaneously, *e.g.*, body
301 temperature, heat flux, blood and tissue oxygenation, blood metabolites and gases, gastric
302 pH and motility, or diving air volume and respiratory rate, could help to achieve this by
303 providing a more comprehensive representation of an individuals' physiological status [108–
304 110].

305

306 Heart rate measurements allow to validate behavioural indicators of emotional
307 arousal and activation of the physiological stress response. Whereas commonly used

308 physiological measures that require laboratory analysis of hormonal changes are expensive,
309 time consuming, or practically not feasible, behavioural observations and analyses of certain
310 indicative behaviours, such as vigilance, can be used to analyse responses to different
311 stimuli. Correlating behavioural observations with simultaneous measures of heart rate
312 provides an important validation for using behavioural indicators of individual arousal and
313 stress. In horses, heart rate and heart rate variability are correlated with snorting in stressful
314 conditions [111], ear posture is indicative of emotional arousal in dairy cows [112], and in
315 greylag geese, the maximum heart rate during aggressive encounters is positively related to
316 frequency of shaking and duration of vigilance after the conflict [22]. However, other studies
317 found no relationship between considered behavioural measures and heart rate in some
318 contexts [113,114]. If a robust relationship between frequency or intensity of behavioural
319 measures and emotional arousal is validated, behavioural observations can be used to
320 assess levels of arousal at low material cost. However, more studies reporting heart rate are
321 needed to carefully validate behavioural indicators of stress under consideration of factors
322 like species, context, individual variation.

323

324 More research is needed to investigate in which contexts emotional arousal and
325 activation of the physiological stress response is adaptive and helps an animal to cope with
326 stressors, and in which contexts is the activation of the physiological stress response
327 maladaptive and has negative impacts on an individual's health [106]. Here, long-term
328 monitoring over months or years is technologically feasible and could, especially in managed
329 animal species (*e.g.*, farm animals, animals in shelters), be linked to outcomes of daily
330 routines or veterinary inspections. Long-term monitoring of heart rate would also allow to
331 disentangle short-term reactivity to environmental stimuli from long-term activation of the

332 physiological stress response, which is not well understood yet [11,99]. Heart rate
333 recordings could be incorporated in automated health surveillance processes in a wide
334 variety of different settings [115,116].

335

336 A major constraint to assess heart rate is the availability of suitable devices. In this
337 review I have presented research applying different biologging technology, ranging from
338 fully implantable transmitters to wearable heart rate belts that can be applied non-
339 invasively (Table 1). Different technology makes measuring heart rate possible in a wide
340 range of species [108,117], including fish [82], marine mammals and turtles [83,84],
341 domestic pets and farmed animals [85], but different approaches have specific social,
342 ethical, and regulatory challenges [118]. For example, implanting transmitters is an invasive
343 process and might not be ethically acceptable in all contexts and species. Commercially
344 available wearable technology, such as heart rate belts, are not easily applicable to wild
345 animals because they often need readjustment and manual removal. Especially for small
346 species, *e.g.*, birds, there are additional ethical considerations to be made regarding to the
347 weight of the device. To minimise ethical risks of prolonged invasive measuring techniques,
348 robust statistical methods to analyse the collected data are needed, which can help to
349 refine study design in accordance with the 3Rs (reduce, refine, replace) [119,120]. Next to
350 ethical considerations, different devices also differ in the price range and method of actual
351 heart rate recording. Most heart rate equipment records an electrocardiogram [121], some
352 require microphones to acoustically record the frequency of heartbeats [122]. All technical
353 solutions measuring heart rate in non-human animals need to be carefully corrected for
354 outlier values, which can occur when the algorithm used to measure the electrocardiogram
355 is not carefully validated for the species in question or when used in un-restrained animals

356 can occur when signal is temporarily lost [123]. Therefore, similar to other physiological
357 parameters, heart rate measurements require careful validation and removal of biologically
358 not meaningful outliers [121,123,124].

359

360 To summarise, using heart rate to gain an improved understanding of how
361 individuals cope with challenges in their environment is of interest for several areas of
362 evolutionary biology, including research on social behaviour, animal cognition, and
363 individual differences. For example, understanding the adaptive costs and benefits of social
364 behaviour is a central topic in evolutionary ecology, or quantifying individual levels of stress
365 in response to anthropogenic disturbances or environmental challenges and evaluating the
366 effectiveness of measures intended to reduce stress is of particular importance in applied
367 animal welfare research and conservation. Technological advances in biologging can help to
368 further advance the application of heart rate monitors in diverse areas of animal behaviour
369 research and contribute to studying emotional arousal in different contexts.

370

371 Data accessibility: This article has no additional data.

372 Competing interests: I declare I have no competing interests.

373

374 Funding: This work received no funding.

375

376 Acknowledgements: I thank Friederike Hillemann for her valuable input on the manuscript. I

377 also thank Lucy Hawkes, Vincent A. Viblanc and an anonymous reviewer for their very

378 helpful comments.

379

380 **References**

381 1. Seyle H. 1976 *The stress of life*. New York: McGraw-Hill.

- 382 2. von Holst D. 1998 The concept of stress and its relevance for animal behavior. In
383 *Advances in the Study of Behavior*, pp. 1–131. Academic Press.
- 384 3. Spodick DH, Raju RL, Bishop RL, Rifkin RD. 1992 Operational definition of normal
385 sinus heart rate. *The American Journal of Cardiology* **69**, 1245–1246.
386 (doi:doi:10.1016/0002-9149(92)90947-w)
- 387 4. Anderson DJ, Adolphs R. 2014 A framework for studying emotions across species. *Cell*
388 **157**, 187–200. (doi:10.1016/j.cell.2014.03.003)
- 389 5. Veissier I, Boissy A. 2007 Stress and welfare: Two complementary concepts that are
390 intrinsically related to the animal’s point of view. *Physiology & Behavior* **92**, 429–433.
- 391 6. von Borell E *et al.* 2007 Heart rate variability as a measure of autonomic regulation of
392 cardiac activity for assessing stress and welfare in farm animals — A review. *Physiology*
393 *& Behavior* **92**, 293–316. (doi:10.1016/j.physbeh.2007.01.007)
- 394 7. Appelhans BM, Luecken LJ. 2006 Heart rate variability as an index of regulated
395 emotional responding. *Review of General Psychology* **10**, 229–240. (doi:10.1037/1089-
396 2680.10.3.229)
- 397 8. Romero LM, Dickens MJ, Cyr NE. 2009 The reactive scope model — A new model
398 integrating homeostasis, allostasis, and stress. *Hormones and Behavior* **55**, 375–389.
399 (doi:10.1016/j.yhbeh.2008.12.009)
- 400 9. Gaidica M, Dantzer B. 2020 Quantifying the autonomic response to stressors—One way
401 to expand the definition of “stress” in animals. *Integrative and Comparative Biology* **60**,
402 113–125. (doi:10.1093/icb/icaa009)
- 403 10. Halsey LG *et al.* 2019 Flexibility, variability and constraint in energy management
404 patterns across vertebrate taxa revealed by long-term heart rate measurements. *Funct*
405 *Ecol* **33**, 260–272. (doi:10.1111/1365-2435.13264)
- 406 11. Wascher CAF, Kotrschal K, Arnold W. 2018 Free-living greylag geese adjust their heart
407 rates and body core temperatures to season and reproductive context. *Sci Rep* **8**, 2142.
408 (doi:10.1038/s41598-018-20655-z)
- 409 12. Ellenberg U, Mattern T, Seddon PJ. 2013 Heart rate responses provide an objective
410 evaluation of human disturbance stimuli in breeding birds. *Conservation Physiology* **1**,
411 cot013–cot013. (doi:10.1093/conphys/cot013)
- 412 13. Ely CR, Ward DH, Bollinger KS. 1999 Behavioral correlates of heart rates of free-living
413 greater white-fronted geese. *The Condor* **101**, 390–395. (doi:10.2307/1370002)
- 414 14. Baudinette RV. 1978 Scaling of heart rate during locomotion in mammals. *J Comp*
415 *Physiol B* **127**, 337–342. (doi:10.1007/BF00738418)
- 416 15. Marchant JN, Mendl MT, Rudd AR, Broom DM. 1995 The effect of agonistic
417 interactions on the heart rate of group-housed sows. *Applied Animal Behaviour Science*
418 **46**, 49–56. (doi:10.1016/0168-1591(95)00636-2)

- 419 16. MacArthur RA, Johnston RH, Geist V. 1979 Factors influencing heart rate in free-
420 ranging bighorn sheep: a physiological approach to the study of wildlife harassment.
421 *Can. J. Zool.* **57**, 2010–2021. (doi:10.1139/z79-265)
- 422 17. Boccia ML, Reite M, Laudenslager M. 1989 On the physiology of grooming in a pigtail
423 macaque. *Physiology & Behavior* **45**, 667–670. (doi:10.1016/0031-9384(89)90089-9)
- 424 18. Boysen ST, Berntson GG. 1989 Conspecific recognition in the chimpanzee (Pan
425 troglodytes): Cardiac responses to significant others. *Journal of Comparative Psychology*
426 **103**, 215.
- 427 19. Boysen ST, Berntson GG. 1986 Cardiac correlates of individual recognition in the
428 chimpanzee (Pan troglodytes). *Journal of Comparative Psychology* **100**, 321.
- 429 20. Wascher CAF, Scheiber IBR, Weiß BM, Kotrschal K. 2009 Heart rate responses to
430 agonistic encounters in greylag geese, *Anser anser*. *Animal Behaviour* **77**, 955–961.
431 (doi:10.1016/j.anbehav.2009.01.013)
- 432 21. Viblanc VA, Valette V, Kauffmann M, Malosse N, Groscolas R. 2012 Coping with social
433 stress: heart rate responses to agonistic interactions in king penguins. *Behavioral Ecology*
434 **23**, 1178–1185. (doi:10.1093/beheco/ars095)
- 435 22. Wascher CAF, Fraser ON, Kotrschal K. 2010 Heart rate during conflicts predicts post-
436 conflict stress-related behavior in greylag geese. *PLoS ONE* **5**, e15751.
437 (doi:10.1371/journal.pone.0015751)
- 438 23. Li H, Listeman LR, Doshi D, Cooper RL. 2000 Heart rate measures in blind cave
439 crayfish during environmental disturbances and social interactions. *Comparative*
440 *Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **127**, 55–70.
441 (doi:10.1016/S1095-6433(00)00241-5)
- 442 24. Wascher CAF, Arnold W, Kotrschal K. 2008 Heart rate modulation by social contexts in
443 greylag geese (*Anser anser*). *Journal of Comparative Psychology* **122**, 100–107.
444 (doi:10.1037/0735-7036.122.1.100)
- 445 25. Wascher CAF, Kotrschal K. 2013 The costs of sociality measured through heart rate
446 modulation. In *The Social Life of Greylag Geese*, pp. 142–154. Cambridge: Cambridge
447 University Press.
- 448 26. Laister S, Stockinger B, Regner A-M, Zenger K, Knierim U, Winckler C. 2011 Social
449 licking in dairy cattle—Effects on heart rate in performers and receivers. *Applied Animal*
450 *Behaviour Science* **130**, 81–90.
- 451 27. Aureli F, Preston SD, De Waal F. 1999 Heart rate responses to social interactions in free-
452 moving rhesus macaques (*Macaca mulatta*): A pilot study. *Journal of Comparative*
453 *Psychology* **113**, 59–65.
- 454 28. Wascher CAF, Weiß BM, Arnold W, Kotrschal K. 2012 Physiological implications of
455 pair-bond status in greylag geese. *Biol. Lett.* **8**, 347–350. (doi:10.1098/rsbl.2011.0917)

- 456 29. Sgoifo A, Pozzato C, Costoli T, Manghi M, Stilli D, Ferrari PF, Ceresini G, Musso E.
457 2001 Cardiac autonomic responses to intermittent social conflict in rats. *Physiology &*
458 *Behavior* **73**, 343–349. (doi:10.1016/S0031-9384(01)00455-3)
- 459 30. Wascher CAF, Scheiber IBR, Kotrschal K. 2008 Heart rate modulation in bystanding
460 geese watching social and non-social events. *Proc. R. Soc. B.* **275**, 1653–1659.
461 (doi:10.1098/rspb.2008.0146)
- 462 31. Höjesjö J, Axelsson M, Dahy R, Gustavsson L, Johnsson JI. 2015 Sight or smell?
463 Behavioural and heart rate responses in subordinate rainbow trout exposed to cues from
464 dominant fish. *PeerJ* **3**, e1169. (doi:10.7717/peerj.1169)
- 465 32. Turbill C, Ruf T, Rothmann A, Arnold W. 2013 Social dominance is associated with
466 individual differences in heart rate and energetic response to food restriction in female
467 red deer. *Physiological and Biochemical Zoology* **86**, 528–537. (doi:10.1086/672372)
- 468 33. Shettleworth SJ. 2001 Animal cognition and animal behaviour. *Animal Behaviour* **61**,
469 277–286. (doi:10.1006/anbe.2000.1606)
- 470 34. Désiré L, Veissier I, Després G, Boissy A. 2004 On the way to assess emotions in
471 animals: Do lambs (*Ovis aries*) evaluate an event through its suddenness, novelty, or
472 unpredictability? *Journal of Comparative Psychology* **118**, 363–374. (doi:10.1037/0735-
473 7036.118.4.363)
- 474 35. van den Buuse M, van Acker SABE, Fluttert M, Kloet ERD. 2001 Blood pressure, heart
475 rate, and behavioral responses to psychological “novelty” stress in freely moving rats.
476 *Psychophysiology* **38**, 490–499.
- 477 36. Langbein J, Nürnberg G, Manteuffel G. 2004 Visual discrimination learning in dwarf
478 goats and associated changes in heart rate and heart rate variability. *Physiology &*
479 *Behavior* **82**, 601–609. (doi:10.1016/j.physbeh.2004.05.007)
- 480 37. Mengoli M, Pageat P, Lafont-Lecuelle C, Monneret P, Giacalone A, Sighieri C, Cozzi A.
481 2014 Influence of emotional balance during a learning and recall test in horses (*Equus*
482 *caballus*). *Behavioural Processes* **106**, 141–150. (doi:10.1016/j.beproc.2014.05.004)
- 483 38. Hagen K, Broom DM. 2004 Emotional reactions to learning in cattle. *Applied Animal*
484 *Behaviour Science* **85**, 203–213.
- 485 39. Glassman LW, Hagmann CE, Qadri MA, Cook RG, Romero LM. 2019 The effect of
486 learning on heart rate and behavior of European starlings (*Sturnus vulgaris*). *J. Exp.*
487 *Zool.* **331**, 506–516. (doi:10.1002/jez.2319)
- 488 40. Kendall-Bar JM, Vyssotski AL, Mukhametov LM, Siegel JM, Lyamin OI. 2019 Eye state
489 asymmetry during aquatic unihemispheric slow wave sleep in northern fur seals
490 (*Callorhinus ursinus*). *PLoS ONE* **14**, e0217025. (doi:10.1371/journal.pone.0217025)
- 491 41. Aulsebrook AE, Connelly F, Johnsson RD, Jones TM, Mulder RA, Hall ML, Vyssotski
492 AL, Lesku JA. 2020 White and Amber Light at Night Disrupt Sleep Physiology in Birds.
493 *Current Biology* **30**, 3657–3663.e5. (doi:10.1016/j.cub.2020.06.085)

- 494 42. Connelly F, Johnsson RD, Aulsebrook AE, Mulder RA, Hall ML, Vyssotski AL, Lesku
495 JA. 2020 Urban noise restricts, fragments, and lightens sleep in Australian magpies.
496 *Environmental Pollution* **267**, 115484. (doi:10.1016/j.envpol.2020.115484)
- 497 43. van Hasselt SJ, Rusche M, Vyssotski AL, Verhulst S, Rattenborg NC, Meerlo P. 2020
498 Sleep time in the European starling is strongly affected by night length and moon phase.
499 *Current Biology* **30**, 1664-1671.e2. (doi:10.1016/j.cub.2020.02.052)
- 500 44. Maros K, Pongracz P, Bardos G, Molnar C, Farago T. 2008 Dogs can discriminate barks
501 from different situations. *Appl. Anim. Behav. Sci.* **114**, 159–167.
- 502 45. Nakagawa S, Waas J, Miyazaki M. 2001 Heart rate changes reveal that little blue penguin
503 chicks (*Eudyptula minor*) can use vocal signatures to discriminate familiar from
504 unfamiliar chicks. *Behavioral Ecology and Sociobiology* **50**, 180–188.
505 (doi:10.1007/s002650100355)
- 506 46. Quaranta A, Siniscalchi M, Vallortigara G. 2007 Asymmetric tail-wagging responses by
507 dogs to different emotive stimuli. *Current Biology* **17**, R199–R201.
508 (doi:10.1016/j.cub.2007.02.008)
- 509 47. Trösch M, Pellon S, Cuzol F, Parias C, Nowak R, Calandreau L, Lansade L. 2020 Horses
510 feel emotions when they watch positive and negative horse–human interactions in a video
511 and transpose what they saw to real life. *Anim Cogn* **23**, 643–653. (doi:10.1007/s10071-
512 020-01369-0)
- 513 48. Edgar JL, Lowe JC, Paul ES, Nicol CJ. 2011 Avian maternal response to chick distress.
514 *Proc. R. Soc. B.* **278**, 3129–3134. (doi:10.1098/rspb.2010.2701)
- 515 49. Briefer EF, Tettamanti F, McElligott AG. 2015 Emotions in goats: mapping
516 physiological, behavioural and vocal profiles. *Animal Behaviour* **99**, 131–143.
517 (doi:10.1016/j.anbehav.2014.11.002)
- 518 50. Reefmann N, Bütikofer Kaszàs F, Wechsler B, Gygas L. 2009 Physiological expression
519 of emotional reactions in sheep. *Physiology & Behavior* **98**, 235–241.
520 (doi:10.1016/j.physbeh.2009.05.017)
- 521 51. Zupan M, Buskas J, Altimiras J, Keeling LJ. 2016 Assessing positive emotional states in
522 dogs using heart rate and heart rate variability. *Physiology & Behavior* **155**, 102–111.
523 (doi:10.1016/j.physbeh.2015.11.027)
- 524 52. Reefmann N, Wechsler B, Gygas L. 2009 Behavioural and physiological assessment of
525 positive and negative emotion in sheep. *Animal Behaviour* **78**, 651–659.
526 (doi:10.1016/j.anbehav.2009.06.015)
- 527 53. Careau V, Thomas D, Humphries MM, Reale D. 2008 Energy metabolism and animal
528 personality. *Oikos* **117**, 641–653.
- 529 54. Kralj-Fisčer S, Weiß BM, Kotrschal K. 2010 Behavioural and physiological correlates of
530 personality in greylag geese (*Anser anser*). *J Ethol* **28**, 363–370.
- 531 55. Sgoifo A, Costoli T, Meerlo P, Buwalda B, Pico'-Alfonso MA, De Boer S, Musso E,
532 Koolhaas J. 2005 Individual differences in cardiovascular response to social challenge.

- 533 *Neuroscience & Biobehavioral Reviews* **29**, 59–66.
534 (doi:10.1016/j.neubiorev.2004.07.001)
- 535 56. Korte SM, Ruesink W, Blokhuis HJ. In press. Heart rate variability during manual
536 restraint in chicks from high- and low-feather pecking lines of laying hens. *Physiology &*
537 *Behavior* **65**, 649–652.
- 538 57. Ellenberg U, Mattern T, Seddon PJ. 2009 Habituation potential of yellow-eyed penguins
539 depends on sex, character and previous experience with humans. *Animal Behaviour* **77**,
540 289–296. (doi:10.1016/j.anbehav.2008.09.021)
- 541 58. Johnsson JI, Höjesjö J, Fleming IA. 2001 Behavioural and heart rate responses to
542 predation risk in wild and domesticated Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **58**,
543 788–794. (doi:10.1139/f01-025)
- 544 59. Jean-Joseph H, Kortekaas K, Range F, Kotrschal K. 2020 Context-specific arousal during
545 resting in wolves and dogs: Effects of domestication? *Front. Psychol.* **11**, 568199.
546 (doi:10.3389/fpsyg.2020.568199)
- 547 60. Viblanc VA, Smith AD, Gineste B, Groscolas R. 2012 Coping with continuous human
548 disturbance in the wild: insights from penguin heart rate response to various stressors.
549 *BMC Ecol* **12**, 10. (doi:10.1186/1472-6785-12-10)
- 550 61. Roche DG, Careau V, Binning SA. 2016 Demystifying animal ‘personality’ (or not): why
551 individual variation matters to experimental biologists. *J Exp Biol* **219**, 3832–3843.
552 (doi:10.1242/jeb.146712)
- 553 62. Viblanc VA, Smith AD, Gineste B, Kauffmann M, Groscolas R. 2015 Modulation of
554 heart rate response to acute stressors throughout the breeding season in the king penguin
555 *Aptenodytes patagonicus*. *Journal of Experimental Biology* **218**, 1686–1692.
556 (doi:10.1242/jeb.112003)
- 557 63. Dickens MJ, Nephew BC, Romero LM. 2006 Captive european starlings (*Sturnus*
558 *vulgaris*) in breeding condition show an increased cardiovascular stress response to
559 intruders. *Physiological and Biochemical Zoology* **79**, 937–943. (doi:10.1086/506007)
- 560 64. Portugal SJ, Green JA, Cassey P, Frappell PB, Butler PJ. 2009 Predicting the rate of
561 oxygen consumption from heart rate in barnacle geese *Branta leucopsis*: effects of
562 captivity and annual changes in body condition. *Journal of Experimental Biology* **212**,
563 2941–2948. (doi:10.1242/jeb.034546)
- 564 65. Linek N, Bjarnason Á, Partecke J, Wikelski M. submitted Heart rate and body
565 temperature measurements in a free-living, small songbird in response to environmental
566 variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*
- 567 66. Cyr NE, Wikelski M, Romero LM. 2008 Increased energy expenditure but decreased
568 stress responsiveness during molt. *Physiological and Biochemical Zoology* **81**, 452–462.
569 (doi:10.1086/589547)
- 570 67. Portugal SJ, White CraigR, Green JA, Butler PJ. 2018 Flight feather moult drives
571 minimum daily heart rate in wild geese. *Biol. Lett.* **14**, 20180650.
572 (doi:10.1098/rsbl.2018.0650)

- 573 68. Welbers AAMH, van Dis NE, Kolvoort AM, Ouyang J, Visser ME, Spoelstra K,
574 Dominoni DM. 2017 Artificial light at night reduces daily energy expenditure in breeding
575 great tits (*Parus major*). *Front. Ecol. Evol.* **5**, 55. (doi:10.3389/fevo.2017.00055)
- 576 69. Vaugeois M, Venturelli PA, Hummel SL, Accolla C, Forbes VE. 2020 Population
577 context matters: Predicting the effects of metabolic stress mediated by food availability
578 and predation with an agent- and energy budget-based model. *Ecological Modelling* **416**,
579 108903. (doi:10.1016/j.ecolmodel.2019.108903)
- 580 70. Hicks O, Burthe SJ, Daunt F, Newell M, Chastel O, Parenteau C, Green JA. 2018 The
581 role of parasitism in the energy management of a free-ranging bird. *J Exp Biol* **221**,
582 jeb190066. (doi:10.1242/jeb.190066)
- 583 71. Beerda B, Schilder MBH, van Hooff JARAM, de Vries HW, Mol JA. 1998 Behavioural,
584 saliva cortisol and heart rate responses to different types of stimuli in dogs. *Applied*
585 *Animal Behaviour Science* **58**, 365–381. (doi:10.1016/S0168-1591(97)00145-7)
- 586 72. Bowman A, Dowell FJ, Evans NP. 2017 ‘The effect of different genres of music on the
587 stress levels of kennelled dogs’. *Physiology & Behavior* **171**, 207–215.
588 (doi:10.1016/j.physbeh.2017.01.024)
- 589 73. Amaya V, Paterson MBA, Descovich K, Phillips CJC. 2020 Effects of olfactory and
590 auditory enrichment on heart rate variability in shelter dogs. *Animals* **10**, 1385.
591 (doi:doi:10.3390/ani10081385)
- 592 74. Meijer M, Kramer K, Remie R. 2006 The effect of routine experimental procedures on
593 physiological parameters in mice kept under different husbandry conditions. *Animal*
594 *Welfare* **15**, 31–38.
- 595 75. Pollard JC, Littlejohn RP. 1995 Effects of social isolation and restraint on heart rate and
596 behaviour of alpacas. *Applied Animal Behaviour Science* **45**, 165–174.
- 597 76. Boissy A, Le Neindre P. 1997 Behavioral, cardiac and cortisol responses to brief peer
598 separation and reunion in cattle. *Physiology & Behavior* **61**, 693–699.
599 (doi:10.1016/S0031-9384(96)00521-5)
- 600 77. Watson SL, Shively CA, Kaplan JR, Line SW. 1998 Effects of chronic social separation
601 on cardiovascular disease risk factors in female cynomolgus monkeys. *Atherosclerosis*
602 **137**, 259–266. (doi:10.1016/S0021-9150(97)00277-3)
- 603 78. Grandi LC, Ishida H. 2015 The physiological effect of human grooming on the heart rate
604 and the heart rate variability of laboratory non-human primates: A pilot study in male
605 rhesus monkeys. *Front. Vet. Sci.* **2**. (doi:10.3389/fvets.2015.00050)
- 606 79. Schmied C, Waiblinger S, Scharl T, Leisch F, Boivin X. 2008 Stroking of different body
607 regions by a human: Effects on behaviour and heart rate of dairy cows. *Applied Animal*
608 *Behaviour Science* **109**, 25–38. (doi:10.1016/j.applanim.2007.01.013)
- 609 80. Coulon M, Nowak R, Peyrat J, Chandèze H, Boissy A, Boivin X. 2015 Do lambs
610 perceive regular human stroking as pleasant? Behavior and heart rate variability analyses.
611 *PLoS ONE* **10**, e0118617. (doi:10.1371/journal.pone.0118617)

- 612 81. Line SW, Morgan KN, Markowitz H, Strong S. 1990 Increased cage size does not alter
613 heart rate or behavior in female rhesus monkeys. *Am. J. Primatol.* **20**, 107–113.
614 (doi:10.1002/ajp.1350200205)
- 615 82. Hinds SB, Raimond S, Purcell BK. 2007 The effect of harp music on heart rate, mean
616 blood pressure, respiratory rate, and body temperature in the African green monkey. *J*
617 *Med Primatol* **36**, 95–100. (doi:10.1111/j.1600-0684.2006.00157.x)
- 618 83. Ditmer MA, Vincent JB, Werden LK, Tanner JC, Laske TG, Iaizzo PA, Garshelis DL,
619 Fieberg JR. 2015 Bears show a physiological but limited behavioral response to
620 unmanned aerial vehicles. *Current Biology* **25**, 2278–2283.
- 621 84. Talling JC, Waran NK, Wathes CM, Lines JA. 1996 Behavioural and physiological
622 responses of pigs to sound. *Applied Animal Behaviour Science* **48**, 187–201.
623 (doi:10.1016/0168-1591(96)01029-5)
- 624 85. Graham AL, Cooke SJ. 2008 The effects of noise disturbance from various recreational
625 boating activities common to inland waters on the cardiac physiology of a freshwater
626 fish, the largemouth bass (*Micropterus salmoides*). *Aquatic Conserv: Mar. Freshw.*
627 *Ecosyst.* **18**, 1315–1324. (doi:10.1002/aqc.941)
- 628 86. Le Grand L, Thorsen NH, Fuchs B, Evans AL, Laske TG, Arnemo JM, Sæbø S, Støen O-
629 G. 2019 Behavioral and physiological responses of Scandinavian brown bears (*Ursus*
630 *arctos*) to dog hunts and human encounters. *Front. Ecol. Evol.* **7**, 134.
631 (doi:10.3389/fevo.2019.00134)
- 632 87. Ropert-Coudert Y, Brooks L, Yamamoto M, Kato A. 2009 ECG response of koalas to
633 tourists proximity: A preliminary study. *PLoS ONE* **4**, e7378.
634 (doi:10.1371/journal.pone.0007378)
- 635 88. Nimon AJ, Schroter RC, Stonehouse B. 1995 Heart rate of disturbed penguins. *Nature*
636 **374**, 415.
- 637 89. Ellenberg U, Mattern T, Seddon PJ. 2013 Heart rate responses provide an objective
638 evaluation of human disturbance stimuli in breeding birds. *Conservation Physiology* **1**,
639 cot013–cot013. (doi:10.1093/conphys/cot013)
- 640 90. Weimerskirch H, Shaffer SA, Mabile G, Martin J, Boutard O, Rouanet JL. 2002 Heart
641 rate and energy expenditure of wandering albatross. *Journal of Experimental Biology* **205**,
642 475–483.
- 643 91. Borneman TE, Rose ET, Simons TR. 2014 Minimal changes in heart rate of incubating
644 American Oystercatchers (*Haematopus palliatus*) in response to human activity. *The*
645 *Condor* **116**, 493–503. (doi:10.1650/CONDOR-14-48.1)
- 646 92. Wascher CAF, Scheiber IBR, Braun A, Kotrschal K. 2011 Heart rate responses to
647 induced challenge situations in greylag geese (*Anser anser*). *Journal of Comparative*
648 *Psychology* **125**, 116–119. (doi:10.1037/a0021188)
- 649 93. Ellenberg U, Mattern T, Houston DM, Davis LS, Seddon PJ. 2012 Previous experiences
650 with humans affect responses of Snares penguins to experimental disturbance. *J Ornithol*
651 **153**, 621–631. (doi:10.1007/s10336-011-0780-4)

- 652 94. Holmes N, Giese M, Kriwoken LK. 2005 Testing the minimum approach distance
653 guidelines for incubating Royal penguins *Eudyptes schlegeli*. *Biological Conservation*
654 **126**, 339–350. (doi:10.1016/j.biocon.2005.06.009)
- 655 95. Baldock NM, Silby RM. 1990 Effects of handling and transportation on the heart rate and
656 behaviour of sheep. *Applied Animal Behaviour Science* **28**, 15–39.
- 657 96. Parrott RF, Hall SJG, Lloyd DM. 1998 Heart rate and stress hormone responses of sheep
658 to road transport following two different loading procedures. *Animal Welfare* **7**, 257–267.
- 659 97. Zebunke M. 2013 Effects of cognitive enrichment on behavioural and physiological
660 reactions of pigs. *Physiology & Behavior* **118**, 70–79.
- 661 98. Banhazi TM, Lehr H, Black JL, Crabtree H, Schofield P, Tscharke M, Berckmans D.
662 2012 Precision livestock farming: an international review of scientific and commercial
663 aspects. *International Journal of Agricultural and Biological Engineering* **5**, 1–9.
- 664 99. Trondrud LM, Pigeon G, Evans A, Arnold W, Albon S, Krol E, Speakman J, Loe LE.
665 submitted Seasonal adjustments in energy expenditure in a high-arctic ungulate revealed
666 via measurements of body Albon S, Krol E, Speakman J & Loe LE. *Philosophical*
667 *Transactions of the Royal Society B: Biological Sciences*
- 668 100. Jorquera-Chavez M, Fuentes S, Dunshea FR, Warner RD, Poblete T, Jongman EC.
669 2019 Modelling and validation of computer vision techniques to assess heart rate, eye
670 temperature, ear-base temperature and respiration rate in cattle. *Animals* **9**, 1089.
671 (doi:10.3390/ani9121089)
- 672 101. Lewis CRG, Hulbert LE, McGlone JJ. 2008 Novelty causes elevated heart rate and
673 immune changes in pigs exposed to handling, alleys, and ramps. *Livestock Science* **116**,
674 338–341. (doi:10.1016/j.livsci.2008.02.014)
- 675 102. Lierz M, Gooss O, Hafez HM. 2006 Noninvasive heart rate measurement using a
676 digital egg monitor in chicken and turkey embryos. *Journal of Avian Medicine and*
677 *Surgery* **20**, 141–146. (doi:10.1647/2005-017R.1)
- 678 103. Palme R. 2019 Non-invasive measurement of glucocorticoids: Advances and
679 problems. *Physiology & Behavior* **199**, 229–243. (doi:10.1016/j.physbeh.2018.11.021)
- 680 104. Seyle H. 1973 The evolution of the stress concept. *American Scientist* **61**, 692–699.
- 681 105. Wisniewska D, McDonald B. submitted Estimating energy intake and expenditure in
682 free-ranging marine predators: a review. *Philosophical Transactions of the Royal Society*
683 *B: Biological Sciences*
- 684 106. Proudfoot K, Habing G. 2015 Social stress as a cause of diseases in farm animals:
685 Current knowledge and future directions. *The Veterinary Journal* **206**, 15–21.
686 (doi:10.1016/j.tvjl.2015.05.024)
- 687 107. Kaplan JR, Manuck SB, Clarkson TB, Lusso FM, Taub DM. 1982 Social status,
688 environment, and atherosclerosis in cynomolgus monkeys. *Arteriosclerosis* **2**, 359–368.

- 689 108. Williams CL, Ponganis PJ. submitted Diving physiology of marine mammals and
690 birds: The development of biologging techniques. *Philosophical Transactions of the*
691 *Royal Society B: Biological Sciences*
- 692 109. Laske T, Garshelis D, Iaizzo PA, Iles T. submitted An engineering perspective on the
693 development and evolution of implantable cardiac monitors in free living animals.
694 *Philosophical Transactions of the Royal Society B: Biological Sciences*
- 695 110. Clark TD, Shen Y, Kusy B. submitted Multi-sensor implantable technology to
696 understand animal-environment interactions and revolutionise ‘smart farming’ Authors:
697 Clark TD, Shen Y & Kusy B. *Philosophical Transactions of the Royal Society B:*
698 *Biological Sciences*
- 699 111. Scopa C, Palagi E, Sighieri C, Baragli P. 2018 Physiological outcomes of calming
700 behaviors support the resilience hypothesis in horses. *Sci Rep* **8**, 17501.
701 (doi:10.1038/s41598-018-35561-7)
- 702 112. Lambert H. 2019 Positive and negative emotions in dairy cows: Can ear postures be
703 used as a measure? *Behav Proc* **158**, 172–180.
- 704 113. Squibb K. 2018 Poker Face: Discrepancies in behaviour and affective states in horses
705 during stressful handling procedures. *Applied Animal Behaviour Science* **202**, 34–38.
- 706 114. Safryghin A, Hebesberger DV, Wascher CAF. 2019 Testing for behavioral and
707 physiological responses of domestic horses (*Equus caballus*) across different contexts –
708 consistency over time and effects of context. *Front. Psychol.* **10**, 849.
709 (doi:10.3389/fpsyg.2019.00849)
- 710 115. Berezowski J, Rüegg SR, Faverjon C. 2019 Complex system approaches for animal
711 health surveillance. *Front. Vet. Sci.* **6**, 153. (doi:10.3389/fvets.2019.00153)
- 712 116. Bartlett PC, Van Buren JW, Neterer M, Zhou C. 2010 Disease surveillance and
713 referral bias in the veterinary medical database. *Preventive Veterinary Medicine* **94**, 264–
714 271. (doi:10.1016/j.prevetmed.2010.01.007)
- 715 117. Williams H, Shipley JR, Rutz C, Wikelski M, Wilkes M, Hawkes L. in press Future
716 trends in measuring physiology in free-living animals. *Phil. Trans. R. Soc. B*
- 717 118. Palmer A, Greenhough B. submitted Out of the lab, into the field: perspectives on
718 social, ethical, and regulatory challenges in wildlife research. *Philosophical Transactions*
719 *of the Royal Society B: Biological Sciences*
- 720 119. Harrison XA. In press. Best statistical practice for handling physiological data
721 collected from wild animals. *Phil. Trans. R. Soc. B*
- 722 120. Holton M, Wilson R, Teilmann J, Siebert U. in press Animal tag technology keeps
723 coming of age: an engineering perspective. *Phil. Trans. R. Soc. B*
- 724 121. Bjarnason Á, Gunnarsson A, Árnason T, Oddgeirsson M, Sigmarsson AB,
725 Gunnarsson Á. 2019 Validation of ECG-derived heart rate recordings in Atlantic cod
726 (*Gadus morhua* L.) with an implantable data logging system. *Anim Biotelemetry* **7**, 13.
727 (doi:10.1186/s40317-019-0176-4)

- 728 122. Nimon AJ, Schroter RC, Oxenham RK. 1996 Artificial eggs: measuring heart rate and
729 effects of disturbance in nesting penguins. *Physiology & Behavior*, 60(3), 1019-1022.
730 *Physiology & Behavior* **60**, 1019–1022.
- 731 123. Schöberl I, Kortekaas K, Schöberl FF, Kotrschal K. 2015 Algorithm-supported visual
732 error correction (AVEC) of heart rate measurements in dogs, *Canis lupus familiaris*.
733 *Behav Res* **47**, 1356–1364. (doi:10.3758/s13428-014-0546-z)
- 734 124. Marchant-Forde RM, Marlin DJ, Marchant-Forde JN. 2004 Validation of a cardiac
735 monitor for measuring heart rate variability in adult female pigs: accuracy, artefacts and
736 editing. *Physiology & Behavior* **80**, 449–458. (doi:10.1016/j.physbeh.2003.09.007)
- 737

738 **Tables and Figures**

739 Table 1: Summary of studies investigating individual heart rate in different species and
 740 contexts, and the type of technology used to measure heart rate.

Context	Species	Technology	Reference
social behaviour	blind cave crayfish, <i>Orconectes australis packardi</i>	implanted wires connected to external impedance detectors	Li et al. 2000
	cattle, <i>Bos taurus</i>	wearable heart rate belt	Laister et al. 2011
	goats, <i>Capra hircus</i>	wearable heart rate belt	Briefer et al. 2015
	greater white-fronted geese, <i>Anser albifrons</i>	implanted radio- transmitter	Ely et al. 1999
	greylag geese, <i>Anser anser</i>	implanted radio- transmitter	Wascher et al. 2008
	king penguins, <i>Aptenodytes patagonicus</i>	implanted electrodes connected to external recorder	Viblanc et al. 2012
	pigtail macaque, <i>Macaca nemestrina</i>	implanted radiotransmitter	Boccia et al. 1989
	rats, <i>Rattus norvegicus</i>	implanted radio- transmitter	Sgoifo et al. 2001
	red deer, <i>Cervus elaphus</i>	rumen-located transmitters	Turbill et al. 2013
	rhesus Macaques, <i>Macaca mulatta</i>	implanted radiotransmitter	Aureli et al. 1999
anthropogenic disturbance	Adélie penguins, <i>Pygoscelis adeliae</i>	artificial eggs	Nimon et al. 1995
	American black bears, <i>Ursus americanus</i>	implanted radio- transmitter	Dietmer et al. 2015
	American oystercatchers, <i>Haematopus palliatus</i>	artificial eggs	Borneman et al. 2014
	bighorn sheep, <i>Ovis canadensis</i>	wearable heart rate belt	MacArthur et al. 1979
	brown bears, <i>Ursus arctos</i>	implanted radio- transmitter	Le Grand et al. 2019
	koalas, <i>Phascolarctos cinereus</i>	wearable heart rate belt	Ropert- Coudert et al. 2009
	largemouth bass, <i>Micropterus salmoides</i>	implanted radio- transmitter	Graham & Cooke 2008

	wandering albatrosses, <i>Diomedea exulans</i>	implanted electrodes connected to external recorder	Weimerskirch et al. 2002
	Yellow-eyed penguin, <i>Megadyptes antipodes</i>	artificial eggs	Ellenberg et al. 2013
cognitive task	cattle, <i>Bos taurus</i>	wearable heart rate belt	Hagen et al. 2004
	chimpanzee, <i>Pan troglodytes</i>	electrodes attached to skin surface, connected to cardiometer	Boysen & Berntson 1986, 1989
	chickens, <i>Gallus gallus domesticus</i>	electrodes attached to skin surface, connected to cardiometers	Edgar et al. 2011
	dogs, <i>Canis familiaris</i>	electrodes attached to skin surface, connected to cardiometers	Maros et al. 2008
	dogs, <i>Canis familiaris</i>	wearable heart rate belt	Siniscalchi et al. 2013
	greylag geese, <i>Anser anser</i>	implanted radio-transmitter	Wascher et al. 2008
	European Starlings, <i>Sturnus vulgaris</i>	implanted radio-transmitter	Glassman et al. 2019
	horses, <i>Equus caballus</i>	wearable heart rate belt	Mengoli et al. 2014; Trösch et al. 2020
	little blue penguin chicks, <i>Eudyptula minor</i>	electrodes attached to skin surface, connected to cardiometers	Nakagawa et al. 2001
	Nigerian dwarf goats, <i>Capra hircus</i>	wearable heart rate belt	Langbein et al. 2004
	rainbow trout, <i>Oncorhynchus mykiss</i>	aquarium with the electrode cage	Höjesjö et al. 2015
	rats, <i>Rattus norvegicus</i>	implanted radio-transmitter	Van den Buuse et al. 2001
	sheep, <i>Ovis aries</i>	electrodes attached to skin surface, connected to cardiometer	Désiré et al. 2004
individual differences	chicken, <i>Gallus gallus domesticus</i>	implanted radio-transmitter	Korte et al. 1999
	greylag geese, <i>Anser anser</i>	implanted radio-transmitter	Kralj-Fisˇer et al. 2010

	rats, <i>Rattus norvegicus</i>	implanted radio-transmitter	Sgoifo et al. 2001
environmental enrichment	African green monkeys, <i>Chlorocebus aethiops</i>	implanted radio-transmitter	Hinds et al. 2007
	dogs, <i>Canis familiaris</i>	wearable heart rate belt	Amaya et al. 2020; Bowman et al. 2017
housing condition	cattle, <i>Bos taurus</i>	electrodes attached to skin surface, connected to cardiometer	Boissy & Le Neindre, 1997
	mice, <i>Mus musculus</i>	implanted radio-transmitter	Meijer et al. 2006
	rhesus monkeys, <i>Mucaca mulatta</i>	implanted radio-transmitter	Line et al. 1990
precision livestock farming	Atlantic salmon, <i>Salmo salar</i>	implanted radio-transmitter	Brijs et al. 2021
	cattle, <i>Bos taurus</i>	wearable heart rate belt	Jorquera-Chavez et al. 2019
	chickens, <i>Gallus gallus domesticus</i>	digital egg monitor	Lierz et al. 2006
	domestic pigs, <i>Sus domesticus</i>	wearable heart rate belt	Lewis et al. 2008

741

742

743 Table 2: Example heart rates during resting and agonistic interactions in different species.

Species	Resting heart rate	Heart rate during agonistic interactions	Reference
bighorn sheep (<i>Ovis canadensis canadensis</i>)	52	66	MacArthur et al. 1979
blind cave crayfish (<i>Orconectes australis packardi</i>)	78	163	Li et al. 2000
domestic pig (<i>Sus scrofa</i>)	52	129	Marchant et al. 1995
greater whitefronted geese (<i>Anser albifrons</i>)	100	400	Ely et al. 1999
greylag geese (<i>Anser anser</i>)	84	157	Wascher et al. 2008
king penguins (<i>Aptenodytes patagonicus</i>)	67	82	Viblanc et al. 2012
pigtail macaque (<i>Macaca nemestrina</i>)	133	176	Boccia et al. 1989

744

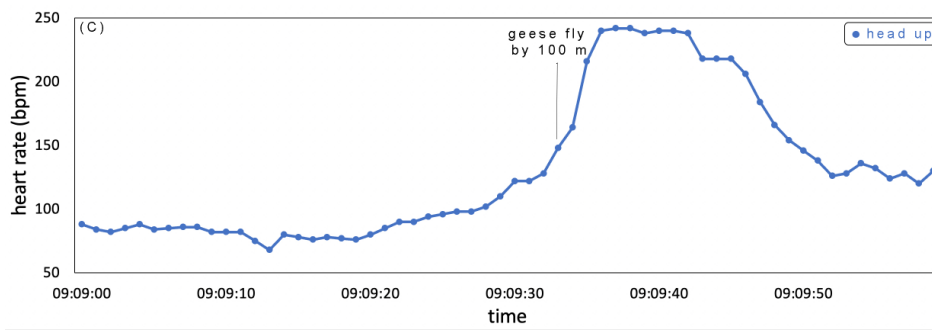
745

aggression

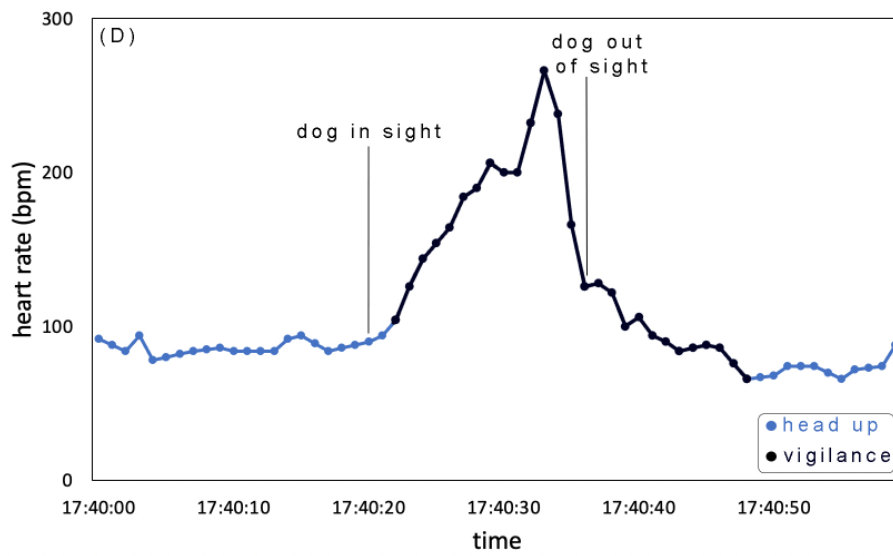
746



747



748



749

750 Figure 1. Examples of heart rate modulation in greylag geese. (A) Aggressive interaction,
751 focal individual walking towards another individual in a threat posture, other individual
752 walks away. (B) Departure event of focal individual. Different behavioural states are shown
753 in different colours. (C) Bystander event, approximately 100 metres from the focal
754 individuals a group of geese fly by. (D) Goose flock is approached by a dog.