

1 The 24/7 approach to promoting optimal welfare for captive wild animals

2 Sabrina Brando<sup>a</sup> and Hannah M. Buchanan-Smith<sup>b</sup>

3 <sup>a</sup>AnimalConcepts, Lancasterdreef 90, 8251 TJ Dronten, The Netherlands,

4 [sbrando@animalconcepts.eu](mailto:sbrando@animalconcepts.eu)

5 <sup>b</sup>Psychology, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA,

6 Scotland, [h.m.buchanan-smith@stir.ac.uk](mailto:h.m.buchanan-smith@stir.ac.uk)

7

8

9 Corresponding author:

10 Sabrina Brando  
11 AnimalConcepts  
12 Lancasterdreef 90  
13 8251 TJ Dronten  
14 The Netherlands  
15 +31633008373  
16 [www.animalconcepts.eu](http://www.animalconcepts.eu)  
17 [sbrando@animalconcepts.eu](mailto:sbrando@animalconcepts.eu)

18

19

20 Accepted for publication in *Behavioural Processes* by Elsevier. The version of  
21 record is available at: <https://doi.org/10.1016/j.beproc.2017.09.010>

22

23

## 24 ABSTRACT

25 We have an ethical responsibility to provide captive animals with environments that  
26 allow them to experience good welfare. Husbandry activities are often scheduled for  
27 the convenience of care staff working within the constraints of the facility, rather than  
28 considering the biological and psychological requirements of the animals themselves.  
29 The animal welfare 24/7 across the lifespan concept provides a holistic framework to  
30 map features of the animal's life cycle, taking into account their natural history, in  
31 relation to variations in the captive environment, across day and night, weekdays,  
32 weekends, and seasons. In order for animals to have the opportunity to thrive, we  
33 argue the need to consider their lifetime experience, integrated into the environments  
34 we provide, and with their perspective in mind. Here, we propose a welfare  
35 assessment tool based upon 14 criteria, to allow care staff to determine if their  
36 animals' welfare needs are met. We conclude that animal habitat management will be  
37 enhanced with the use of integrated technologies that provide the animals with more  
38 opportunities to engineer their own environments, providing them with complexity,  
39 choice and control.

40

41 Keywords: Animal welfare, Birth to death, Habitat management, Technology, Zoo,  
42 24/7 across lifespan

43

44

45

46 Highlights:

- 47 • New holistic conceptual framework in caring for captive wild animals 24/7  
48 across lifespan is proposed.
- 49 • Considers individual's life cycle needs and preferences influenced by a range  
50 of variations.
- 51 • An animal welfare assessment tool with 14 welfare criteria is proposed.
- 52 • Highlights importance of habitat management and use of technologies.

53

54

55

56

57

58

59

60

61

62

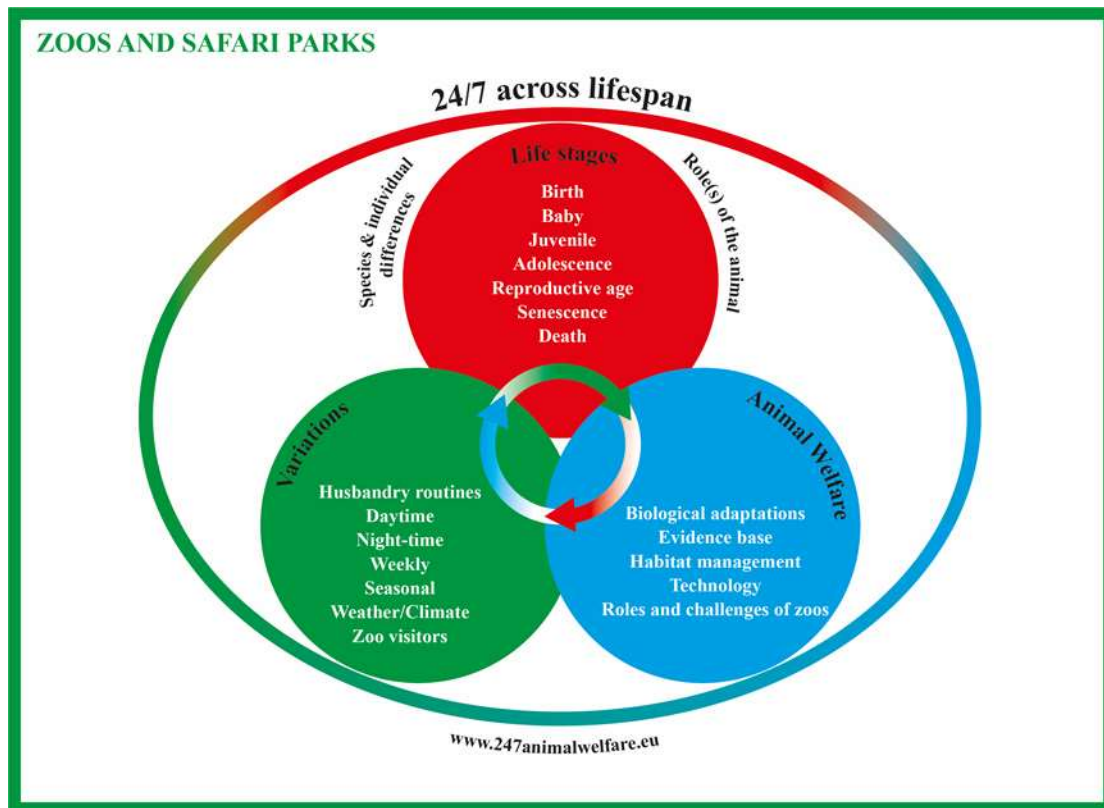
63

64

## 65 **1. Introduction: A holistic approach to animal welfare**

66 Care staff spends a limited number of hours at a zoo, wildlife centre, or sanctuary.  
67 The animals however, are there 24/7, year round for life unless they are part of a  
68 reintroduction program (or escape!). Indeed, the human working day dictates the care  
69 provided to captive animals. Husbandry activities typically occur during 6-8 daylight  
70 hours, which are not necessarily biologically relevant times for the animals. Care staff  
71 are not normally present to observe and provide for the needs and preferences of  
72 captive animals most of the time (i.e. 16-18 h/day). Given that animal care personnel  
73 are fundamental to promoting good welfare, we propose a tool for care staff to  
74 determine how well they are providing habitats that meet animals' needs.

75 This paper proposes a new, holistic conceptual framework to help optimise how we  
76 care for animals in zoos. We focus on the animal's perspective; how are animals  
77 affected by different aspects of their life cycle, and how do these aspects vary across,  
78 for example, day and night, seasons, and the role the animal has been assigned. We  
79 discuss how to promote good animal welfare using our proposed 24/7 across the  
80 lifespan framework. The framework (Figure 1) requires consideration and integration  
81 of life stages, in relation to species and individual differences, and the roles animals  
82 play, variations, and other factors affecting animal welfare. We start by describing  
83 how we see the concept of animal welfare within this 24/7 framework, and the  
84 challenges we face in promoting optimal welfare in zoo environments. We discuss  
85 examples of good practice and propose future directions.



86

87 **Figure 1.** 24/7 across lifespan framework, illustrating the different aspects that should  
88 be considered and integrated.

### 89 *1.1 Applying the concept of animal welfare*

90 Defining and measuring animal welfare is not straightforward (e.g. Mason and Mendl,  
91 1993; reviewed in Fraser, 2009). An animal's welfare is generally accepted to lie on a  
92 continuous scale between bad and good (Broom, 1999), and behavioural,  
93 physiological, psychological, and biochemical measures need to be integrated to  
94 provide a holistic view (Broom, 2007, 2014). Despite this agreement, there is still  
95 debate about the importance of the three different approaches to welfare that include  
96 whether the animal is able to lead a natural life (e.g. Duncan and Petherick, 1991),  
97 how the animal feels (e.g. Dawkins, 1998; Duncan and Petherick, 1991), and the  
98 biological functioning approach (e.g. Broom, 1986). Fraser (2009) provides an

99 excellent critique of the merits and limitations of the approaches. The approaches are  
100 now seen as dynamically integrated elements within the whole animal, and methods  
101 to measure welfare should incorporate all three approaches (e.g. Mellor, 2016).  
102 Promoting natural adaptations will likely lead to better welfare reflected by the  
103 feelings and biological functioning approaches. 24/7 across the lifespan takes this  
104 holistic perspective.

105 More pragmatically, a range of factors influences the choice of methods to measure  
106 welfare. These include availability of technology; human expertise and time; and the  
107 relationship with the animals. We strongly recommend that when changes are made to  
108 the environment that the animals' welfare be evaluated to ensure the changes have the  
109 desired overall positive effect. Behaviour can be systematically quantified (see Martin  
110 and Bateson, 2007 for methods) or measured using a Qualitative Behavioural  
111 Assessment approach (see Wemelsfelder, 2007). Behavioural observations have  
112 many advantages for animal care staff. Unlike some physiological and physical health  
113 measures, recording behaviour is non-invasive, often non-intrusive, accessible,  
114 immediate and informative of welfare state. Behaviour is the ultimate phenotype - not  
115 only is it the result of the animal's own decision-making processes, it is also the  
116 expression of emotions (Darwin, 1872; Dawkins, 2004).

117 Whilst many may consider it ideal for animals only to display positive welfare states  
118 (e.g. comfort, satisfaction), we note that some (short-term) negative welfare states are  
119 essential; they are instincts that promote survival. For example, thirst encourages  
120 water seeking, or hunger promotes exploration and food seeking (Mellor, 2016). The  
121 concept of "optimal" welfare is therefore one that includes some negative welfare  
122 states.

123 To illustrate this, Rabin (2003) emphasizes the importance of maintaining behavioural  
124 diversity in light of conservation goals by the development of natural behaviour  
125 management programs. These programs contain naturalistic stimuli that will  
126 encourage the performance of a wide range of behaviours, some of which might be in  
127 conflict with short-term animal welfare objectives such as exposing animals to  
128 predatory stimuli. Rabin (2003) argues that animals destined for release should be  
129 exposed to both positive and negative stimuli during sensitive periods that require  
130 behaviour releasing mechanisms. Thus, some stressors are required to promote  
131 resilience and coping in animals (see Section 2.2); the key for good welfare is whether  
132 the animal has perceived control. It is the balance between positive and negative  
133 experiences that reflects the overall welfare state (Spruijt et al., 2001), and welfare is  
134 good when the balance is strongly positive (Mellor, 2016, p. 21).

135 Our goal in 24/7 across the lifespan is to provide environments in which animals can  
136 thrive, understanding that at any one time point welfare may vary for individual  
137 animals within the same group (e.g. dominant *versus* subordinate). However, when  
138 considering the lifespan holistically and within the framework we provide, we argue  
139 the balance of positive to negative experiences at all stages of the life cycle will  
140 improve.

#### 141 *1.2 Challenges in zoos*

142 Humans are inevitably a critical part of the lives of all captive wild animals, and their  
143 actions impact animal welfare. Humans design enclosures, decide on animals' social  
144 companionship (or otherwise), have control over the type of food, frequency and  
145 method of delivery. Humans decide whether to provide dynamic challenges and  
146 environmental enrichment. Key concepts behind environments that promote good

147 welfare are complexity and novelty, choice, and control, and their relationship to  
148 predictability (Buchanan-Smith, 2010a). These concepts underpin Poole's (1998) four  
149 basic needs of mammals, namely security (a safe area in which to rest and feel  
150 secure), complexity, achievement (control), and novelty (to satisfy curiosity and  
151 prevent boredom). Both social and physical complexity is critical to promote positive  
152 affective states. However, provision of suitably complex environments that animals  
153 can control has to be understood in the context of the many challenges zoos face to  
154 remain competitive and viable ventures.

155 Modern zoos have clearly defined goals reflected in their mission statements, these  
156 being conservation, research, education and recreation or entertainment (Buchanan-  
157 Smith et al., 2001; Patrick et al., 2007). Miller (2012), who surveyed zoo visitors after  
158 viewing a video of a tiger pacing, found that poor welfare and related behaviours are  
159 not only detrimental for the animals in the zoo, but they can also cause a significant  
160 decrease in people's perception of the level of care the animals receive, and their  
161 willingness to support zoos. Good animal welfare underpins zoos' goals, by providing  
162 environments that encourage visitor learning through the enjoyment and interest  
163 generated from watching animals in environments that promote natural behavioural  
164 diversity and good infant rearing conditions. Good welfare also promotes more  
165 ecologically valid research findings on healthy animals (Buchanan-Smith et al.,  
166 2001). Therefore, promoting good animal welfare is fundamental not only for the  
167 individual animal, but also to achieve high standards in successful conservation,  
168 research, education, and entertainment programs.

169 Besides education, research and conservation, zoos must entertain the public, as they  
170 are usually financially reliant on paying visitors. Despite best efforts, there are often



171 financial constraints and competition from other animal-related activities the public  
172 could choose to visit (e.g. amusement park, petting farm). Building or maintaining  
173 new enclosures is extremely expensive, and staff often have limited time to engage in  
174 all animal welfare activities they might wish to (Brando, 2016a). Fulfilling both the  
175 goals of high standards of animal welfare as well as adhering to mission statements  
176 can be challenging, as the goals can be conflicting when trying to meet visitor, staff,  
177 and animal needs and preferences. Animal visibility is an important aspect in  
178 maintaining visitor satisfaction and achieving educational goals, but animals might  
179 choose to be out of sight from the public. Creative solutions such as one-way glass  
180 nesting boxes that allow for visibility while an animal is inside (without direct visitor  
181 access to avoid tapping on the glass to wake up and/or activate the animals) can help  
182 overcome some of the conflicts between different goals.

## 183 **2. Considering 24/7 welfare across lifespan**

### 184 *2.1 Species, including developmental and social, considerations*

185 The natural history of an animal, its biology, ecology and diet, sensory systems,  
186 natural habitat, social structure, major life history events, activity patterns, and  
187 human-animal interactions are among the many topics taken into account when  
188 developing species-specific animal welfare programs (see our website  
189 [247animalwelfare.eu](http://247animalwelfare.eu) for a worked example with common marmosets). Looking at the  
190 life cycle of a species, we find different life stages commonly divided into birth, baby,  
191 juvenile, adolescence, reproductive age, senescence and death (see Table 1). When we  
192 consider different life stages we can identify key features and considerations likely to  
193 be of importance to the welfare of the species. On our website, we provide a table  
194 highlighting examples of these features across a wide range of species. To manage a

195 species appropriately in captivity, it is important to find out about each of these key  
196 considerations and develop a management plan accordingly. This includes  
197 consideration of nutritional requirements such as adequate concentrations of protein  
198 for growth and development (NRC, 2003), attention to vitamin requirements such as  
199 vitamin D for bone growth and maintenance of mature bone tissue, and calcium for  
200 growth and during lactation (Hosey et al., 2009).

201 A defining characteristic of a species is their social structure. Ensuring animals are  
202 housed in appropriate social groups is therefore critical to welfare. Compatible  
203 conspecifics are known to buffer stress (e.g. Smith et al, 1998), and present  
204 opportunities for positive welfare-enhancing behaviours (such as grooming, play, and  
205 mating). Despite this, most enrichment literature focuses on physical rather than  
206 social environment (e.g. de Azevedo et al., 2007). One reason may be the potential  
207 harm from social enrichment, including problems with introducing individuals, and  
208 competition for dominance and associated risks of serious injury, together with  
209 concerns about disease transmission. Additionally, acquiring sufficient numbers of  
210 individuals to form natural groups, combined with lack of available space in captivity  
211 may prevent optimal social group composition and size. None-the-less keeping  
212 animals in appropriate social groupings, and with the required space and complexity  
213 to allow individuals to choose to spend time together or apart, is likely to be the most  
214 important welfare consideration.

215 Social considerations 24/7 across the lifespan may require social housing to vary,  
216 depending for example on reproductive stage, or mating season. Many of the  
217 subheadings in Table 1 indicate the range of social considerations at different life  
218 stages. For example, some species require seclusion from others for the birth

219 environment (e.g. snow leopard: O'Connor and Freeman, 1982). In other species, we  
220 know the importance of same age play mates for normal development (e.g. baboons:  
221 Cheney, 1978) or of gaining experience of rearing offspring to become a good parent  
222 (e.g. callitrichids: Buchanan-Smith, 2010b). Social considerations extend throughout  
223 the life including coping with illness and at the end of life with the death of a  
224 conspecific (e.g. chimpanzees: Anderson et al., 2010). As species do not live in  
225 isolation from each other in the wild, the formation of mixed-species groups that  
226 naturally associate may also improve welfare (e.g. Leonardi et al., 2010; Daoudi et al.,  
227 2017).

228 **Table 1** Examples of key features at different stages of an animal's life.

<b>Life stage</b>	<b>Examples key features/considerations in captivity</b>
Birth	Age of mother Mother and father experience Social group and infant experience (e.g. cooperative rearers; aunts) Nutritional requirements of mother Nutritional requirements of offspring Comfort (thermal and physical) Seclusion of physical birth environment (e.g. nesting materials) Human-animal interaction Infant mortality, including infanticide/cannibalism Imprinting
Baby	Mother's experience and dominance Number of other relatives/allies/foes Social group and members experience of infant care Age of weaning and mother's nutritional requirements until weaning
Juvenile	Juvenile mortality Availability of same age play mates Space and time to play Cognitive development opportunities Social learning
Adolescence	Mother's experience and dominance Friendships Social groupings (e.g. relatives/allies/foes)
Reproductive age	Social structure and possibilities to mate (e.g. social sexual suppression by dominants) Bachelor groups Inbreeding avoidance; protection of young (e.g. infanticide)
Senescence	Social structure and behaviour Physical decline (reduced mobility, pain) Behaviour and physical aspects Aging rates and nutrition Cognitive decline (memory etc.)
Death	Social aspects sickness and dying Euthanasia

229

230 *2.2 Individual differences*

231 We must accept that individuals, human and non-human, vary in their biological  
232 capacity for good welfare. There are genes that predispose animals to good or poor  
233 physical health (e.g. susceptibility to disease), and also those that predispose them to  
234 experience degrees of "happiness" or subjective wellbeing (SWB) (Weiss et al., 2002,  
235 2008). For example, negative welfare states (e.g. anxiety) are strongly associated with

236 the “Neuroticism” personality factor in humans (Costa and McCrae, 1980). Similarly,  
237 good subjective wellbeing in humans is predicted strongly by the personality  
238 dimension Extraversion (e.g. Costa and McCrae, 1980) and, less so to Agreeableness  
239 and Conscientiousness (e.g. DeNeve and Cooper, 1998; McCrae and Costa, 1991). A  
240 personality structure similar to humans has been found in chimpanzees and other  
241 primates (chimpanzee: King and Landau, 2003; capuchin: Morton et al., 2013). In  
242 chimpanzees, the “Dominance”, “Extraversion” and “Dependability” factors predict  
243 SWB (King and Landau, 2003). These traits are genetically inherited (chimpanzees:  
244 Weiss et al., 2002), and there is an association between happiness and longevity  
245 (orang-utans: Weiss et al., 2011).

246 Individual differences can also have an effect on social relationships and breeding  
247 success. Carlstead et al. (1999) did a cross-institutional analysis of environments and  
248 breeding success, in combination with behavioural profiling of black rhinoceros. They  
249 found that both individual temperament traits such as “dominant” and “fear”, and  
250 characteristics of the captive environments such as wall and enclosure size, have an  
251 impact on a pair’s breeding success. Personality has been shown to influence the  
252 quality of social relationships (e.g. capuchins; Morton et al., 2015) and breeding  
253 success (e.g. cheetahs: Wielebnowski, 1999; pandas; Martin et al, 2017). As such, it is  
254 likely that personality profiling will be used in the future, together with genetic  
255 considerations from studbook analyses to determine social compatibility in breeding  
256 programmes.

257 Understanding the development of individual animal personalities is still a new field,  
258 as is integrating gene and experiential factors including individuals' control over their  
259 own environment (Stamps and Groothuis, 2010). Our approach in 24/7 is to attempt to

260 provide animals with an environment that is designed on an understanding of  
261 individual differences. An environment that provides sufficient complexity, choice  
262 and control will allow animals to thrive within their own capacity, and to develop  
263 abilities to cope with the challenges they may face in a captive environment. Early life  
264 is a critical stage in this regard.

265 Early experiences affect the brain, given its plasticity when developing (Knudsen,  
266 2004). For example, there is considerable research using non-human primates and  
267 rodents as models that shows that early life stress (e.g. parental loss, neglect, or  
268 abuse) can enhance fear and anxiety. It can also lead to impaired cognition, loss of  
269 sensitivity to reward, abnormal brain neurochemistry and neurobiology, and alter  
270 hypothalamic-pituitary-adrenal (HPA) axis baseline activity, as well as reactivity  
271 (Pryce et al., 2002; reviewed in Parker and Maestriperi, 2011). Although there is  
272 ample evidence that severe early life stress can have deleterious consequences, there  
273 is also some empirical research that illustrates that exposure to some mild or moderate  
274 early life stress may provide resilience to subsequent stressors encountered in  
275 adulthood (reviewed in Parker and Maestriperi, 2011). It is a fine balance to provide  
276 the best early life care to enable the animal to cope as an adult in their future  
277 environment.

### 278 *2.3 The role of animal*

279 Animals do not choose the role they get assigned in a zoo, people do this for them.  
280 Some of the common roles animals are assigned to fulfil are: exhibit animal, petting  
281 zoo/touch pool animal, ambassador, interaction (e.g. photo opportunity) and show  
282 animal, research animal, breeder, and reintroduction candidate, but this list is by no  
283 means exhaustive. Roles may require animals to move between zoos regularly, as

284 they are important to the genetic diversity of the captive populations. Roles may  
285 require a predominately hands-off approach when animals are raised in environments  
286 that prepare them for successful release, such as the “mother condor puppet” feeding  
287 method for California condor chicks (Kasielke, 2007, p.151). Alternatively they may  
288 receive anti-predator training, as is used with the greater rhea, to improve introduction  
289 success (de Azevedo et al., 2012). Other roles take animals into human arms, when  
290 children and adults in petting zoos cradle rabbits, or dolphins are kissed in interactive  
291 programs. It is important to emphasize that animals can have multiple roles  
292 (simultaneously and/or consecutively), such as the bottlenose dolphin being part of a  
293 breeding program, a participant in research projects and an interaction/show animal.  
294 The impacts of cumulative stress on animals that are assigned multiple roles need to  
295 be considered.

296 To illustrate the impact of the role assigned, we shall use an example of domestic rats.  
297 Rats are often bred in zoos as food for other animals, and mostly housed in simple and  
298 small cages. The same rats can also be display animals in zoos however, housed in  
299 larger and complex exhibits with reversed light-cycle, showcasing the highly  
300 adaptable, curious, active and social nature of the animal. These same rats can  
301 become food for other animals in the zoo when they are old and not suitable to be on  
302 display anymore. The role the animal is assigned by humans will affect his/her quality  
303 of life, and we need a better understanding of what the implications of role(s) on  
304 animal welfare are and how it affects an animal 24/7 across the lifespan. Some well-  
305 known animal roles are briefly discussed with examples.

306 *2.3.1 The use of animals in education, interactive exhibits and shows*

307 The purpose for outreach and interactive programs through touch pools and other  
308 education programs with hands-on experiences may be laudable. It is important to  
309 educate children that, for example, snakes are not slimy, but should be admired and  
310 protected. There is also evidence that keeping animals in the classroom improves the  
311 children's learning outcomes, for example using more science facts and vocabulary in  
312 student writing (Trainin et al., 2005). It also positively affects the cognitive and/or  
313 emotional impact and welfare of humans participating in interactive programs and  
314 petting zoos (e.g. DebRoy and Roberts, 2006; Sahrman et al., 2016).

315 Staff are likely to select animals that tolerate being touched and handled, and can cope  
316 with the loud noises and sudden events. However, despite efforts to ensure proper  
317 handling, inexperienced children may scream, drop, scare, or hurt animals. Animals  
318 may be transported to schools, during which their welfare requires careful  
319 consideration, whilst others live semi-permanently in classrooms (e.g. Trainin et al.,  
320 2005). Many ambassador animals used in interactive programmes with humans may  
321 have compromised welfare. Such environments may limit their range of movements,  
322 provide them little choice and control, and force them to live in social groups that are  
323 not species-specific. Schools may have inadequate knowledge of how to best keep  
324 them, for example with regards to nutrition, or how to assess their welfare, especially  
325 of exotics (e.g. reptiles, invertebrates). On the other hand, the programs might provide  
326 opportunities for positive human-animal interactions and relationships, opportunities  
327 to gain access to desirable activities, such as foraging and interactions with  
328 environmental enrichment, and therefore have a positive effect on animal welfare  
329 (Miller et al., 2011).



330 Dogu et al. (2011) claim that “*Animals in touch exhibits are usually tough enough to*  
331 *be touched often without experiencing high levels of stress, however management at*  
332 *touch exhibits and safe touching practices are important to ensure the safety of the*  
333 *animals by guests*” (p. 4). Robust evidence to support the claim that the animals are  
334 not experiencing high stress is lacking. It is unfortunate that with the amount and  
335 variety of species of zoo animals being used in the many types of programs, such as  
336 touch pools, petting zoos, interactive and education programs, there are only a handful  
337 of peer-reviewed publications describing research on the impact on animal welfare.

338 Supporting a lack of negative effect, Baird et al. (2016) found no direct welfare  
339 issues, measured by behaviour and faecal glucocorticoid metabolites (FGM) in  
340 armadillos used as education animals. However, they found the overall amount of  
341 handling that an animal experienced (for education programs or for husbandry) had a  
342 positive correlation with FGM. These findings show that handling negatively impacts  
343 welfare, but was not related to maintaining the animals for educational purposes in  
344 this study.

345 Many zoos have exhibits, such as petting areas, where humans are allowed close  
346 proximity, and often, physical contact with the animals. These species are usually  
347 domesticated, or semi-domesticated and some zoos sanction feeding. Research into  
348 the welfare effects is inconsistent. Anderson et al. (2002, 2004) found that visitors  
349 negatively influenced the behaviour of goats and sheep in a petting zoo, specifically  
350 when no retreat area was available. In contrast, Farrand et al. (2014) found that the  
351 public did not affect the behaviour of goats and llamas. However, pigs showed  
352 decreased inactivity and social behaviour, both affiliative and aggressive. The  
353 presence of a retreat area, which the public cannot enter, gives the animals some

354 control over their interactions with visitors and may have ameliorated some negative  
355 effects. Majchrzak et al. (2015) found that performing rides did not increase cortisol  
356 levels in camels, claiming the rides were more akin to environmental enrichment.  
357 However no behavioural data were collected to help interpret the findings. It is widely  
358 accepted that the use of cortisol as a sole measure does not provide enough  
359 information to understand animal welfare and caution against using a one-method  
360 approach (e.g. Novak et al., 2013). There are many reasons that glucocorticoid  
361 measurements may increase including but not limited to seasonal variation in sex  
362 hormones, activity levels, and/or the stress response. A multi-method integrated  
363 approach is fundamental for a holistic understanding of animal welfare (Mason and  
364 Mendl, 1993).

365 Public presentations and shows are popular with the public and still commonplace.  
366 Whilst the chimpanzee tea party is an event of the past in modern zoos, displays with  
367 birds of prey, parrots and small mammals, as well as various marine mammal shows  
368 still take place. Although such displays can be educational, highlighting and showing  
369 skills and adaptations, they also raise specific welfare concerns (Brando, 2016b).  
370 Shows can often attract large and noisy crowds, and the method of showing animals  
371 has the potential for negative impact.

372 For example, with birds of prey, frequently used old-fashioned and classical falconry  
373 methods require that the diet is restricted to ensure the birds are hungry and “work”  
374 during the shows and return to the handler (Ford, 1992). Bird of prey training  
375 focusing on positive reinforcement is on the rise and weight management to the  
376 detriment of the bird is recommended against (IAATE, 2008). Birds of prey may be  
377 hooded (eyes covered to limit sensory input) to prevent them becoming distracted or

378 frightened (Ford, 1992), and parrots might be feather clipped to prevent them from  
379 flying away. Housing may be designed to make interactions easy and quick with high  
380 visitor visibility, and birds of prey are often tethered to perches limiting movement, or  
381 held in small crates and holding areas between presentations and shows. Whilst many  
382 birds appear to adapt as long periods of being stationary and without food intake may  
383 be part of their natural history, food restriction, tethering and hooding, may have  
384 negative welfare consequences. Scientific research on these topics is currently  
385 lacking. Their participation in shows may disrupt their desired activity patterns, but  
386 often provides the only opportunity for the animals to fly freely. Restricted housing  
387 for easy access and handling is not limited to birds of prey, but is also common in  
388 other species used in education programs, including small mammals such as rats and  
389 armadillos.

390 Marine mammal shows are popular and California sea lions are a frequently used  
391 show animal. Their participation in presentations is usually voluntary and rewarded  
392 with food. Indeed, there is evidence from a range of species that positive  
393 reinforcement training can be beneficial for animal welfare (e.g. Brando, 2010, 2012;  
394 Desportes et al., 2007; Kastelein and Wiepkema, 1988; Melfi, 2013). However, the  
395 use of sea lions in shows may lead to physical and social access being restricted at  
396 certain times (including night-time) to facilitate shows and their preparation. The  
397 effects of shows, interaction and “swim with” programs are still ill understood and  
398 different effects have been reported (e.g. positive effects: Miller et al., 2011; negative:  
399 Kyngdon et al., 2003). Allowing animals choice (i.e. independent of food reward) to  
400 not engage with shows, in petting zoos or other activities should be available.  
401 Animals who do not want to participate, for example, could go to a certain place in  
402 the exhibit, or request another enrichment activity by pressing a lever.

### 403 2.3.2 *The use of animals in research*

404 As well as education, one of the roles of zoos is to engage in research to further our  
405 scientific understanding of the animals themselves, and many animals are the subject  
406 of intensive research on behaviour, nutrition, reproduction and genetics. Most data  
407 are collected non-invasively through observations, analyses of studbooks, or  
408 biological samples are collected during veterinary interventions, so no additional  
409 handling or restraint is required. Indeed, many animals are trained to cooperate with  
410 research (e.g. hydro-dynamic trail following in seals: Dehnhardt et al., 2001;  
411 underwater visual acuity in manatees: Bauer et al., 2003; shape representation in a  
412 grey parrot: Pepperberg and Nakayama, 2016). Animals are increasingly being tested  
413 individually in purpose-built research centres within zoos (e.g. chimpanzees: Herrelko  
414 et al., 2012; capuchins: Morton et al., 2016). The animals volunteer to participate,  
415 which suggests it is enriching for them, and their social interactions and natural  
416 activity budgets on research participation days suggests their welfare is better than on  
417 non-research days (e.g. baboons: Fagot et al., 2014; chimpanzees: Yamanashi and  
418 Hayashi, 2011). However, we must continue to monitor their behaviour (and other  
419 parameters where possible) during research. Whilst some research is automated, much  
420 still requires interactions with humans and this has been shown to have a negative  
421 impact on welfare, increasing agonistic behaviour, and decreasing pro-social  
422 behaviours (chimpanzees: Chelluri et al., 2013). The authors emphasise the  
423 importance of understanding the influence of all forms of interactions, and to include  
424 positively intended interactions in animal welfare assessment. Research participation  
425 may also impact welfare negatively if it causes the animal frustration through  
426 unfairness of reward (e.g. Brosnan and de Waal, 2014), and if the task challenge is too  
427 difficult (Meehan and Mench, 2007). For example, Leavens et al. (2001) found that

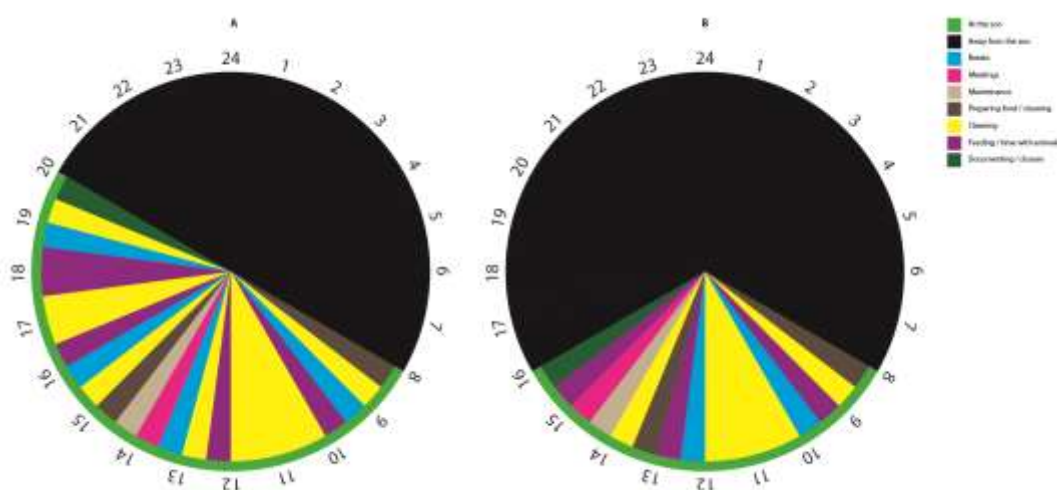
428 anxiety-related self-directed scratching increased with cognitive challenge in  
429 chimpanzees, and Wagner et al. (2016) found it increased when the response was  
430 incorrect in both gorillas and chimpanzees. The length of time away from the group is  
431 also critical, as it may affect normal conspecific social interactions, and return to the  
432 group after individual testing has been shown to increase both positive and negative  
433 interactions, which could be related to the food reward used and received during  
434 testing and shifting (capuchins: Ruby and Buchanan-Smith, 2015).

### 435 2.3.3 *The role of animals: Conclusion*

436 To conclude, the role an animal gets assigned needs to be decided as soon as possible  
437 in his/her life, to ensure they are best prepared. Ideally, the role should be one they  
438 enjoy and not just tolerate. Regular handling and feeding of animals, starting early in  
439 life promotes better human animal interactions (e.g. cattle: Jago et al. 1999; chickens:  
440 Jones, 1993; rats: Cloutier et al., 2012; rabbits: Podberscek et al., 1991; red-tailed  
441 hawks: Baird et al. 2016), and may make the animals more suitable as candidates for  
442 outreach or petting zoos. However, too much human contact, as is often the case  
443 during hand-rearing, can lead to imprinting on humans, inability to integrate  
444 successfully with conspecifics, development of stereotypies, and problems with  
445 successful reproduction (e.g. parrots: Schmid et al., 2006; gibbons: Pirovino et al.,  
446 2011). Some decisions on how to treat animals are not easy, as the animal's welfare  
447 may conflict with educational or entertainment goals, and a decision not to hand-rear  
448 (e.g. after a mother dies, or neglects the young) may lead to the animal dying. If we  
449 are to take animal welfare seriously, we should consider whether early interventions  
450 are required, and critically review the whole life experience from the 24/7 perspective  
451 of the animals.

## 452 2.4 Variations

453 As we have noted, the hours caregivers and veterinarians are at the zoo are limited to,  
 454 on average, approximately 8 hours a day, and predominately during daytime hours.  
 455 Additionally, the time at the zoo is divided over many tasks such as cleaning,  
 456 preparing food, maintenance, meetings, activities such as ‘zookeeper for a day’, as  
 457 well as coffee breaks and lunch. This leaves little time to observe, interact and  
 458 dynamically provide for animals and their environments. Daytime hours at the zoo  
 459 can also vary with regards to the seasons, as opening and closing times change with  
 460 daylight hours in some geographical areas (see Figures 2A and 2B which illustrate the  
 461 longer operating hours in summer compared to winter).



462

463 **Figure 2.** Example of an average (A) summer and (B) winter day considering  
 464 different activities and time with the animals (personal observations, Brando, based  
 465 on 25 years of practical experiences in zoos).

466 There are many variations to consider over a 24-hour period, over the week and  
 467 across the seasons, which are influenced by the geographical location and climate.

468 Animals can be categorised in relation to their activity patterns: diurnal, nocturnal,  
469 crepuscular (active at dawn and dusk), matutinal (dawn and morning), vespertine  
470 (dusk and night) and cathemeral (when activity is distributed roughly evenly  
471 throughout the 24-hour cycle). It is important to acknowledge differences within  
472 activity budgets, and these in turn can differ per individual. Disruption of natural  
473 circadian rhythms can create welfare issues, including increased susceptibility to  
474 disease (humans: review in Bechtold et al., 2010) and mood disorders. For example,  
475 rats exposed to constant light for 8 weeks, or constant darkness developed depression-  
476 and anxiety-like behaviour, characterised by anhedonia – the inability to feel pleasure  
477 in normally pleasurable activities (Tapia-Osorio et al., 2013). Abou-Ismaïl et al.  
478 (2008) found that rat welfare is better if husbandry routines are performed during the  
479 dark (active) rather than light (inactive) phase.

480 Nocturnal animals are usually kept on reverse light cycles under artificial light (i.e.  
481 dark during the day so visitors may see their active period), but it means they can  
482 rarely use outdoor enclosures which are in daylight and may overwhelm their  
483 sensitive visual systems (Erkert, 1989). The effect of artificial blue light may also  
484 have negative effects on the activity budgets, health and reproduction of nocturnal  
485 species (Fuller, 2014). In addition to visual adaptations, there are other biological  
486 adaptations to fit with their activity patterns. One example, is the afternoon gum-  
487 eating behaviour performed by saddle back and moustached tamarins, likely to be a  
488 strategy to prolong the time that the gum stays in the gut (i.e. overnight), so the  
489 tamarins benefit from microbial fermentation (Heymann and Smith, 1999). Such  
490 examples highlight the importance of the range of considerations required to optimise  
491 animal welfare in management practices.

492 *2.4.1 Variations in relation to husbandry routines*

493 Human induced variations, as well as variations in animal activity patterns means  
494 there are numerous husbandry aspects and management routines to consider in  
495 relation to animal welfare. Kawata (2008) emphasises the need to understand the  
496 feeding ecology of animals in the wild to promote their welfare in zoos. The way  
497 animals feed, what they feed on, under which conditions, frequencies and time spans,  
498 what the seasonal variations are, and other relevant information should be obtained  
499 and integrated into husbandry programmes.

500 We will illustrate this with an example of animal feeding repertoires. Many species  
501 housed in zoos would naturally be feeding, or engaging in their natural feeding  
502 repertoire, at times that zoo care professionals are not usually at work. In the wild,  
503 some animals start feeding very early, other species feed when the sun goes down or  
504 at night, while other species might forage throughout a 24-hour timeframe. The  
505 feeding repertoire may include many facets like feelings of hunger, anticipating food,  
506 gathering, manipulation, hiding and recovering food, to digestive behaviours and  
507 processes. Animals could be eating throughout the day and every day, or gorge feed  
508 with meals spread weeks apart, and this in turn can be seasonally dependent. Feeding  
509 can be a solitary or social event, and can have social functions to strengthen bonds or  
510 maintain hierarchies. These are only a few of the many considerations regarding an  
511 animal's feeding repertoire.

512 Due to caregiver routines and working hours, species-specific and appropriate feeding  
513 presentation might be different to what is preferred or necessary for the species in  
514 question. Unless provided for through the use of technology, such as timed feeders  
515 and foraging opportunity devices (e.g. Brando, 2009; Krebs and Watters, 2016),



516 animals might want to forage and eat but will not have access to food until the  
517 caregiver arrives. Non-technology solutions are also possible, such as providing food  
518 in ice blocks for the slow release of food after the keepers have left for the day. Not  
519 being able to forage and feed when the animal desires and/or food not being presented  
520 in species-appropriate manners can result in undesired behaviours such as stereotypies  
521 (e.g. okapi and giraffe, Bashaw et al., 2001).

522 Providing opportunities that prolong exploring and increase foraging time, processing  
523 and the consumption of food are some of the aims of food related environmental  
524 enrichment programs. Modifying the spatial or temporal distribution of food can  
525 increase the duration of feeding related behaviours in chimpanzees, bears and  
526 elephants (Morimura and Ueno, 1999). The provision of a species-specific foraging  
527 diet for rhinoceros can reduce obesity and avoid over supplementation of energy and  
528 minerals found in grain and pellets (Clauss and Hatt, 2006).

529 Unpredictability of feeding times due to changing caregiver routines can increase or  
530 induce stress-related behaviour (Waite and Buchanan-Smith, 2001). However, food  
531 delivered on a very predictable schedule can also result in undesired behaviours.

532 Bloomsmith and Lambeth (1995) studied the response of chimpanzees to predictable  
533 and unpredictable feeding schedules and found more abnormal behaviour and  
534 inactivity in the pre-feeding period in the predictable schedule due to anticipation.

535 Feeding enrichment designed to increase temporal variability of feeding times  
536 (change from feeding at set times), and to increase the number of feeding times/day is  
537 proposed by Swaisgood and Shepherdson (2005).

538 Altman et al. (2005) found that changing the feeding schedule of lions from daily  
539 feeding to a gorge and fast schedule was beneficial. The lions paced less on fasting

540 days, as compared to being fed everyday, and showed an overall increase in  
541 digestibility and an increase in appetitive active behaviours. Feeding routines can  
542 therefore have overall animal welfare benefits on non-feeding days.

543 Furthermore, staff shortages, extended maintenance of the enclosure, weather,  
544 presence of infants and visitor considerations all impact on whether animals are  
545 granted access to indoor and/or outdoor areas, and the effects on animal welfare vary.  
546 Locking or keeping animals inside can result in behaviours associated with negative  
547 welfare (e.g. gorillas, Hoff et al., 1994). Some animals are required to be ‘locked out’  
548 on exhibit during zoo opening hours to increase the chance that animals can be seen  
549 by visitors. Giving animals the choice to move between on- and off-exhibits is  
550 important. Giant pandas displayed fewer signs of behavioural agitation and lower  
551 urinary cortisol in a free choice condition between off- and on-exhibit enclosures,  
552 than when they were locked outside on exhibit (Owen et al., 2005). The use of  
553 preference and choice tests will aid our understanding of what animals want, and  
554 provide the necessary information for suitable conditions for indoor-outdoor  
555 environments, rather than blindly following traditions or species guidelines (i.e. input  
556 parameters described in guidelines have not all been empirically tested using animal-  
557 based parameters).

#### 558 *2.4.2 Variations between day and night*

559 Although the use of night cameras is increasing, it is remarkable how little practical  
560 and scientific knowledge is available of what animals do when animal care staff is not  
561 there. The majority of research on zoo animals has been conducted during daytime,  
562 therefore biasing the research evidence towards human working hours rather than  
563 following the animal’s life cycle and activity budget. When we are considering animal

564 welfare over the 24-hour period, the question arises, ‘what do animals do at night’? It  
565 is likely that most caretakers and curators do not know.

566 Sleep occurs in mammals, birds, and invertebrates (Vorster and Born, 2015). Many  
567 functions of sleep remain unclear but they are likely to relate to energy conservation  
568 and nervous system recuperation (Siegel, 2005). The quality and quantity of sleep an  
569 animal has can have physiological, behavioural and psychological consequences, and  
570 affects the vast majority of body functions, including immunity, hormonal regulation,  
571 metabolism, thermoregulation and pain thresholds. Sleep also supports consolidation  
572 of newly acquired information in memory (Diekelmann and Born, 2010). Sleep  
573 deprivation, or disturbance can affect attention in many animals (Kirszenblat and  
574 Swinderen, 2015), decrease cognitive performance (Alhola and Polo-Kantola, 2007),  
575 and increase sensitivity to pain (Karmann et al., 2014). Sleep and rest are therefore  
576 fundamental to good welfare and a lack of sleep, or repeated disturbances, can lead to  
577 bad welfare and impaired performance.

578 Provision of appropriate sleeping sites is critical. Features such as height,  
579 concealment, lack of disturbance, hygiene, and comfort, together with required  
580 nest/bedding materials, must be considered (e.g. Anderson, 1998, 2000; red-bellied  
581 tamarins, Caine et al. 1992). Sleeping site preferences may vary in relation to risk and  
582 season (e.g. gorillas, Lukas et al., 2003), and in relation to evening events held in  
583 zoos.

584 Understanding how social factors affect sleeping and sleeping site selection is also  
585 important to ensure that the captive environment has appropriate and sufficient resting  
586 and sleeping areas for different kin groups. Vessey (1973) observed sleeping clusters  
587 to consist mainly of kin in free-ranging macaques. Similarly, snub-nosed monkeys of

588 the same matriline slept in the branches of the same sleeping tree, and night-time  
589 grouping patterns were generally similar to those observed during daytime (Cui et al.,  
590 2006). Therefore, plenty of sleeping sites should be available to accommodate social  
591 sleeping behaviours.

592 Open access between indoor and outdoor areas can influence sleeping patterns. Drury  
593 and Buchanan-Smith (2008) found that captive giraffes showed a pattern for longer  
594 sleep in more frequent bouts, a more natural sleep architecture, when they had open  
595 access between the indoor and outdoor area. They recommend that giraffes are not  
596 confined indoors overnight, but are given the choice to access outdoor areas. Another  
597 aspect to consider is light. Fading artificial light in and out is beneficial, so diurnal  
598 primates are not plunged in and out of lightness and darkness in enclosures without  
599 natural light (Buchanan-Smith, 1997).

600 The examples above illustrate that sleep and rest have predominantly been studied in  
601 relation to behaviour, social aspects, and how environmental parameters such as the  
602 location of nest boxes, impact animal sleep. More research is needed to understand  
603 how animals spend their time at night, whether animals are hungry or overfeeding,  
604 and to evaluate the value and use of the provided environmental enrichment. We need  
605 a better understanding of whether the sleeping and resting places offered are adequate  
606 for good quality rest and sleep, social requirements and/or individual preferences, and  
607 how this relates to welfare.

#### 608 2.4.3 *Weekly variations*

609 Visitor numbers often change between weekdays and weekends, usually with more  
610 visitors on the weekend. Sometimes certain weekdays are busier than others when it

611 comes to school groups, educational programs, and animal presentations. Availability  
612 of care staff and veterinarians may also vary across the week. There are 102 days per  
613 year of ‘weekend days’, when time for optimal care might be significantly reduced.

614 Although fewer care staff at weekends may have negative consequences for welfare,  
615 it can also have the opposite effect, and record analyses is a fruitful database to  
616 analyse weekly variations. Lambeth et al. (1997) found laboratory-housed  
617 chimpanzee wounding was reduced on weekend days when human husbandry  
618 activities were lower. In zoo-housed chimpanzees, Wagner and Ross (2008) found  
619 parturitions were equally distributed across the week, indicating that there was no  
620 effect. These examples of record analysis illustrate the breadth and wealth of  
621 information contained within them and analyses can provide insights for practical  
622 applications.

#### 623 *2.4.4 Seasonal variations in relation to husbandry routines, visitors, geographical* 624 *location and weather*

625 Depending on geographical location, many seasonal variations exist, such as daylight  
626 hours and climatic variations, with the changing seasons also affecting enclosure  
627 quality, quantity and outdoor access. For example, in countries in northern Europe  
628 (e.g. Finland) days can be very long, even having 24-hour daylight in summer, while  
629 winter days are shortened to a few daylight hours. If zoos operate with the closed  
630 access policy (i.e. animals do not have free access between indoor and outdoor areas  
631 whenever they want to), the length of opening hours will have an effect on the  
632 animals opportunity to choose where they want to be. There is evidence that a  
633 combination of indoor and outdoor housing does improve welfare for a variety of  
634 primate species, and for some outdoor access is of particular importance (e.g.

635 common marmosets; Pines et al., 2007). Outdoor facilities should provide shelter,  
636 heating and protection to allow access in inclement weather. Particular care must be  
637 taken for smaller monkey species like the Callitrichidae, or carried infants,  
638 particularly those unable to return inside of their own volition when they get cold.

639 Geographical area and associated weather also influences the amount of time that  
640 animals can spend outdoors, and may impact on adaptations for seasonal breeding.  
641 Indoor illumination by artificial fluorescent lighting may be operated by automatic  
642 time switches that are adjusted seasonally to mimic the natural changes in day length  
643 in the species' habitat, and technology can be used to increase the options for control  
644 over environmental parameters (additional light and localised heat for common  
645 marmosets: Buchanan-Smith and Badihi, 2012). Animals are likely to spend less time  
646 in outdoor exhibits during heavy rains, snow, strong winds, hail, and very cold spells,  
647 or if temperatures rise and shade is unavailable. Provision of features like heat lamps,  
648 shade, vegetation, misting systems, different humidity zones, a fan, spray showers,  
649 and open access between indoor and outdoor areas allow animals to choose different  
650 thermal zones and to optimise enclosure use.

651 Variations across day and night, the week, year and seasons can be geographically  
652 dependent, and should be reviewed for each species on an individual facility basis.  
653 Tailored programs to suit an individual facility will assist in providing the most  
654 optimal environment to promote animal welfare.

### 655 *2.5 Zoo visitors*

656 Visitor numbers the type of audience, behaviour and noise levels varies across the  
657 seasons, with spring and autumn seeing more people at the weekends, while school

658 trips are mostly planned on weekdays. The summer season is often busier with  
659 activities such as photo opportunities and night-zoo events, and in winter visitor  
660 numbers decrease or are reduced to none if the zoo closes for the season, ceasing all  
661 public activities like sea lion or bird of prey shows.

662 Visitor effects have predominantly been studied in primates, with effects ranging  
663 from negative and neutral to positive (Davey, 2006; Fernandez et al., 2009; Hosey,  
664 2000). There are species and individual differences in response to visitors, with life  
665 experience influencing how animals respond. Enclosure design, and allowing animals  
666 to choose not to be on view to visitors (or using camouflaged nets to conceal and  
667 quieten visitors) can be effective at reducing negative behavioural consequences  
668 (Blaney and Wells, 2004; Davey, 2007).

669 However, there is sometimes a conflict, with management worried about animal  
670 visibility when animals choose to spend time out of view, or sleep hidden in their  
671 favourite spot in the back of the enclosure. Sometimes the use of a sprinkler system or  
672 other deterrent is used to reduce the time animals spend in areas where they are not  
673 visible for the public. Although this might achieve the goal of increasing visibility, we  
674 encourage methods that positively achieve goals for both animals and people, with  
675 animal welfare at the heart of considerations and solutions. When animals spend time  
676 in places that are off-limit to the public or in harder to observe areas technology, such  
677 as live-streaming cameras and plasma screens, can be used to make the animals  
678 visible for the interested public (as used in the giant panda enclosure at Ocean Park in  
679 Hong Kong). Enclosure design offering a variety of concealment options like  
680 vegetation, open dens, and providing shaded elevated platforms while maintaining the  
681 animals in view can be designed to meet both animal and visitor needs.

### 682 **3. Animal welfare assessments: A practical evaluative framework**

683 Within the constraints of attempting to take the animal's perspective (but supporting  
684 critical anthropomorphism, Burghardt, 1985), understanding individual differences  
685 and seasonal changes, we developed an assessment criteria framework as a tool to  
686 assist care staff consider the experiences of animals, through a thorough  
687 understanding of natural history and biological adaptations. In this section we  
688 compare our framework with others available, and introduce a practical online tool.

#### 689 *3.1 Animal Welfare Frameworks*

690 The first welfare framework was developed for farm animals (Brambell, 1965). Farm  
691 animals make up the majority of kept animals (e.g. Fraser and MacRae, 2011) and the  
692 early attempt to promote welfare was encapsulated in the Five Freedoms (Brambell,  
693 1965). More recently these have been extended to a Five Domains model (Mellor,  
694 2016) and a 12 welfare criteria (Welfare Quality, 2009). We have combined these two  
695 approaches, and adapted and extended the 12 welfare criteria to assess any captive  
696 animal in our 24/7 approach (see below). We focus here on zoo-housed animals, but  
697 the approach is applicable to any captive animal.

698 Other zoo welfare frameworks have also been developed recently. We recognise that  
699 efforts to promote optimal welfare in zoos must be comprehensive, coordinated and  
700 there must be commitment at all levels for it to be successful at institution level.

701 Kagan et al. (2015, p. S2) provide an excellent high-level framework, with “four  
702 major components: institutional philosophy and policy, reflecting values commitment  
703 and capacity building; pragmatic structure and resources; execution and evaluation”.

704 Capacity building, staff training, leadership and communication feature as key



705 concepts, and we fully recognise and support this in our 24/7 approach. Kagan et al.  
706 (2015) also provide the Detroit Zoological Society assessment checklist for both the  
707 Institutional Policies and Programmatic Structure. If completed, this should provide  
708 the basis for the development of a clear action plan if deficiencies are identified.

709 Justice et al. (2017) have adapted the Animal Welfare Assessment Grid (AWAG),  
710 originally developed for animals in research programmes (Honest and Wolfensohn,  
711 2010), for use in zoos. The AWAG takes four components into account: Physical  
712 parameters (e.g. general condition, clinical assessment); Psychological parameters  
713 (e.g. positive and negative behaviours in a range of contexts); Environmental  
714 parameters (e.g. enclosure design, group size); and Procedural parameters (e.g.  
715 restraint, sedation). This type of approach has been validated with laboratory-housed  
716 macaques used in research (Wolfensohn et al. 2015). The welfare assessment grid has  
717 a distinct advantage of providing a visual representation of an animal's welfare, and  
718 provides a temporal component to allow changes to be tracked over time (Honest and  
719 Wolfensohn, 2010). A specific scoring system has also been developed to evaluate  
720 quality of life in geriatric zoo-housed mammals to support decision-making for  
721 euthanasia (Föllmi et al., 2007).

722 Our 24/7 approach has several features in common with those of Kagan et al. (2015)  
723 and Justice et al. (2017). They all feature a wide range of considerations (including  
724 social, physical and husbandry considerations, human-animal interactions) and with  
725 an important focus on individual animal agency. Their checklists can be applied to  
726 any animal, and their use will be helpful in the development of an action plan for  
727 improvement, and to set priorities. We fully support both of their evidence-based  
728 approaches. What the 24/7 approach adds is the need to fully research the natural

729 history and adaptations as a starting point prior to any assessment, and to consider  
730 welfare across the life-course and the impact of variations described in this paper.

731 For 24/7, we propose that welfare assessments should be planned at specific times, at  
732 important changes and/or transitions (e.g. particular requirements such as shelter,  
733 heating or cooling might be necessary with a change of season). A change in the care  
734 staff is another example. When someone who has cared for certain individuals for  
735 many years is retiring, early planning and continued animal welfare assessment can  
736 help identify, prevent and address possible negative impacts. Assessment is also  
737 needed when an animal is moved in or out of the group (through death or transfer).  
738 Revisiting the workshop questions at pre-determined times would increase the  
739 likelihood that an animal's needs and preferences are attended to as much as  
740 possible.

### 741 *3.2 The 24/7 across the lifespan approach*

742 Understanding how to assess and promote captive wild animal welfare from a 24/7  
743 approach is one of major challenges and responsibilities of modern zoos and  
744 sanctuaries today. Preferably, animal welfare assessment decisions and their  
745 implementation is informed and based on science, considering both resource (input)  
746 and animal-based (outcome) parameters. Gaps in knowledge, as well as concerns and  
747 conflicts need to be identified to produce an Institutional philosophy and policy (e.g.  
748 see Kagan et al., 2015) that can be consistently applied through a culture of care.

749 To develop these high standards and professional animal care programs, it is critical  
750 to understand an animal's ecology, behaviour, biology, sensory systems, social life,  
751 and nutritional needs. We base our approach on the 12-point welfare assessment

752 criteria framework. In 2004, a large multi-country and multi-institution project in  
753 Europe was initiated, named Welfare Quality®, science and society improving animal  
754 welfare in the food quality chain (Welfare Quality, 2009). The goal of the project was  
755 to develop European standards for on-farm welfare assessment, product information  
756 systems that create transparency about the welfare of farm animals during production,  
757 as well as practical strategies for improving animal welfare. The project took five  
758 years to complete and identified four key principles: good feeding, good housing,  
759 good health and appropriate behaviour. The principles incorporate, expand and update  
760 the Five Freedoms. Within these 4 key principles, 12 animal welfare assessment  
761 criteria were defined.

762 We have adapted these 12 welfare assessment criteria to be more relevant to zoo  
763 animal welfare. We propose two additional criteria (Table 2: criteria no. 2 on feeding  
764 and no. 7 on perceived control) to determine whether welfare needs are met.

765 The orange-winged Amazon parrot was chosen as an example species, to illustrate the  
766 adapted animal welfare assessment criteria (Table 2). The reason for choosing this  
767 species is that there has been a considerable amount of research done on different  
768 aspects of the behaviour, biology and care in captivity, such as environmental  
769 enrichment, feeding, and health, which makes completing the criteria easier and  
770 decisions for care evidence-based (Melfi, 2009). This parrot species is a resident  
771 breeding bird in South America, Tobago and Trinidad, reaching up to sixty years of  
772 age. In the wild, the diet consists primarily of all types of fruits, nuts, seeds, blossoms,  
773 leaf buds and berries, feeding solely during the day, early in the morning or late in the  
774 afternoon (Pet information Animal World, 2016). They travel in social groups and  
775 live in large communities, in semi-open country and forests (Austin, 2014). They are

776 a popular species in zoos and as companion animals. However, a species dedicated  
777 husbandry manual for the orange-winged Amazon parrot could not be located at the  
778 time of writing and should be professionally developed to ensure a standardized  
779 approach to promoting good welfare for orange-winged Amazon parrots (or any other  
780 animal species kept in captivity for that matter).

781 **Table 2**

782 Illustrated example of the 14 welfare criteria with the orange-winged Amazon parrot  
783 (adapted from Welfare Quality ®).

Orange-winged Amazon parrot ( <i>Amazona amazonica</i> ) (unless otherwise stated).		
Welfare Principles	Welfare Criteria	Example evidence reference
Good feeding: Are the animals properly fed and supplied with water?	<p>1. Absence of prolonged hunger (i.e. mimic natural feeding intervals). Other end of the spectrum should also be considered, i.e. prevention of obesity.</p> <p>2. Access to appropriate food and species-typical foraging opportunities (i.e. they should have a nutritionally suitable and appropriate diet &amp; delivery).</p> <p>3. Absence of prolonged thirst (i.e. they should have a sufficient and accessible water supply).</p>	<p>Over-sized pellets provide foraging-like opportunities reducing inactivity and encourages a more naturalistic activity budget (Rozek et al., 2010). These parrots usually feed early morning (30 minutes after sunrise when leave roost) and late afternoon so attempts should be made to mimic these intervals in captivity.</p> <p>Information on breadth of diet and utilisation of palms for fruit foraging (Bonadie and Bacon, 2000). Captive parrot nutrition: Interactions between anatomy, physiology, and behaviour (Matson and Koutsos, 2008). Over-sized pellets elicit comparable podomandibulation (handling with beak and foot) behaviour (Rozek and Millam, 2011). Clean drinking water must be available at all times and refreshed at least daily (Kalmar et al., 2010).</p>
Good housing: Are the animals properly housed?	<p>4. Animals should have comfort when they are resting and sleeping (i.e. physically comfortable and relaxed, not always vigilant).</p> <p>5. Animals should have thermal comfort (i.e. they should neither be too hot nor too cold, and have thermal zones to choose from).</p> <p>6. Animals should have enough space to be able to move around freely in relation to natural locomotion (e.g. leap distance, orientation of substrates etc.), and in context of indoor-outdoor space restrictions.</p> <p>7. Animals should have perceived control (i.e. complex enclosure giving them choice over what and when they do things).</p>	<p>On Trinidad palms function as roosting and nesting sites (Bonadie and Bacon, 2000).</p> <p>Temperature, humidity, and environmental housing parameters (Kalmar et al., 2010).</p> <p>Habitat use in and around two lowland Atlantic forest reserves in Brazil (Marsden et al., 2000).</p> <p>Preferences for cage enrichment devices (Kim et al., 2009).</p>

Good health: Are the animals healthy?	<p>8. Animals should be free of major injuries (e.g. skin damage and locomotory disorders).</p> <p>9. Animals should be free from disease (i.e. appropriate standards of hygiene and care).</p> <p>10. Animals should not suffer pain induced by inappropriate management, handling, catching, or transport.</p> <p>11. Animals should be treated well in all situations (i.e. care staff should promote good human-animal relationships, with the animal's perspective as the focus).</p>	<p>Development of a reference for xeroradiographic and conventional radio-graphic anatomy and its importance to clinical evaluation (Smith et al., 1990).</p> <p>The basic cage care includes daily cleaning of the water and food dishes. Weekly wash of all the perches and dirty toys, and the floor should be washed about every other week. A total hosing down and disinfecting of an aviary should be done yearly, replacing anything that needs to be freshened, such as old dishes, toys and perches.</p> <p>Normal haematological parameters (Tell et al., 1997).</p> <p>Capture, restraint, sample collection, high-quality nutrition, and intellectual stimulation: An overview of avian care and husbandry (Schulte and Rupley, 2004).</p> <p>Short neonatal handling of parent-reared birds increases tameness and improves adaptation to life in captivity (Aengus and Millam, 1999).</p>
Appropriate behaviour: Does the behaviour of the animals reflect optimized emotional states?	<p>12. Animals should be able to express normal, non-harmful, social behaviours (e.g. preening, breeding).</p> <p>13. Animals should be able to express other normal behaviours (i.e. it should be possible to express species-specific natural behaviours such as exploring, problem solving).</p> <p>14. Negative emotions such as fear, distress, frustration or boredom/apathy should be avoided whereas positive emotions such as security or contentment should be promoted.</p>	<p>Pair housing significantly improves environmental quality and positively affects animal welfare (Meehan et al., 2003).</p> <p>Captive animals show a preference for morning bathing compared to other times of the day (Murphy et al., 2011).</p> <p>Environmental enrichment and social manipulations (including misting, fruit supplementation, nest hole restriction, enlarged nest boxes, and pair separation/reunification) increases reproductive performances (Millam et al., 1995).</p> <p>Social play behaviour of two juvenile white-fronted Amazon Parrots (<i>Amazona albifrons</i>) includes bill-nibbling, pseudo-copulation, play-solicitation, play-biting and fighting and foot-clawing, possibly to increase social ties between birds and develop adult behaviours used in epigamic and agonistic contexts (Skeate, 1985).</p> <p>Cognitive flexibility, memory, lateralization and individual differences (Cussen and Mench, 2014).</p> <p>Colour, hardness, size and material all influence environmental device use (Kim et al., 2009).</p> <p>Level of novelty experienced during early life affects neophobia development (Fox and Millam, 2004).</p> <p>Social play analysis in different species of parrots, e.g. play chases, play fighting, wild careering flights, physical interactions (rolling on the back and jumping on the belly) (Diamond and Bond, 2003).</p> <p>Novelty and individual differences influence neophobia (Fox and Millam, 2007).</p> <p>Genetics, environmental aspects, and neighbours affect the severity of stereotypies and feather picking (Garner et al., 2006).</p>

787 As previously noted, we have a dedicated website for the 24/7 welfare across lifespan  
788 approach: [www.247animalwelfare.eu](http://www.247animalwelfare.eu). Amongst other materials, this website provides  
789 a link to an interactive and evaluative workshop using common marmosets as an  
790 example. The “Wild *versus* Captive” workshop provides an evidence base to highlight  
791 where there may be a mismatch between the wild and captivity, and so potentially  
792 highlight a welfare problem.

#### 793 **4. Conclusion and future directions**

794 The essence of care for any animal is habitat management (Ahlering and Faaborg,  
795 2006). The concept of habitat management is well known in species conservation,  
796 although this term can have different interpretations. What is of interest to zoo  
797 professionals is the approach used in planning and designing environments, including  
798 microhabitats that incorporate the needs of a particular animal. Habitat management,  
799 such as features used by adult animals during nesting, requires an understanding that  
800 animals have specific habitat requirements at different life stages (Berkeley et al.,  
801 2007). Habitat management in zoos provides for species-specific needs and should be  
802 modified to reflect and respond to individual needs and preferences over time.

803 Rather than caregivers providing the bulk of the care, the environment can be  
804 designed to provide for activities and opportunities to the animals to choose. The shift  
805 to habitat management should be further developed in zoos, reflecting a 24/7 across  
806 lifespan approach. Coe (1989, 1996, 2003, 2011), an experienced landscape and zoo  
807 architect, has long designed and written about the importance of environments that  
808 strongly contribute to the mental and physical wellbeing of animals, including urban  
809 wildlife in zoos. Coe (2009) describes the design of environments that specifically  
810 suit particular life stages, such as an exhibit for bachelor groups of gorillas. Coe

811 (2006) proposes naturalistic and functional enrichment through built in features that  
812 elicit enduring interest for animals, reflecting biological relevance, such as a basking  
813 rock, shade and cooler places, artificial mound feeders, swaying branches, and  
814 (infrared) motion detector or lever activating water jets as provided for otters,  
815 penguins, chimpanzees and elephants. Coe recently designed the trail systems at the  
816 Philadelphia Zoo, when he wondered, “Why stop with rotating exhibits? Why not just  
817 connect everything in the zoo to everything else and let the animals have the run of  
818 the place?” (Philly.com, 2015). Although final control obviously is in the hands of  
819 professional zoo staff, ensuring practical aspects such as the health and safety of  
820 animals, staff and visitors, these trails provide additional complexity, choice and  
821 control to animals as they have more habitat options available, views and inter-species  
822 interactions.

823 Habitat management will also be more optimal with the use of integrated  
824 technologies. Partly self-sustaining environments that function in a semi-autonomous  
825 manner provide a wide variety of opportunities, choice and control for animals over  
826 24 hours (Brando, 2009; Krebs and Watters, 2016). The implementation of different  
827 types of technologies, such as: timers (lemurs: Sommerfeld et al., 2005); infra-red  
828 motion sensor beams (otters and other aquatic species: Coe, 2006); touch sensors  
829 (marmosets: Buchanan-Smith and Badihi, 2012); lever pulling (elephants: Markowitz  
830 reviewed in Maple, 2007); automated feeding stations with individual transponder  
831 chip (common brushtail possum: Isaac et al., 2004); automated showers (cows:  
832 Legrand et al., 2011); echolocation activated devices to activate a water jet stream  
833 (dolphin: Amundin et al., 2008); and computer screens to play games or request fish  
834 or toys (primates: Fagot and Bonté, 2010; dolphin: Starkhammar et al., 2007) are



835 some of the available options. Such technologies give animals control over their  
836 environments, and direct reliance on humans is reduced.

837 Decision-making with regard to animal welfare should preferably be done from an  
838 evidence-based approach (Melfi, 2009), even if many practical, although not officially  
839 researched and tested handling and care strategies are already being successfully used  
840 with a variety of species. We believe it is important to verify these long-standing  
841 practices through systematic research, and analyses of long-term and cross-  
842 institutional records. Data should be collected for all species, including at night using  
843 24-hour observations, and across the weeks and seasons.

844 Decisions about animal care should also be revisited in the light of ethics to ensure  
845 appropriate treatment when caring for and interacting with animals, and used to  
846 defend high quality of care being provided. For example, decisions to cease keeping  
847 certain species could flow from ethical considerations with regards to providing, or  
848 failing to provide, an environment that allows for good animal welfare. A decision not  
849 to keep a certain species often originates from restrictions and limitations, as in the  
850 case of being a smaller city zoo, or a zoo without the necessary expertise, or due to  
851 geographical location, and not because the species is unlikely to thrive even in the  
852 best captive conditions. This philosophy reflects the commitment to high animal  
853 welfare standards above the need to house species because the public wants to see  
854 them.

855 In conclusion, caring for zoo animals involves considering the cradle to grave  
856 experience of individual animals. It is a dynamic process requiring changes to  
857 accommodate individual needs and preferences, which may change over time, as well  
858 as constant updating as more evidence becomes available. Those caring for zoo

859 animals should therefore aspire to promote predominantly good animal welfare, 24/7  
860 across their entire lifespan using the criteria proposed.

## 861 **Acknowledgments**

862 We thank Dr. Lou Tasker for her enthusiasm, critical insights into the concept, and  
863 constructive editing of a draft of the paper. Dr. Hayley Ash, Mark Kingston Jones,  
864 Martina Schiestl and Chris Lucas also provided valuable feedback on earlier versions  
865 of this concept and manuscript. We thank Remco van Asch for designing the artwork  
866 and figures. This research did not receive any specific grant from funding agencies in  
867 the public, commercial, or not-for-profit sectors.

## 868 **References**

- 869 Abou-Ismaïl, U.A., Burman, O.H., Nicol, C.J., & Mendl, M., 2008. Let sleeping rats  
870 lie: does the timing of husbandry procedures affect laboratory rat behaviour,  
871 physiology and welfare? *Applied Animal Behaviour Science*, 111, 329-341.
- 872 Aengus, W.L. and Millam, J.R., 1999. Taming parent-reared orange-winged  
873 Amazon parrots by neonatal handling. *Zoo Biology*, 18, 177-187.
- 874 Ahlering, M.A., Faaborg, J., 2006. Avian habitat management meets conspecific  
875 attraction: If you build it, will they come? *The Auk* 123, 301-312.
- 876 Alhola, P., Polo-Kantola, P., 2007. Sleep deprivation: Impact on cognitive  
877 performance. *Neuropsychiatric Disease and Treatment* 3, 553-567.

- 878 Altman, J.D., Gross, K.L. and Lowry, S.R., 2005. Nutritional and behavioral effects  
879 of gorge and fast feeding in captive lions. *Journal of Applied Animal Welfare*  
880 *Science*, 8, 47-57.
- 881 Amundin, A., Starkhammar, J., Evander, M., Almqvist, M., Lindström, K., Persson,  
882 H.W., 2008. An echolocation visualization and interface system for dolphin  
883 research. *The Journal of the Acoustical Society of America* 123, 1188-1194.
- 884 Anderson, J.R., 1998. Sleep, sleeping sites, and sleep- related activities: awakening to  
885 their significance. *American Journal of Primatology*, 46, 63-75.
- 886 Anderson, J.R., 2000. Sleep-related behavioural adaptations in free-ranging  
887 anthropoid primates. *Sleep Medicine Reviews*, 4, 355-373.
- 888 Anderson, J.R., Gillies, A., Lock, L.C., 2010. *Pan* thanatology. *Current Biology* 20,  
889 R349-R351.
- 890 Anderson, U.S., Benne, M., Bloomsmith, M.A., Maple, T.L., 2002. Retreat space and  
891 human visitor density moderate undesirable behavior in petting zoo animals.  
892 *Journal of Applied Animal Welfare Science* 5, 125-137.
- 893 Anderson, U.S., Maple, T.L., Bloomsmith, M.A., 2004. A close caregiver nonhuman  
894 animal distance does not reduce undesirable behavior in contact yards goats  
895 and sheep. *Journal of Applied Animal Welfare Science* 7, 59-69.
- 896 Austin, R., 2014. *Amazona amazonica*  
897 [https://sta.uwi.edu/fst/lifesciences/documents/Amazona\\_amazonica.pdf](https://sta.uwi.edu/fst/lifesciences/documents/Amazona_amazonica.pdf)  
898 (accessed 15.07.2016).

- 899 Baird, B.B., Kuhar, C.W., Lukas, K.E., Amendolagine, L.A., Fuller, G.A., Nemet, J.,  
900 Willies, M.A., Schook, M.W., 2016. Program animal welfare: Using  
901 behavioral and physiological measures to assess the well-being of animals  
902 used for education programs in zoos. *Applied Animal Behaviour Science* 17,  
903 150–162.
- 904 Bashaw, M.J., Tarou, L.R., Maki, T.S., Maple, T.L., 2001. A survey assessment of  
905 variables related to stereotypy in captive giraffe and okapi. *Applied Animal*  
906 *Behaviour Science* 73, 235-247.
- 907 Bauer, G.B., Colbert, D.E., Gaspard III, J.C., Littlefield, B., Fellner, W., 2003.  
908 Underwater Visual Acuity of Florida Manatees (*Trichechus manatus*  
909 *latirostris*). *International Journal of Comparative Psychology* 16, 130-142.
- 910 Bechtold, D.A., Gibbs, J.E., Loudon, A.S., 2010. Circadian dysfunction in disease.  
911 *Trends in Pharmacological Sciences* 31, 191-198.
- 912 Berkeley, L.I., McCarty, J.P., LaReesa Wolfenberger, L., 2007. Postfledging survival  
913 and movement in dickcissels (*Spiza americana*): Implications for habitat  
914 management and conservation. *The Auk* 2, 396-409.
- 915 Blaney, E.C., Wells, D.L., 2004. The influence of a camouflage net barrier on the  
916 behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal*  
917 *Welfare* 13, 111-118.
- 918 Bloomsmith, M.A., Lambeth, S.P., 1995. Effects of predictable versus unpredictable  
919 feeding schedules on chimpanzee behaviour. *Applied Animal Behaviour*  
920 *Science* 44, 65-74.

- 921 Bonadie, W.A., Bacon, P.R., 2000. Year-round utilisation of fragmented palm swamp  
922 forest by Red-bellied macaws (*Ara manilata*) and orange-winged parrots  
923 (*Amazona amazonica*) in the Nariva Swamp (Trinidad). *Biological*  
924 *Conservation* 95, 1-5.
- 925 Brambell, F.W.R., 1965. Report of the technical committee to enquire into the welfare  
926 of animals kept under intensive livestock husbandry systems. London, UK;  
927 Her Majesty's Stationary Office.
- 928 Brando, S.I.C.A., 2009. Exploring choice and control opportunities applied in  
929 enrichment and training. Paper presented at International Conference on  
930 Environmental Enrichment, Paignton, UK.
- 931 Brando, S.I.C.A., 2010. Advances in husbandry training in marine mammal care  
932 programs. *International Journal of Comparative Psychology* 23, 777-791.
- 933 Brando, S.I.C.A., 2012. Animal learning and training: Implications for animal  
934 welfare. *Veterinary Clinics of North America: Exotic Animal Practice* 15,  
935 387-98.
- 936 Brando, S.I.C.A. 2016a. An evaluation of zoo animal welfare assessment from  
937 inspection to daily practices with recommendations for a holistic approach.  
938 MSc. Thesis Animal Studies. Retrieved from  
939 <http://animalconcepts.eu/MScThesisBrando2016/>
- 940 Brando, S.I.C.A. 2016b. Wild Animals in Entertainment, in: Bovenkerk, B., Keulartz,  
941 J. (Eds.), *Animal Ethics in the Age of Humans. Blurring boundaries in human-*  
942 *animal relationships*. Springer, Dordrecht, pp. 295-318.

- 943 Brosnan S.F., de Waal F.B., 2014. Evolution of responses to (un) fairness. *Science*  
944 346, 1251776.
- 945 Broom, D.M., 1986. Indicators of poor welfare. *British Veterinary Journal* 142, 524-  
946 526.
- 947 Broom, D.M., 1999. Animal welfare: the concept of the issues, in: Dolins, F.L. (Ed.),  
948 *Attitudes to Animals: Views in Animal Welfare*. Cambridge University Press,  
949 Cambridge, pp. 129-143.
- 950 Broom, D.M., 2007. Quality of life means welfare: how is it related to other concepts  
951 and assessed? *Animal Welfare* 16s, 45-53.
- 952 Buchanan-Smith, H.M., 1997. Considerations for the housing and handling of New  
953 World primates in the laboratory, in: Reinhardt, V. (Ed.), *Comfortable*  
954 *quarters for laboratory animals*. Washington, DC, pp. 75–84.
- 955 Buchanan-Smith, H.M., Stronge, J., Challis, M., 2001. The roles of zoos: examples  
956 from Belfast Zoological Gardens, in: Rushton, B.S., Hackney, P., Tyrie, C.R.  
957 (Eds.), *Biological Collections and Biodiversity*. Westbury Academic and  
958 Scientific Publishing, Otley, West Yorkshire, pp. 163-170.
- 959 Buchanan-Smith, H.M., 2010a. Environmental Enrichment for Primates in  
960 Laboratories. *Advances in Science and Research* 5, 41-56.
- 961 Buchanan-Smith, H.M., 2010b. Marmosets and tamarins, in: Hubrecht, R.C.,  
962 Kirkwood, J. (Eds.), *The UFAW Handbook on the Care and Management of*  
963 *Laboratory and Other Research Animals*. Wiley-Blackwell, pp. 543-563.

- 964 Buchanan-Smith, H.M., Badihi, I., 2012. The psychology of control: Effects of  
965 control over supplementary light on welfare of marmosets. *Applied Animal*  
966 *Behaviour Science* 137, 166-174.
- 967 Burghardt, G.M., 1985. Animal awareness: Current perceptions and historical  
968 perspective. *American Psychologist* 40, 905-919.
- 969 Caine, N.G., Potter, M.P., Mayer, E., 1992. Sleeping site selection by captive  
970 tamarins (*Saguinus labiatus*). *Ethology* 90, 63-71.
- 971 Carlstead, K., Fraser, J., Bennett, C., Kleiman, D.G., 1999. Black rhinoceros (*Diceros*  
972 *bicornis*) in U.S. zoos: II. Behavior, breeding success, and mortality in relation  
973 to housing facilities. *Zoo Biology* 18, 35-52.
- 974 Chelluri, G.I., Ross, S.R., Wagner, K.E., 2013. Behavioural correlates and welfare  
975 implications of informal interactions between caretakers and zoo-housed  
976 chimpanzees and gorillas. *Applied Animal Behaviour Science* 147, 306-315.
- 977 Cheney, D.L., 1978. The play partners of immature baboons. *Animal Behaviour* 26,  
978 1038-1050.
- 979 Clauss, M., Hatt, J.M., 2006. The feeding of rhinoceros in captivity. *International Zoo*  
980 *Yearbook* 40, 197-209.
- 981 Cloutier, S., Panksepp, J., Newberry, R.C., 2012. Playful handling by caretakers  
982 reduces fear of humans in the laboratory rat. *Applied Animal Behaviour*  
983 *Science* 140, 161-171.
- 984 Coe, J.C., 1989. Naturalizing habitats for captive primates. *Zoo Biology* 8, 117-125.

- 985 Coe, J.C., 1996. One hundred years of evolution in great ape facilities in American  
986 zoos. Proceedings of the AZA 1995 Western Regional Conference, Denver,  
987 Colorado. <http://www.joncoedesign.com/pub/technical.htm> (accessed  
988 03.08.2016).
- 989 Coe, J.C., 2003. Steering the ark toward Eden: design for animal well-being. Journal  
990 of the American Veterinary Medical Association 223, 977-980.
- 991 Coe, J.C., 2006. Naturalistic Enrichment. Presented at Australasian Regional  
992 Association of Zoological Parks and Aquaria Conference, Perth.  
993 <http://www.joncoedesign.com/pub/technical.htm> (accessed 03.08.2016).
- 994 Coe, J.C., 2009. Third generation conservation: Accommodating wildlife in our daily  
995 lives. Presented at Australasian Regional Association of Zoological Parks and  
996 Aquaria Conference, Gold Coast, Australia.
- 997 Coe, J.C., 2011. Architects and Enrichment. Presented at the 10th International  
998 Conference on Environmental Enrichment, Portland, Oregon.
- 999 Costa Jr., P.T., McCrae, R.R., 1980. Influence of extraversion and neuroticism on  
1000 subjective wellbeing: Happy and unhappy people. Journal of Personality and  
1001 Social Psychology 38, 668-678.
- 1002 Cui, L.W., Quan, R.C., Xiao, W., 2006. Sleeping sites of black and white snub nosed  
1003 monkeys (*Rhinopithecus bieti*) at Baimi Snow Mountain, China. Journal of  
1004 Zoology 270, 192-198.



- 1005 Cussen, V.A., Mench, J.A., 2014. Performance on the Hamilton search task, and the  
1006 influence of lateralization, in captive orange-winged Amazon parrots  
1007 (*Amazona amazonica*). *Animal Cognition* 17, 901-909.
- 1008 Daoudi, S., Badihi, G., & Buchanan-Smith, H. M. (2017). Is mixed-species living  
1009 cognitively enriching? Enclosure use and welfare in two captive groups of  
1010 tufted capuchins (*Sapajus apella*) and squirrel monkeys (*Saimiri*  
1011 *sciureus*). *Animal Behavior and Cognition*, 4, 51-69.
- 1012 Darwin, C., 1872/1965. *The expression of the emotions in man and animals*.  
1013 University of Chicago Press, Chicago.
- 1014 Davey, G., 2006. Visitor behavior in zoos: A review. *Anthrozoös* 19, 143-157.
- 1015 Davey, G., 2007. Visitors' effects on the welfare of animals in the zoo: A review.  
1016 *Journal of Applied Animal Welfare Science* 10, 169-183.
- 1017 Dawkins, M.S., 1998. Evolution and animal welfare. *Quarterly Review of Biology* 73,  
1018 305-328.
- 1019 Dawkins, M.S., 2004. Using behaviour to assess animal welfare. *Animal Welfare* 13,  
1020 S3-S8.
- 1021 De Azevedo, C. S., Cipreste, C. F., & Young, R. J. (2007). Environmental  
1022 enrichment: a GAP analysis. *Applied Animal Behaviour Science*, 102, 329-  
1023 343.

- 1024 De Azevedo., C.S., Lima M.F., da Silva, V.C., Young, R.J., Rodrigues M., 2012.  
1025 Visitor influence on the behavior of captive greater rheas (*Rhea americana*).  
1026 Journal of Applied Animal Welfare Science 15, 113-125.
- 1027 DebRoy, C., Roberts, E., 2006. Screening Petting Zoo Animals for the Presence of  
1028 Potentially Pathogenic *Escherichia coli*. Journal of Veterinary Diagnostic  
1029 Investigation 18, 597-600.
- 1030 Dehnhardt, G., Mauck, B., Hanke, W., Bleckmann, H., 2001. Hydrodynamic trail-  
1031 following in harbor seals (*Phoca vitulina*). Science 366, 3077-3084.
- 1032 DeNeve, K.M., Cooper, H., 1998. The happy personality: A meta-analysis of 137  
1033 personality traits and subjective well-being. Psychological Bulletin 124, 197-  
1034 229.
- 1035 Desportes, G., Buholzer, L., Anderson-Hansen, K., Blanchet, M.A., Acquarone, M.,  
1036 Shephard, G. Brando, S.I.C.A., Vossen, A., Siebert, U., 2007. Decrease stress:  
1037 Train your animals: The effect of handling methods on cortisol levels in  
1038 harbour porpoises (*Phocoena phocoena*) under human care. Aquatic Mammals  
1039 33, 286-292.
- 1040 Diamond, J., Bond, A.B., 2003. A comparative analysis of social play in birds.  
1041 Behaviour 140, 1091-1115.
- 1042 Diekelmann, S., Bron, J., 2010. The memory function of sleep. Nature Reviews  
1043 Neuroscience 11, 114-126.

- 1044 Dogu, H., Wehman, S., Fagan, J.M., 2011. Touch Exhibits for Aquatic Animals. Best  
1045 Management Practices for Touch Exhibits of AZA Accredited Aquariums, 1-  
1046 16.
- 1047 Drury, L., Buchanan-Smith, H.M., 2008. The effects of 24 hour outdoor access on  
1048 deep sleep in giraffe. Poster presented at the Scottish Conference on Animal  
1049 Behaviour, Stirling, Scotland.
- 1050 Duncan, I.J.H., Petherick, J.C., 1991. The implications of cognitive processes on  
1051 animal welfare. *Journal of Animal Science* 69, 5017-5022.
- 1052 Erkert, H.G., 1989. Lighting requirements of nocturnal primates in captivity: a  
1053 chronobiological approach. *Zoo Biology* 8, 179-191.
- 1054 Fagot, J., Bonté, E., 2010. Automated testing of cognitive performance in monkeys:  
1055 Use of a battery of computerized test systems by a troop of semi-free-ranging  
1056 baboons (*Papio papio*). *Behavior Research Methods* 42, 507-516.
- 1057 Fagot, J., Gullstrand, J., Kemp, C., Defilles, C., Mekaouche, M., 2014. Effects of  
1058 freely accessible computerized test systems on the spontaneous Behaviour and  
1059 stress level of Guinea baboons (*Papio papio*). *American Journal of*  
1060 *Primatology* 76, 56-64.
- 1061 Farrand, A., Hosey, G., Buchanan-Smith, H.M., 2014. The visitor effect in petting  
1062 zoo-housed animals: Aversive or enriching? *Applied Animal Behaviour*  
1063 *Science* 151, 117-127.

- 1064 Fernandez, E.J., Tamborski, M.A., Pickens, S.R., Timberlake, W., 2009. Animal–  
1065 visitor interactions in the modern zoo: Conflicts and interventions. *Applied*  
1066 *Animal Behaviour Science* 120, 1-8.
- 1067 Föllmi, J., Steiger, A., Walzer, C., Robert, N., Geissbühler, U., Doherr, M.G.,  
1068 Wenker, C., 2007. A scoring system to evaluate physical condition and quality  
1069 of life in geriatric zoo mammals. *Animal Welfare* 16, 309-318.
- 1070 Ford, E., 1992. *Falconry. Art and practice.* Blandford Press, London.
- 1071 Fox, R.A., Millam, J.R., 2004. The effect of early environment on neophobia in  
1072 orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal*  
1073 *Behaviour Science* 89, 117-129.
- 1074 Fox, R.A., Millam, J.R., 2007. Novelty and individual differences influence  
1075 neophobia in orange-winged Amazon parrots (*Amazona amazonica*). *Applied*  
1076 *Animal Behaviour Science* 104, 107-115.
- 1077 Fraser, D., 2009. Assessing animal welfare: Different philosophies, different scientific  
1078 approaches. *Zoo Biology* 28, 507-518.
- 1079 Fraser, D., MacRae, A.M., 2011. Four types of activities that affect animals:  
1080 Implications for animal welfare science and animal ethics philosophy. *Animal*  
1081 *Welfare*, 20, 581-590.
- 1082 Fuller, G.A., 2014. The night shift: lighting and nocturnal Strepsirrhine care in zoos  
1083 (Unpublished Doctoral dissertation, Case Western Reserve University).

- 1084 Garner, J.P., Meehan, C.L., Famula, T.R., Mench, J.A., 2006. Genetic, environmental,  
1085 and neighbor effects on the severity of stereotypies and feather picking in  
1086 Orange-winged Amazon parrots (*Amazona amazonica*): An epidemiological  
1087 study. *Applied Animal Behaviour Science* 96, 153-168.
- 1088 Herrelko, E.S., Vick, S.J., Buchanan-Smith, H.M., 2012. Cognitive research in zoo-  
1089 housed chimpanzees: influence of personality and impact on welfare.  
1090 *American Journal of Primatology* 74, 828-840.
- 1091 Heymann, E.W., Smith, A.C., 1999. When to feed on gums: temporal patterns of  
1092 gummivory in wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis*  
1093 (*Callitrichinae*). *Zoo Biology* 18, 459-472.
- 1094 Hoff, M.P., Forthman, D.L., Maple, T.L., 1994. Dyadic interactions of infant lowland  
1095 gorillas in an outdoor exhibit compared to an indoor holding area. *Zoo*  
1096 *Biology* 13, 245–256.
- 1097 Honess, P., Wolfensohn, S., 2010. The extended welfare assessment grid: a matrix for  
1098 the assessment of welfare and cumulative suffering in experimental  
1099 animals. *ATLA-Alternatives to Laboratory Animals*, 38, 205-212.
- 1100 Hosey, G.R., 2000. Zoo animals and their human audiences: what is the visitor effect?  
1101 *Animal Welfare* 9, 343-357.
- 1102 Hosey, G., Melfi, V., Pankhurst, S. 2009. *Zoo animals: behaviour, management, and*  
1103 *welfare*. Oxford University Press, Oxford.
- 1104 IAATE: International Association of Avian Trainers and Educators, 2008. Position  
1105 Statement Food Management and Weight Management.

- 1106 [http://www.iaate.org/pdfs/PositionStatement\\_FoodWeightManagement.pdf](http://www.iaate.org/pdfs/PositionStatement_FoodWeightManagement.pdf)  
1107 (accessed 09.06.2016).
- 1108 Isaac, J.L., Johnson, C.N., Grabau, P.J., Krockenberger, A.K., 2004. Automated  
1109 feeders: new technology for food supplementation experiments with  
1110 mammals. *Wildlife Research* 31, 437- 441.
- 1111 Jago, J.G., Krohn, C.C., Matthews, L.R., 1999. The influence of feeding and handling  
1112 on the development of the human–animal interactions in young cattle. *Applied*  
1113 *Animal Behaviour Science* 62, 137-151.
- 1114 Jones, R.B., 1993. Reduction of the domestic chick's fear of human beings by regular  
1115 handling and related treatments. *Animal Behaviour* 46, 991-998.
- 1116 Justice, W.S.M., O'Brien, M.F., Szyszka, O., Shotton, J., Gilmour, J.E.M., Riordan, P.,  
1117 Wolfensohn, S. 2017. Adaptation of the animal welfare assessment grid  
1118 (AWAG) for monitoring animal welfare in zoological collections. *The*  
1119 *Veterinary Record* published online May 9.
- 1120 Kagan, R., Carter, S., Allard, S., 2015. A universal animal welfare framework for  
1121 zoos. *Journal of Applied Animal Welfare Science*, 18, S1-S10.
- 1122 Kalmar, I.D., Janssens, G.P., Moons, C.P., 2010. Guidelines and ethical  
1123 considerations for housing and management of psittacine birds used in  
1124 research. *ILAR Journal* 51, 409-423.
- 1125 Karmann, A.J., Kundermann, B., Lautenbacher, S., 2014. Sleep deprivation and pain:  
1126 a review of the newest literature. *Schmerz* 2, 141-6.

- 1127 Kasielke, S. 2007. Condors. Hand-Rearing Birds, 1 ed. Wiley-Blackwell, Iowa.
- 1128 Kastelein, R.A., Wiepkema, P.R., 1988. The significance of training for the behaviour  
1129 of Steller sea lions (*Eumetopias jubata*) in human care. Aquatic Mammals 14,  
1130 39-41.
- 1131 Kawata, K., 2008. Zoo Animal Feeding: A natural history viewpoint. Der  
1132 Zoologische Garten 78, 17-42.
- 1133 Kim, L.C., Garner, J.P., Millam, J.R., 2009. Preferences of orange-winged Amazon  
1134 parrots (*Amazona amazonica*) for cage enrichment devices. Applied Animal  
1135 Behaviour Science 120, 216-223.
- 1136 King, J.E., Landau, V.I., 2003. Can chimpanzee (*Pan troglodytes*) happiness be  
1137 estimated by human raters? Journal of Research in Personality 37, 1-15.
- 1138 Kirszenblat, L., van Swinderen, B., 2015. The yin and yang of sleep and attention.  
1139 Trends in Neurosciences 38, 776-86.
- 1140 Knudsen, E.I., 2004. Sensitive periods in the development of the brain and behavior.  
1141 Journal of Cognitive Neuroscience 16, 1412-1425.
- 1142 Krebs, B.L., Watters, J., 2016. Using technology driven environments to promote  
1143 animal well-being in zoos. Paper presented at the Human Computer  
1144 Interactions Conference, San Jose, California.
- 1145 Kyngdon, D. J., Minot, E. O., Stafford, K. J., 2003. Behavioural responses of captive  
1146 common dolphins *Delphinus delphis* to a 'Swim-with-Dolphin' programme.  
1147 Applied Animal Behaviour Science, 81, 163-170.

- 1148 Lambeth, S., Bloomsmith, M.A., Alford, P., 1997. Effects of human activity on  
1149 chimpanzee wounding. *Zoo Biology*, 16, 327-333.
- 1150 Leavens, D.A., Aureli, F., Hopkins, W.D., Hyatt, C.W., 2001. Effects of cognitive  
1151 challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*).  
1152 *American Journal of Primatology* 55, 1-14.
- 1153 Legrand, A., Schütz, K.E., Tucker, C.B., 2011. Using water to cool cattle: Behavioral  
1154 and physiological changes associated with voluntary use of cow showers.  
1155 *Journal of Dairy Science* 94, 3376-86.
- 1156 Leonardi, R., Buchanan-Smith, H. M., Dufour, V., MacDonald, C., & Whiten, A.  
1157 (2010). Living together: behavior and welfare in single and mixed species  
1158 groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri*  
1159 *sciureus*). *American Journal of Primatology*, 72, 33-47.
- 1160 Lukas, K.E., Stoinski, T.S., Burks, K., Snyder, R., Maple, T.L., 2003. Nest Building  
1161 in captive *Gorilla gorilla gorilla*. *International Journal of Primatology* 24,  
1162 103-123.
- 1163 Majchrzak, Y.N., Mastro Monaco, G.F., Korver, W., Burness, G., 2015. Use of  
1164 salivary cortisol to evaluate the influence of rides in dromedary camels.  
1165 *General and Comparative Endocrinology* 211, 123-130.
- 1166 Maple, T., 2007. Towards a science of welfare for animals in the zoo. *Journal of*  
1167 *Applied Animal Welfare Science* 10, 63-70.



- 1168 Marsden, S.J., Whiffin, M., Sadgrove, L., Guimaraes Jr., P., 2000. Parrot populations  
1169 and habitat use in and around two lowland Atlantic forest reserves, Brazil.  
1170 *Biological Conservation* 96, 209-217.
- 1171 Martin, P., Bateson, P., 2007. *Measuring Behaviour: An Introductory Guide*, third ed.  
1172 Cambridge University Press, Cambridge.
- 1173 Martin-Wintle, M.S., Shepherdson, D., Zhang, G., Huang, Y., Luo, B., Swaisgood,  
1174 R.R. 2017. Do opposites attract? Effects of personality matching in breeding  
1175 pairs of captive giant pandas on reproductive success. *Biological*  
1176 *Conservation*, 207, 27-37.
- 1177 Mason, G.J., Mendl, M., 1993. Why is there no simple way of measuring animal  
1178 welfare? *Animal Welfare* 2, 301-319.
- 1179 Matson, K.D., Koutsos, E.A., 2008. Captive Parrot Nutrition: Interactions with  
1180 Anatomy, Physiology, and Behavior, in: Luescher, A. (Ed.), *Manual of Parrot*  
1181 *Behavior*. Wiley-Blackwell, pp. 49-58.
- 1182 McCrae, R.R., Costa Jr., P.T., 1991. Adding Liebe and Arbeit: The full five-factor  
1183 model and wellbeing. *Personality and Social Psychology Bulletin* 17, 227-232.
- 1184 Meehan, C.L., Garner, J.P., Mench, J.A., 2003. Isosexual pair housing improves the  
1185 welfare of young Amazon parrots. *Applied Animal Behaviour Science* 81, 73-  
1186 88.
- 1187 Meehan, C.L., Mench, J.A., 2007. The challenge of challenge: can problem solving  
1188 opportunities enhance animal welfare? *Applied Animal Behaviour Science*  
1189 102, 246-261.

- 1190 Melfi, V.A., 2009. There are big gaps in our knowledge, and thus approach, to zoo  
1191 animal welfare: a case for evidence-based zoo animal management. *Zoo*  
1192 *Biology* 28, 574-588.
- 1193 Melfi, V., 2013. Is training zoo animals enriching? *Applied Animal Behaviour*  
1194 *Science* 147, 299-305.
- 1195 Mellor, D.J., 2016. Updating animal welfare thinking: moving beyond the “Five  
1196 Freedoms” towards “A Life Worth Living”. *Animals* 6, 21.
- 1197 Millam, J.R., Kenton, B., Jochim, L., Brownback, T., Brice, A.T., 1995. Breeding  
1198 orange-winged Amazon parrots in captivity. *Zoo Biology* 14, 275-284.
- 1199 Miller, L.J., Mellen, J., Greer, T., Kuczaj, S.A., 2011. The effects of education  
1200 programmes on Atlantic bottlenose dolphin (*Tursiops truncatus*) behaviour.  
1201 *Animal Welfare* 20, 159-172.
- 1202 Miller, L.J., 2012. Visitor reaction to pacing behavior: influence on the perception of  
1203 animal care and interest in supporting zoological institutions. *Zoo Biology* 31,  
1204 242-248.
- 1205 Morimura, N., Ueno, Y., 1999. Influences on the feeding behavior of three mammals  
1206 in the Maruyama Zoo: Bears, elephants, and chimpanzees. *Journal of Applied*  
1207 *Animal Welfare Science* 2, 169-186.
- 1208 Morton, F.B., Lee, P.C., Buchanan-Smith, H.M., Brosnan, S.F., Thierry, B., Paukner,  
1209 A., de Waal, F.B.M., Widness, J., Essler, J.L., Weiss, A., 2013. Personality  
1210 structure in brown capuchin monkeys: comparisons with chimpanzees,

- 1211            orangutans, and rhesus macaques. *Journal of Comparative Psychology* 127,  
1212            282-298.
- 1213    Morton, F.B., Weiss, A., Buchanan-Smith, H.M., Lee, P.C., 2015. Capuchin monkeys  
1214            with similar personalities have higher-quality relationships independent of  
1215            age, sex, kinship and rank. *Animal Behaviour*, 105, 163-171.
- 1216    Morton, F.B., Brosnan, S.F., Prétôt, L., Buchanan-Smith, H.M., O'Sullivan, E.,  
1217            Stocker, M., Wilson, V.A., 2016. Using photographs to study animal social  
1218            cognition and behaviour: Do capuchins' responses to photos reflect reality?  
1219            *Behavioural Processes* 124, 38-46.
- 1220    Murphy, S.M., Braun, J.V., Likkam, J.R., 2011. Bathing behavior of captive orange-  
1221            winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour*  
1222            *Science* 132, 200-210.
- 1223    Novak, M.A., Hamel, A.F., Kelly, B.J., Dettmer, A.M., Meyer, J.S., 2013. Stress, the  
1224            HPA axis, and nonhuman primate well-being: a review. *Applied Animal*  
1225            *Behaviour Science* 143, 135-149.
- 1226    National Research Council, Committee on Animal Nutrition 2003. Nutrient  
1227            requirements of Non-human primates. National Academy of Science,  
1228            Washington DC.
- 1229    Oranged-winged Amazon parrot. Pet information Animal World. [http://animal-](http://animal-world.com/encyclo/birds/amazons/orangewingedamazon.php)  
1230            [world.com/encyclo/birds/amazons/orangewingedamazon.php](http://animal-world.com/encyclo/birds/amazons/orangewingedamazon.php) (accessed  
1231            15.07.2016).

- 1232 Owen, M.A., Swaisgood, R.R., Czekala, N.M., Lindburg, D.G., 2005. Enclosure  
1233 choice and well-being in giant pandas: is it all about control? *Zoo Biology* 24,  
1234 475-481.
- 1235 O'Connor, T., Freeman, H., 1982. Maternal behaviour and behavioural development  
1236 in the captive snow leopard (*Panther uncial*). *International Pedigree Book for*  
1237 *Snow leopards* 3, 103-110.
- 1238 Parker, K.J., Maestriperi, D., 2011. Identifying key features of early stressful  
1239 experiences that produce stress vulnerability and resilience in  
1240 primates. *Neuroscience and Biobehavioral Reviews* 35, 1466-1483.
- 1241 Patrick, P.G., Matthews, C.E., Ayers, D.F., Tunnicliffe, S.D., 2007. Conservation and  
1242 education: Prominent themes in zoo mission statements. *The Journal of*  
1243 *Environmental Education* 38, 53-60.
- 1244 Pepperberg, I.M., Nakayama, K., 2016. Robust representation of shape in a Grey  
1245 parrot (*Psittacus erithacus*). *Cognition* 153, 146-60.
- 1246 Philly.com, 2015. Zoo's primates now have trails of their own.  
1247 [http://articles.philly.com/2015-05-15/news/62170932\\_1\\_treetop-trail-peco-](http://articles.philly.com/2015-05-15/news/62170932_1_treetop-trail-peco-primate-reserve-great-ape-trail)  
1248 [primate-reserve-great-ape-trail](http://articles.philly.com/2015-05-15/news/62170932_1_treetop-trail-peco-primate-reserve-great-ape-trail) (accessed 17.07.2016)
- 1249 Pines, M.K., Kaplan, G., Rogers, L.J., 2007. A note on indoor and outdoor housing  
1250 preferences of common marmosets (*Callithrix jacchus*). *Applied Animal*  
1251 *Behaviour Science* 108, 348-353.
- 1252 Pirovino, M., Heistermann, M., Zimmermann, N., Zingg, R., Clauss, M., Codron, D.,  
1253 Kaup, F.J., Steinmetz, H.W., 2011. Fecal glucocorticoid measurements and

- 1254 their relation to rearing, behavior, and environmental factors in the population  
1255 of pileated gibbons (*Hylobates pileatus*) held in European zoos. International  
1256 Journal of Primatology 32, 1161-1178.
- 1257 Podberscek, A., Blackshaw, J., Beattie, A., 1991. The effects of repeated handling by  
1258 familiar and unfamiliar people on rabbits in individual cages and group pens.  
1259 Applied Animal Behaviour Science 28, 365-373.
- 1260 Poole, T.B., 1998. Meeting a mammal's psychological needs: Basic principles.  
1261 Second nature: Environmental enrichment for captive animals. Smithsonian  
1262 Institution Press, pp. 83-94.
- 1263 Pryce, C.R., Rüedi-Bettschen, D., Dettling, A.C., Feldon, J., 2002. Early life stress:  
1264 long-term physiological impact in rodents and primates. Physiology 17, 150-  
1265 155.
- 1266 Rabin, L.A., 2003. Maintaining behavioural diversity in captivity for conservation:  
1267 Natural behaviour management. Animal Welfare 12, 85-94.
- 1268 Rozek, J.C., Danner, L.M., Stucky, P.A., Millam, J.R., 2010. Over-sized pellets  
1269 naturalize foraging time of captive Orange-winged Amazon parrots (*Amazona*  
1270 *amazonica*). Applied Animal Behaviour Science 125, 80-87.
- 1271 Rozek, J.C., Millam, J.R., 2011. Preference and motivation for different diet forms  
1272 and their effect on motivation for a foraging enrichment in captive orange-  
1273 winged Amazon parrots (*Amazona amazonica*). Applied Animal Behaviour  
1274 Science 129, 153-161.

- 1275 Ruby, S., Buchanan-Smith, H.M., 2015. The effects of individual cubicle research on  
1276 the social interactions and individual behavior of brown capuchin monkeys  
1277 (*Sapajus apella*). *American Journal of Primatology* 77, 1097-1108.
- 1278 Sahrman, J.M., Niedbalski, A., Bradshaw, L., Johnson, R., Deem, S.L., 2016.  
1279 Changes in Human Health Parameters Associated With a Touch Tank  
1280 Experience at a Zoological Institution. *Zoo Biology* 35, 4-13.
- 1281 Schmid, R., Doherr, M.G., Steiger, A., 2006. The influence of the breeding method on  
1282 the behaviour of adult African grey parrots (*Psittacus erithacus*). *Applied*  
1283 *Animal Behaviour Science* 98, 293-307.
- 1284 Schulte, M.S., Rupley, A.E., 2004. Avian care and husbandry. *Veterinary Clinics of*  
1285 *North America: Exotic Animal Practice* 2, 315-350.
- 1286 Siegel, J.M., 2005. Clues to the functions of mammalian sleep. *Nature* 437, 1264-  
1287 1271.
- 1288 Skeate, S.T., 1985. Social Play Behaviour in Captive White-fronted Amazon Parrots  
1289 *Amazona albifrons*. *Bird Behavior* 6, 46-48.
- 1290 Smith, B.J., Smith, S.A., Flammer, K., Spaulding, K.A., Smallwood, J.E., 1990. The  
1291 normal xeroradiographic and radiographic anatomy of the orange-winged  
1292 amazon parrot (*Amazona amazonica amazonica*). *Veterinary Radiology* 31,  
1293 114-124.
- 1294 Smith, T. E., McGreer-Whitworth, B., & French, J. A. (1998). Close proximity of the  
1295 heterosexual partner reduces the physiological and behavioral consequences of

- 1296 novel-cage housing in black tufted-ear marmosets (*Callithrix*  
1297 *kuhli*). *Hormones and Behavior*, 34, 211-222.
- 1298 Sommerfeld, R., Bauert, M., Hillmann, E., Stauffacher, M., 2005. Feeding enrichment  
1299 by self-operated food boxes for white-fronted lemurs (*Eulemur fulvus*  
1300 *albifrons*) in the Masoala exhibit of the Zurich Zoo. *Zoo Biology* 25, 145–154.
- 1301 Spruijt, B.M., van den Bos, R., Pijlman, F.T., 2001. A concept of welfare based on  
1302 reward evaluating mechanisms in the brain: anticipatory behaviour as an  
1303 indicator for the state of reward systems. *Applied Animal Behaviour Science*  
1304 71, 145-171.
- 1305 Stamps, J., Groothuis, T.G., 2010. The development of animal personality: relevance,  
1306 concepts and perspectives. *Biological Reviews* 85, 301-325.
- 1307 Starkhammar, J., Amundin, M., Olsén, H., Almqvist, M., Lindström, K., Persson,  
1308 H.W., 2007. Acoustic Touch Screen for Dolphins, First application of ELVIS  
1309 - an Echo-Location Visualization and Interface System.  
1310 <http://lup.lub.lu.se/record/768807> (accessed 15.07.2016).
- 1311 Swaisgood, R. R., Shepherdson, D. J., 2005. Scientific approaches to enrichment and  
1312 stereotypies in zoo animals: what's been done and where should we go next?  
1313 *Zoo Biology* 24, 499-518.
- 1314 Tapia-Osorio, A., Salgado-Delgado, R., Angeles-Castellanos, M., Escobar, C., 2013.  
1315 Disruption of circadian rhythms due to chronic constant light leads to  
1316 depressive and anxiety-like behaviors in the rat. *Behavioural Brain Research*  
1317 252, 1-9.

- 1318 Tell, L.A., Kabbur, M.B., Smith, W.L., Dahl, K.H., Cullor, J.S., 1997. A technique  
1319 for isolating heterophils from blood of orange-winged Amazon parrots  
1320 (*Amazona amazonica amazonica*). *Comparative Haematology International* 7,  
1321 47-53.
- 1322 Trainin, G., Wilson, K., Wickless, M., Brooks, D., 2005. Extraordinary animals and  
1323 expository writing: Zoo in the classroom. *Journal of Science Education and*  
1324 *Technology* 14, 299-304.
- 1325 Vessey, S.H., 1973. Night observations of free-ranging rhesus monkeys. *American*  
1326 *Journal of Physical Anthropology* 38, 613-620.
- 1327 Vorster, A.P., Born, J., 2015. Sleep and memory in mammals, birds and invertebrates.  
1328 *Neuroscience & Biobehavioral Reviews* 50, 103-119.
- 1329 Wagner, K.E., Ross, S.R., 2008. Chimpanzee (*Pan troglodytes*) birth patterns and  
1330 human presence in zoological settings. *American Journal of Primatology* 70,  
1331 703-706.
- 1332 Wagner, K.E., Hopper, L.M., Ross, S.R., 2016. Asymmetries in the production of  
1333 self-directed behavior by chimpanzees and gorillas during a computerized  
1334 cognitive test. *Animal Cognition* 19, 343-350.
- 1335 Waitt, C., Buchanan-Smith, H.M., 2001. What time is feeding?: How delays and  
1336 anticipation of feeding schedules affect stump-tailed macaque behavior.  
1337 *Applied Animal Behaviour Science* 75, 75-85.
- 1338 Weiss, A., Adams, M.J., King, J.E., 2011. Happy orang-utans live longer lives.  
1339 *Biology Letters* 7, 872-874



- 1340 Weiss, A., King, J.E., Enns, R.M., 2002. Subjective well-being is heritable and  
1341 genetically correlated with dominance in chimpanzees (*Pan troglodytes*).  
1342 Journal of Personality and Social Psychology 83, 1141-1149.
- 1343 Weiss, A., Bates, T. C., & Luciano, M. (2008). Happiness is a personal (ity) thing:  
1344 The genetics of personality and well-being in a representative  
1345 sample. *Psychological Science*, 19, 205-210.
- 1346 Welfare Quality (2009). Retrieved from  
1347 <http://www.welfarequality.net/everyone/26536/5/0/22>
- 1348 Wemelsfelder, F., 2007. How animals communicate quality of life: the qualitative  
1349 assessment of behaviour. *Animal Welfare* 16S, 25-31.
- 1350 Wielebnowski, N. C. (1999). Behavioral differences as predictors of breeding status  
1351 in captive cheetahs. *Zoo Biology*, 18, 335-349.
- 1352 Wolfensohn, S., Sharpe, S., Hall, I., Lawrence, S., Kitchen, S., Dennis, M., 2015.  
1353 Refinement of welfare through development of a quantitative system for  
1354 assessment of lifetime experience. *Animal Welfare*, 24, 139-149.
- 1355 Yamanashi, Y., Hayashi, M., 2011. Assessing the effects of cognitive experiments on  
1356 the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of  
1357 activity budget between wild and captive chimpanzees. *American Journal of*  
1358 *Primatology* 73, 1231-1238.