

Brereton

1 The Zone Overlap Index: a new measure of shared resource use in the zoo

2 James Edward Brereton^{1,2} and Paul E. Rose^{3,4}

3 ¹University Centre Sparsholt, Westley Lane, Sparsholt, Winchester, Hampshire, SO21 2NF, United
4 Kingdom, .

5 ²Nottingham Trent University, Brackenhurst Lane, Southwell NG25 0QF, United Kingdom.

6 ³Centre for Research in Animal Behaviour, University of Exeter, Exeter EX4 4QG, United Kingdom.

7 ⁴WWT, Slimbridge Wetland Centre, Slimbridge GL2 7BT, United Kingdom.

8 Correspondence: James Edward Brereton, email; James.Brereton@sparsholt.ac.uk

9 **Running title:** *Development of the Zone Overlap Index*

10 **Paper type:** *Technical paper*

11

12 **Abstract**

13 It is important that the environment provided in the zoo is relevant to the species being housed and its
14 suitability be easily assessed by personnel. As shared space and resources can overlap in a zoo's
15 enclosure a tool is required to measure the effects of such overlap between individual animals in a
16 shared enclosure. This paper outlines the Pianka Index (PI), a tool used in ecology to quantify niche
17 overlap, that has value in quantifying the amount of time that animals spend in shared enclosure zones.
18 One limitation to this method, however, is that the established method of determining the PI requires
19 division of the enclosure into equally sized zones, something that is not always relevant to a zoo
20 enclosure. To combat this, we created a modified index, entitled the Zone Overlap Index (ZOI). This
21 modified index is the exact mathematical equivalent of the original index when zone sizes are equal.
22 When zone sizes are unequal, the ZOI generates higher values when animals share smaller, as opposed
23 to larger, zones. This is because animals are more likely to share larger enclosure zones simply by
24 chance, and shared use of smaller zones brings individuals into closer proximity with the potential for

25 competition. To illustrate the application of the ZOI, a series of hypothetical situations were generated
26 to reflect real-world scenarios, demonstrating how this index could be used to better understand zone
27 occupancy overlap in the zoo.

28

29 **Keywords:** compatibility, enclosure design, mixed-species enclosure, Pianka Niche Overlap Index,
30 proximity

31 Research highlights:

- 32 1. *The Pianka Index can be used to quantify space use overlap in exhibits with equal-sized zones.*
- 33 2. *The Zone Overlap Index quantifies space use overlap in exhibits with unequal-sized zones.*
- 34 3. *The Zone Overlap Index places higher weightings on small zones which animals are unlikely*
35 *to share by chance.*

36

37

38

39

40

41

42

43

44

45

46

47

48 **Introduction**

49 The managed environment of the zoo, with its finite space, often results in increased density and social
50 housing for animals (Mason, 2010). This can often present challenges for animal management (Clubb
51 & Mason, 2007; Kroshko et al., 2016). Inappropriate combinations of individuals could result in
52 extreme competition with welfare impacts (Mason, 2010). As such, it is important that animal care staff
53 can assess animal compatibility to reduce the risk of future welfare problems. Although a species' wild
54 social behavior may appear to be a good predictor of their suitability for multi-animal enclosures,
55 research has demonstrated that the creation of mixed-species display is not so clear cut. Some solitary
56 species can be housed in pairs or groups with no identified welfare impact (Macri & Patterson-Kane,
57 2011), whereas social species regularly pose compatibility challenges in captivity (Hosey et al., 2016).
58 At maturity, species often naturally disperse away from natal groups, but the zoo's finite captive
59 environment hampers these attempts (Price & Stoinski, 2007; Morgan & Tromborg, 2007). A clear
60 understanding of animal compatibility and space use is therefore useful for practitioners to promote
61 animal welfare, ensure appropriate animal management and evidence the ecological relevance of
62 enclosure sizes.

63 In the wild, aggression is often triggered by competition over valued and/or limited resources (Tran et
64 al., 2014) such as food or access to potential mates (Stamps, 1977). In the wild, individuals that fit a
65 similar demographic (e.g. similar body size or same sex) (Ward et al., 2006), or species that share
66 similar ecological niches (Tran et al., 2014) are more likely to compete, and this may also stand true in
67 the zoo. Knowledge of the perceived value of an area or resource within an enclosure could be used to
68 reduce competition in captive animals. Understanding how sympatric species avoid competition, and
69 selection of these species for mixed species exhibits, may be appropriate but any usage of shared
70 resources still needs to be measured and interpreted.

71 Valid identification of how and where zoo-housed animals overlap in their space use may be of use to
72 the further development of species-appropriate housing and husbandry. Any valued resources, that are
73 finite in nature, could become the focal point for competition or aggression between the occupants of
74 an enclosure. By highlighting resources that encourage animals to congregate, the distribution and

75 pattern of such valued resources within an enclosure can be evidenced to promote species-typical
76 behavior. There are already a range of tools available to aid researchers in the field of animal space use
77 and welfare (Macri & Patterson-Kane, 2011), and the use of several tools in combination can help to
78 unpick a complex scenario. Behavioral measures and enclosure use analysis are particularly synergistic
79 as they can identify both where and how an animal uses its space (Ross & Lukas, 2008). However, there
80 are currently no tools available that quantify any overlap in space use between individual animals.

81 To aid ecologists in quantifying niche overlap in free-living populations, the Pianka (1973) Niche
82 Overlap Index was developed. Traditionally, this index is used to quantify the dietary overlap between
83 two sympatric species. These Pianka Index (PI) values are useful in that they provide a numerical value
84 for the dietary competition between two animal species (Glen & Dickman, 2008). The Pianka Index
85 assumes that individuals/species with similar diets are likely to compete over ecological niche. This
86 index could be useful if adapted to a new role in the zoo due to its abilities in assessing usage of shared
87 resources, something common to practically all zoo enclosures. Here, the assumption is that animals
88 that spend long periods of time in shared zones are more likely to compete over resources.

89 Consequently, this paper describes the evolution of the PI to enable quantification of enclosure zone
90 overlap in a zoo or aquarium (hereafter “zoo”) context. Literature relating to Pianka’s (1973) Niche
91 Overlap Index was consulted and then a modified version, the Zone Overlap Index (ZOI), was tested
92 on simulated data to assess its practical application.

93

94 **Methods**

95

96 *Pianka’s index*

97 The equation for Pianka’s Niche Overlap Index is:

98
$$O_{jk} = \left(\frac{\sum P_{ij} P_{ik}}{\sum P_{ij}^2 \sum P_{ik}^2} \right)^{1/2}$$

99 Traditionally, P_i is the frequency of occurrence of prey item i in the diet of species j and k (Pianka,
 100 1973). The values generated vary between 0 (no overlap) and 1 (total overlap). For the purposes of
 101 animal space use research, P^i represents the use of enclosure zone i by animals j and k . Here, animals j
 102 and k can be animals from two different species, or two individuals of the same species that share an
 103 exhibit. The equation assumes that all zones are of equal size. In practice, this is rarely the case, so there
 104 was a need to develop an index that could factor in unequal zone sizes.

105

106 *Developing the Zone Overlap Index*

107 A new index, entitled the ZOI, was developed using by adapting the PI. The equation for the index is:

$$108 \quad ZO_{jk} = \left(\frac{\sum Zi(P_{ij} P_{ik})}{\sum ZiP_{ij}^2 \sum ZiP_{ik}^2} \right)^{1/2}$$

109 In this index, P^i is the amount of time that animals j and k spend in zone i in a given study period.

110 Z_i represents the total enclosure size (e.g. m², cm³), divided by the size of zone i .

111 As per the PI, this index generates a value between 0 (total separation) and 1 (total overlap) for animals
 112 j and k . When all zones are of equal size, the PI and the ZOI produce identical values. The more time
 113 that animals j and k spend in shared zones, the higher the generated values. However, when zones are
 114 unequal in size, the two indices differ. The more time that animals j and k spend in shared, smaller
 115 zones, the higher the index values become in contrast to results generated by the PI in the same situation.
 116 Simulation data were developed and expressed graphically to illustrate the workings of both Indices
 117 under different conditions (Supplementary material for Excel file).

118

119 *Scenario 1*

120 A highly simplified enclosure was generated that consisted of only two zones: Zone A and Zone B.
 121 Two animals: Alpha and Beta, occupied this enclosure. Alpha and Beta were observed simultaneously
 122 for sixty sets of one-hour observation periods, using instantaneous focal sampling at one-minute

123 intervals. For each observation, 60 data points were generated per animal per hour. Regardless of the
124 observation, Beta always stayed in zone A. Alpha, by contrast, spent 60 minutes in zone A in the first
125 observation. For the second observation, Alpha spent 59 minutes in zone A, and one minute in zone B.
126 For the third hour, Alpha spent 58 minutes in zone A and 2 minutes in zone B. This pattern is repeated
127 until Alpha spent only 1 minute in zone A, and 59 minutes in zone B. Both PI and ZOI were applied to
128 these data generated.

129

130 *Scenario 2*

131 The zone sizes for the basic, two-zone exhibit introduced in scenario 1 were altered to demonstrate the
132 effect of unequal zones on ZOI values. Three sets of zone sizes were used. For the first simulation, the
133 two zones were equal in size (50m² for each zone). For the second and third simulations, zone A was
134 made larger (90m²) or smaller (10m²) than zone B (10m² or 90m²). The animal space use patterns were
135 identical to those described in Scenario 1.

136

137 *Scenario 3*

138 A more complex situation, in which three animals (Alpha, Beta and Omega) shared an enclosure that
139 contained four zones (zones A to D). As per the first two scenarios, all three animals were observed for
140 one-hour sessions, during which instantaneous focal samples of location are taken every minute. This
141 resulted in 60 data points per animal per hour.

142 In this scenario, Beta stayed in zone A for the entirety of all observations. For the first observation,
143 Alpha and Omega were also observed for all 60 minutes in this zone. However, over the course of the
144 study, both Alpha and Omega slowly dispersed to new zones (in the second hour, Alpha spent 59
145 minutes in zone A and 1 minute in zone C, whereas Omega spent 59 minutes in zone A and 1 minute
146 in zone B). This pattern continued for 60 hours, up until the point that Omega and Alpha spend only
147 one minute in zone A, and the remaining 59 minutes in zone B and C, respectively.

148 Initially, all zone sizes were set to be equal for this scenario. For example, all zone sizes were 25m². PI
 149 values were generated between all animal pairs.

150 To demonstrate the effect of unequal zone size on index values, the four zone sizes were then altered
 151 for a second simulation. This time, zone A was set to 30m², zone B to 60m², zone C to 5m² and zone D
 152 to 5m². The simulation was rerun, using the ZOI for all three pairwise comparisons (Beta-Alpha, Beta-
 153 Omega and Omega-Alpha).

154

155 **Results**

156 ***Scenario 1***

157 Simulations were developed for a simple, two-zone enclosure, to compare the values generated by PI
 158 and ZOI for two animals, Alpha and Beta. When both animals spent all their time in zone A, both the
 159 PI and ZOI value were 1. As Alpha spent progressively more time in zone B, PI and ZOI values dropped.
 160 PI and ZOI values were identical to one another (Table 1).

161

162 Table 1. PI and ZOI values generated from a simulated two-zone exhibit. The table is abridged to show
 163 every tenth hour.

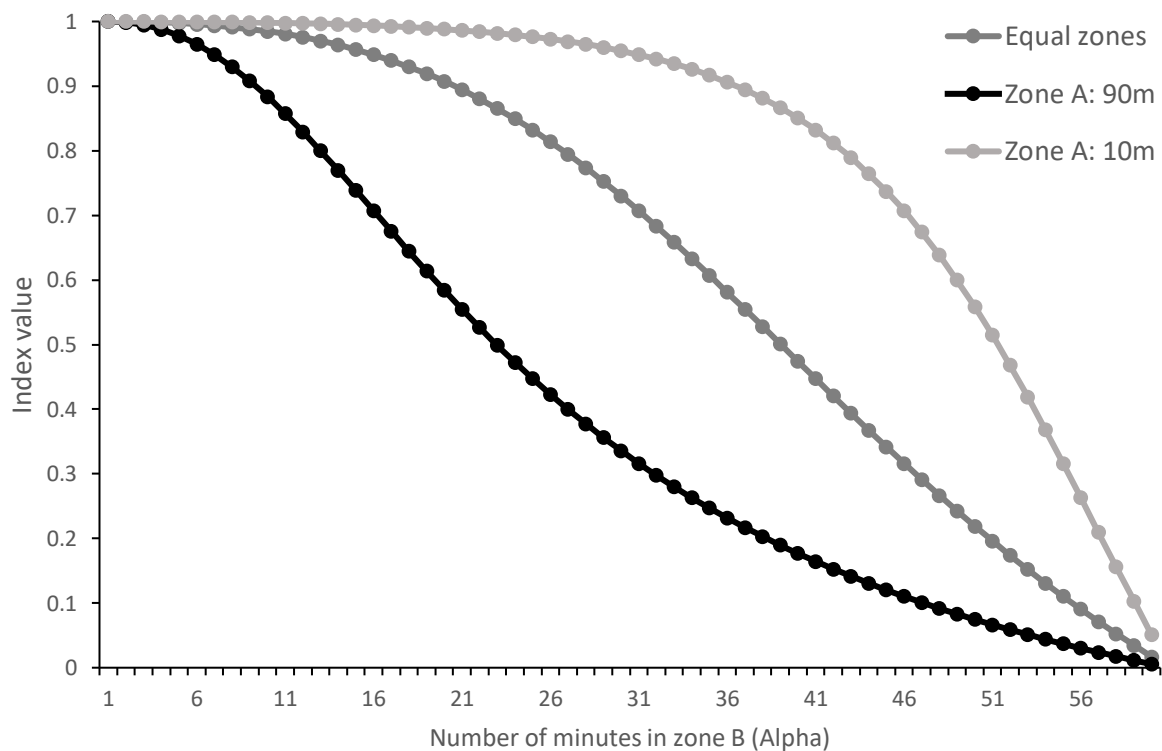
Number of minutes spent by Alpha in zone A	PI	ZOI
60	1.000	1.000
50	0.981	0.981
40	0.894	0.894
30	0.707	0.707
20	0.447	0.447
10	0.196	0.196

164

165

166 **Scenario 2**

167 In this scenario, Beta always occupied zone A for the full hour, but Alpha spent progressively less time
 168 in this zone. In all scenarios, ZOI values dropped as the two animals spent less time in the same zone.
 169 However, the drop was much steeper for the simulation where zone A was larger in size (90m²). By
 170 contrast, ZOI values remained high for longer in the simulation where zone A was smaller (10m²)
 171 (Figure 1).

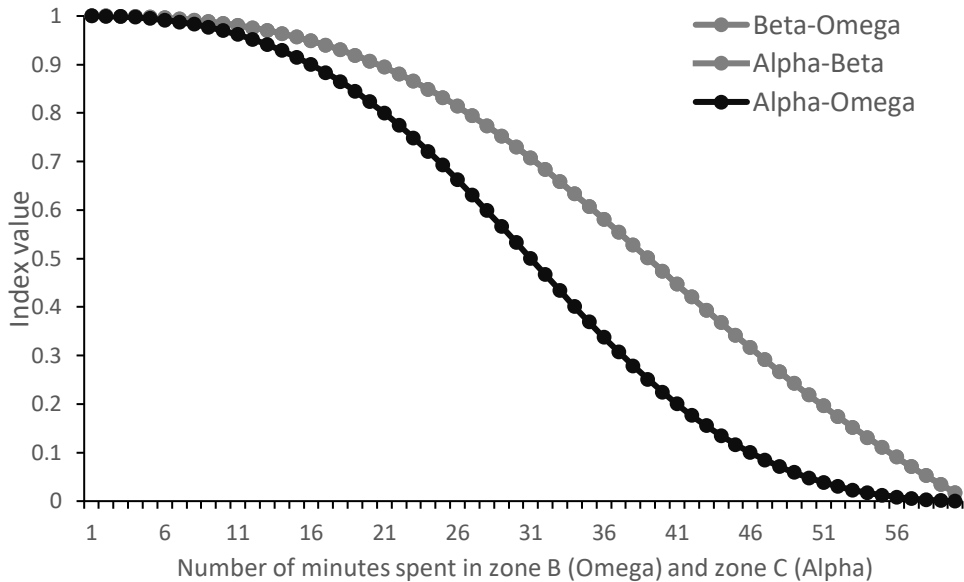


172
 173 Figure 1. Effect of unequal zone size on ZOI. The grey line shows the index values when both zones
 174 are of equal size, and the black and light grey line demonstrate ZOI values when zone A is set to be
 175 larger (90m²) or smaller (10m²).

176
 177 **Scenario 3**

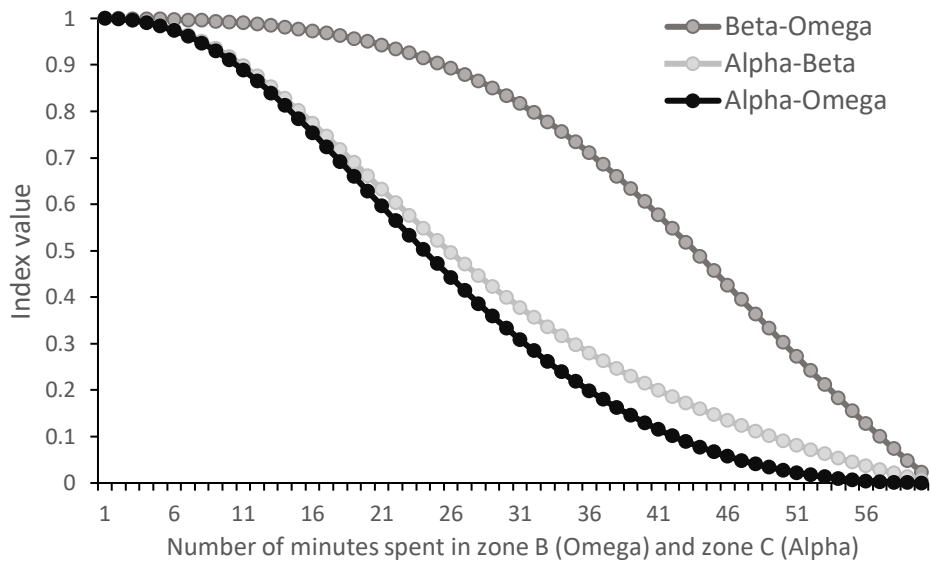
178 For this scenario, three animals (Alpha, Beta and Omega) spent time in a four-zone enclosure. Beta
 179 spent the entire study period in zone A, whereas Alpha and Omega transition from spending all their

180 time in zone A, to spending their time in zone C and B, respectively. Simulations were generated for
 181 this scenario when all zones are of equal size (Figure 2), and when zones were of unequal size (Figure
 182 3). The PI was used for the equal-size zone simulation, and ZOI was used for the unequal-size zone
 183 simulation. The values for Beta-Omega stayed higher for longer than the values for Beta-Alpha.



184
 185 Figure 2. PI values for a simulated four-zone enclosure containing three animals. Here, two animals
 186 (Omega and Alpha) spend progressively less time in zone A (shared with Beta) as the study progresses.
 187 The lines show the PI values for Beta-Omega, Beta-Alpha, and Alpha-Omega combinations. The Beta-
 188 Omega line is invisible because it is hidden behind the Alpha-Beta line, which it is identical to.

189



190

191 Figure 3. ZOI values for a simulated unequal-sized four-zone enclosure containing three animals. Here,
 192 two animals (Omega and Alpha) spend progressively less time in zone A (shared with Beta) as the study
 193 progresses. The lines show the ZOI values for Beta-Omega, Beta-Alpha, and Alpha-Omega
 194 combinations.

195

196 Discussion

197 The PI and ZOI were used to quantify enclosure zone overlap in a range of simulated scenarios. First,
 198 the results demonstrated that PI and ZOI generate identical values when applied to an enclosure
 199 containing equally sized zones. Second, the ZOI generated values closer to 1 when animals spent time
 200 together in smaller zones, and slightly lower values when animals spent time together in the larger zones
 201 (e.g. Table 3). The reason for this is that animals spending time together in smaller areas is less likely
 202 to arise by chance than animals spending time in larger enclosure areas. The PI is therefore valuable for
 203 use in exhibits which can be clearly delineated into equal-sized zones, whereas the ZOI has merit when
 204 assessing exhibits with unequal-sized areas.

205 The PI and ZOI fit a new niche in assessing space overlap (Vieira & Port, 2007), and these methods
 206 could be applied to compare different individuals from the same species, in a shared enclosure. While
 207 there are several existing methods of assessing enclosure use, such as Spread of Participation Index

208 (Plowman, 2003), Electivity Index (Vanderploeg and Scavia, 1979) and Entropy, these methods do not
209 directly compare how individual animals use space. Of the four indices, three assess enclosure use
210 holistically, providing only a single value of evenness of space use. The ZOI therefore is much more
211 appropriate for direct comparisons of zone overlap between animals, as it generates pairwise
212 comparisons which can be quantified between group members.

213 While PI and ZOI incorporate some enclosure use theory, they are not traditional measures of enclosure
214 use. Unlike existing indices, the PI and ZOI do not automatically assume that animals should be using
215 all areas. In fact, a value of 1 (total overlap) can be generated even if animals are using a single zone
216 (e.g. Figure 2). For both indices, this maximum value is generated only when the two animals are using
217 the same zones in the same proportion to one another. Similarly, a value of 0 (no overlap) can be
218 generated for animals provided they never use the same zones. This is useful because it demonstrates
219 that the indices are not sensitive to variation in the size of unused zones.

220 Unlike PI, the ZOI weights zones based on their respective size. This weighting is inverted, so that
221 proportionally smaller enclosure spaces are weighted more heavily. Animals are less likely to spend
222 time together in small enclosure spaces due to chance (Matthiopoulos, 2003; Smith et al., 2021). Smaller
223 spaces that are being shared are therefore more likely to contain highly valued resources, thus increasing
224 the chances of competition.

225 While the PI and ZOI share some similarities with measures of animal sociality and social networks,
226 they fit a different role. Social networks are built on proximity or interaction-information between
227 animals (Wey et al., 2008), neither of which are factored into these indices. The ZOI may generate high
228 values for animals that associate together because they spend time in the same zones. However, the
229 indices will also generate high values for animals that regularly compete for shared, valued exhibits
230 resources. The index therefore generates a measure of overlap, rather than an index of association or
231 competition.

232

233 **Future applications**

234 Given their versatility, there are many scenarios in which the PI and new ZOI could be used to
235 investigate. Three examples of practical application are as follows:

236 1. Mixed species enclosures. The ZOI could be applied to existing mixed-species enclosures to quantify
237 the level of overlap between species. Where several species are maintained in the same enclosure,
238 pairwise comparisons could be made to determine which species overlap most in space use. It is
239 theorized that animals that share a similar ecological niche will use similar resources and zones,
240 resulting in higher competition and therefore higher ZOI values. Future studies, using the Zone Overlap
241 Index in combination with behavioral measures (e.g. of aggression) would have value in testing this,
242 especially in scenarios where compatibility may be challenging, such as canids and ursids (Dorman &
243 Bourne, 2010).

244 2. Compatibility in single species exhibits. Management of endangered species normally sees animals
245 paired for breeding via studbook recommendations that incorporate genetic and demographic
246 information (Ayala-Burbano et al., 2020). However, animals within a pair may not be behaviorally
247 compatible, resulting either in aggression or avoidance (Kozlowski et al., 2015). When used with other
248 measures, such as behavioral observation, the ZOI can quantify use of shared enclosure areas (and this
249 may be indicative of affiliation between individuals in a breeding pair) or for identification of animals
250 that are beginning to split from an existing social group (Hosey et al., 2016), and therefore are ready for
251 movement to a new facility.

252 3. Introductions. Introductions of new animals into established groups can be risky, and competition
253 may cause injury (Berg et al., 2019). As the ZOI defined the degree of overlap in space use (and
254 therefore potential for competition between individual animals) it has an application in assessing where
255 conflict may appear. The ZOI could also aid in identification of potential aggression flashpoints at
256 small but valuable resources.

257

258 **Conclusion**

259 The new ZOI can assess space overlap in co-habiting zoo animals. Several scenarios have been
260 demonstrated to support its usage as a tool to assist in zoo management. The index represents an
261 opportunity to quantify and compare overlapping space use between animals. This identification of
262 valuable resources helps practitioners make informed decisions on enclosure development to ensure
263 resource availability is appropriate for all species being housed.

264

265 **Conflict of Interest**

266 The authors declare no conflict of interest.

267

268 **Ethical statement**

269 No ethical approval was required as the work is a theoretical paper.

270

271 **Data Sharing and Data Accessibility**

272 The simulated data generated for this project are available from the authors upon reasonable request.

273 Additionally, a Pianka Index and Zone Overlap Index generator spreadsheet is available as a
274 supplementary file.

275

276 **Acknowledgments**

277 The authors would like to thank Mrs S Brereton and Mr M Brereton for discussions regarding the
278 development of the index. The authors would also like to thank anonymous reviewers for their
279 constructive comments.

280

281 **References**

- 282 Ayala-Burbano, P. A., Galetti Junior, P. M., Wormell, D., Pissinatti, A., Marques, M. C., & de Freitas,
283 P. D. (2020). Studbook and molecular analyses for the endangered black-lion-tamarin; an integrative
284 approach for assessing genetic diversity and driving management in captivity. *Scientific Reports*, *10*(1),
285 6781. <https://doi.org/10.1038/s41598-020-63542-2>
- 286 Berg, M. R., Heagerty, A., & Coleman, K. (2019). Oxytocin and pair compatibility in adult male rhesus
287 macaques (*Macaca mulatta*). *American Journal of Primatology*, 1-8. <https://doi.org/10.1002/ajp.23031>
- 288 Clubb, R., & Mason, G. J. (2007). Natural behavioural biology as a risk factor in carnivore welfare:
289 How analysing species differences could help zoos improve enclosures. *Applied Animal Behaviour*
290 *Science*, *102*(3), 303–328. <https://doi.org/10.1016/j.applanim.2006.05.033>
- 291 Dorman, N., & Bourne, D. C. (2010). Canids and ursids in mixed-species enclosures. *International Zoo*
292 *Yearbook*, *44*(1), 75–86. <https://doi.org/10.1111/j.1748-1090.2009.00108.x>
- 293 Edwards, M. J., Hosie, C. A., Smith, T. E., Wormell, D., Price, E., & Stanley, C. R. (2021). Principal
294 Component Analysis as a novel method for the assessment of the enclosure use patterns of captive
295 Livingstone’s fruit bats (*Pteropus livingstonii*). *Applied Animal Behaviour Science*, *244*, 1–14. 105479.
296 <https://doi.org/10.1016/j.applanim.2021.105479>
- 297 Glen, A. S., & Dickman, C. R. (2008). Niche overlap between marsupial and eutherian carnivores: does
298 competition threaten the endangered spotted-tailed quoll? *Journal of Applied Ecology*, *45*(2), 700–707.
299 <https://doi.org/10.1111/j.1365-2664.2007.01449.x>
- 300 Hosey, G., Melfi, V., Formella, I., Ward, S. J., Tokarski, M., Brunger, D., Brice, S., & Hill, S. P. (2016).
301 Is wounding aggression in zoo-housed chimpanzees and ring-tailed lemurs related to zoo visitor
302 numbers? *Zoo Biology*, *35*(3), 205–209. <https://doi.org/10.1002/zoo.21277>
- 303 Hurlbert, S. H. (1978). The Measurement of Niche Overlap and Some Relatives. *Ecology*, *59*(1), 67–
304 77. <https://doi.org/10.2307/1936632>

- 305 Kozłowski, C. P., Bauman, K. L., & Asa, C. S. (2015). Reproductive behavior of the great hornbill
 306 (*Buceros bicornis*): Hornbill Reproductive Behavior. *Zoo Biology*, 34(4), 328–334.
 307 <https://doi.org/10.1002/zoo.21221>
- 308 Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrensclager, A., & Mason, G. (2016). Stereotypic
 309 route tracing in captive Carnivora is predicted by species-typical home range sizes and hunting styles.
 310 *Animal Behaviour*, 117, 197–209. <https://doi.org/10.1016/j.anbehav.2016.05.010>
- 311 Macri, A. M., & Patterson-Kane, E. (2011). Behavioural analysis of solitary versus socially housed
 312 snow leopards (*Panthera uncia*), with the provision of simulated social contact. *Applied Animal*
 313 *Behaviour Science*, 130(3), 115–123. <https://doi.org/10.1016/j.applanim.2010.12.005>
- 314 Mason, G. J. (2010). Species differences in responses to captivity: stress, welfare and the comparative
 315 method. *Trends in Ecology & Evolution*, 25(12), 713–721. <https://doi.org/10.1016/j.tree.2010.08.011>
- 316 Matthiopoulos, J. (2003). The use of space by animals as a function of accessibility and preference.
 317 *Ecological Modelling*, 159(2), 239–268. [https://doi.org/10.1016/S0304-3800\(02\)00293-4](https://doi.org/10.1016/S0304-3800(02)00293-4)
- 318 Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour*
 319 *Science*, 102(3–4), 262–302. <https://doi.org/10.1016/j.applanim.2006.05.032>
- 320 Pianka, E. R. (1973). The structure of Lizard Communities. *Annual Review of Ecology and Systematics*,
 321 4(1973), 53–74. https://www.jstor.org/stable/2096804#metadata_info_tab_contents
- 322 Plowman, A. (2013). Diet review and change for monkeys at Paignton Zoo Environmental Park.
 323 *Journal of Zoo and Aquarium Research*, 1(2), 73–77. <https://doi.org/10.19227/jzar.v1i2.35>
- 324 Plowman, A. B. (2003). A note on a modification of the spread of participation index allowing for
 325 unequal zones. *Applied Animal Behaviour Science*, 83(4), 331–336. [https://doi.org/10.1016/S0168-](https://doi.org/10.1016/S0168-1591(03)00142-4)
 326 [1591\(03\)00142-4](https://doi.org/10.1016/S0168-1591(03)00142-4)
- 327 Price, E. E., & Stoinski, T. S. (2007). Group size: Determinants in the wild and implications for the
 328 captive housing of wild mammals in zoos. *Applied Animal Behaviour Science*, 103(3–4), 255–264.
 329 <https://doi.org/10.1016/j.applanim.2006.05.021>

- 330 Ross, S. R., & Lukas, K. E. (2006). Use of space in a non-naturalistic environment by chimpanzees
331 (Pan troglodytes) and lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science*,
332 96(1-2), 143-152. <https://doi.org/10.1016/j.applanim.2005.06.005>
- 333 Stamps, J. A. (1977). The Relationship between Resource Competition, Risk, and Aggression in a
334 Tropical Territorial Lizard. *Ecology*, 58(2), 349–358. <https://doi.org/10.2307/1935609>
- 335 Tran, M. V., O’Grady, M., Colborn, J., Ness, K. V., & Hill, R. W. (2014). Aggression and Food
336 Resource Competition between Sympatric Hermit Crab Species. *PLOS ONE*, 9(3), e91823.
337 <https://doi.org/10.1371/journal.pone.0091823>
- 338 Vanderploeg, H. A., & Scavia, D. (1979). Calculation and use of selectivity coefficients of feeding:
339 Zooplankton grazing. *Ecological Modelling*, 7(2), 135–149. [https://doi.org/10.1016/0304-](https://doi.org/10.1016/0304-3800(79)90004-8)
340 3800(79)90004-8
- 341 Vieira, E. M., & Port, D. (2007). Niche overlap and resource partitioning between two sympatric fox
342 species in southern Brazil. *Journal of Zoology*, 272(1), 57–63. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-7998.2006.00237.x)
343 7998.2006.00237.x
- 344 Ward, A. J. W., Webster, M. M., & Hart, P. J. B. (2006). Intraspecific food competition in fishes. *Fish*
345 *and Fisheries*, 7(4), 231–261. <https://doi.org/10.1111/j.1467-2979.2006.00224.x>