Understanding impacts of zoo visitors: quantifying behavioural changes of two popular zoo species during COVID-19 closures

by Williams, E., Carter, A., Rendle, J. and Ward, S.J.

DOI link to the version of record on the publisher's website

Harper Adams University

8 February 2021

Understanding impacts of zoo visitors: Quantifying behavioural changes of two popular zoo species during COVID-19 closures[1]

[1] This paper is part of the Special Issue 'COVID-19: Rethinking confinement' based on the 2020 ISAE conference

Ellen Williams[1,a*], Anne Carter[1+], Jessica Rendle[2,3+] & Samantha J Ward[1+]

[1]School of Animal, Rural & Environmental Sciences, Nottingham Trent University, Brackenhurst Campus, Nottinghamshire, NG25 0QF, UK; ewilliams@harper-adams.ac.uk; anne.carter@ntu.ac.uk; Samantha.ward@ntu.ac.uk

[2] Twycross Zoo, Atherstone, Warwickshire CV9 3PX, UK; jessica.rendle@twycrosszoo.org

[3] Conservation Medicine, College of Science Health, Education and Engineering, Murdoch University, Perth 6150, Australia

[a]Current address: Department of Veterinary Health & Animal Sciences, Harper Adams University, Newport, Shropshire TF10 8NB

*Corresponding author

Email address: ewilliams@harper-adams.ac.uk

[+]Authors had an equal contribution

Abstract

Visitors are normally a prominent and constant feature in a zoo animals' environment with more than 700 million people visiting zoos and aquariums worldwide, annually. Animal-visitor interactions can be enriching and stimulating and are now considered within the Five Domains of animal welfare assessment. Zoo closures as a result of COVID-19 provided a unique opportunity to monitor the impact of abrupt and prolonged removal of visitors on two popular zoo

33   species. Data were collected at four facilities (n=3 slender-tailed

34   meerkats, n=1 African penguin) during COVID-19 zoo closures and

35   up to one month following reopening to the public. Meerkats

36   showed increased positive social interactions, increased alert

37   behaviours, and reduced environmental interactions in the first

38   month post-opening, as compared to closure periods. They also

39   used more of their enclosures during periods of closure and spent

40   longer than would be expected in zones furthest from visitor

41   viewing areas when facilities reopened. African penguins showed no

42   behavioural change between open and closure periods. Enclosure

43   usage during both observation periods was relatively even and no

44   differences were observed in enclosure use between open and

45   closure periods. These results will enable an advanced

46   understanding of the impact that people have on the behaviour of

47   zoo animals, which has ramifications for animals used in close

48   encounters and other 'visitor experiences' in the future.

49   Understanding relationships between animals and people is

50   applicable in all managed animal settings. The results from this

51   study are of practical use in managing visitor access to animals

52   moving forwards, including enclosure location and design, to ensure

53   a positive visitor experience that does not negatively impact animal

54   behaviour.

55

56   Key words: penguins, meerkats, COVID-19, zoo, behaviour, welfare

57

1. Introduction

Worldwide closure of zoos and aquariums during the COVID-19 pandemic led to an abrupt cessation in visitor interactions for a range of animal species. Visitors are a prominent and constant feature in a zoo animals' environment with more than 700 million people visiting zoos and aquariums worldwide on an annual basis (WAZA, 2020). The animal-visitor relationship can be enriching and stimulating (Sherwen & Hemsworth, 2019). However, existing research provides limited 'visitor free' opportunities, and none of these are within 'normal' zoo opening hours. COVID-19 closures provided a unique opportunity to monitor the impact of abrupt (and prolonged) removal of visitors, and thus enhance our understanding of 'visitor effects' in this true presence/absence study.

Animal responses to visitors under normal zoo-opening hours are varied (Sherwen & Hemsworth, 2019), and even within species, individuals can respond differently (Davey, 2007). Since zoo closures were implemented, anecdotal zoo reports have also indicated mixed behavioural responses in a number of species. Some animals have been 'hiding' from staff due to a lack of people around their enclosures (Steger, 2020), some have been exploring their enclosures more (Gandhiok, 2020) and others have been calling to keepers to attract attention (Mack, 2020). Meerkats (*Suricata suricatta*) at Wellington Zoo were 'keenly aware of the absence of visitors' (Roy, 2020) and at Adelaide Zoo keepers employed novel forms of enrichment outside of the meerkat enclosure after they

84   noticed their meerkats were less active than normal (Eckert, 2020).

85   Meanwhile, Singapore State zoo took their African penguins

86   (*Spheniscus demersus*) on tours around the zoo in a bid to

87   counteract the lack of stimulation from the loss of zoo visitors

88   (Fahey, 2020).

89

90   Slender-tailed meerkats and African penguins are common across

91   zoological facilities (Sherwen et al., 2014; Saiyed et al., 2019) and

92   frequently have high levels of interaction with members of the

93   public. Worldwide there are 493 institutions housing meerkats and

94   297 housing African penguins registered on the ZIMS database, 323

95   and 162 of which are European facilities (Species 360, 2020). Not

96   only are these species popular in terms of presence in zoos, they are

97   also considered to be species that visitors are keen to see and are

98   often used as ambassador species. In a study at Durrell Wildlife Park,

99   57/444 surveyed zoo visitors voted meerkats as one of their

100   favourite animals at the zoo, coming fourth behind western lowland

101   gorillas (*Gorilla gorilla gorilla*), Sumatran orangutans (*Pongo abelii*)

102   and oriental short-clawed otters (*Aonyx cinereus*) (Carr, 2016).

103   Ambassador animals in zoos are those involved in personal

104   experience or encounter programmes (Whitehouse-Tedd et al.,

105   2018). Typically, they involve animals coming into close contact with

106   the public either within their habitat or when brought into the

107   public's space (Powell et al., 2020) and usually involve animals with

108   which the public engage well. Personal experience/encounter

109   programmes are becoming increasingly common in zoological

110 facilities (Ward & Sherwen, 2019), and many facilities that house

111 meerkats and penguins run 'animal encounters' with these species.

112

113 Previous reports suggest that behavioural responses of meerkats

114 and penguins to human-animal interactions during normal zoo

115 opening hours are variable. Sherwen et al. (2014) found meerkats at

116 three separate facilities to be 'behaviourally unresponsive' to

117 changes in visitor behaviour, with no changes in behaviour or

118 enclosure use observed. Others have reported increased faecal

119 glucocorticoid metabolites in relation to increased visitors (Scott et

120 al., 2017). When little penguins (*Eudyptula minor*) had their exhibit

121 closed to the public on five randomised study days they displayed

122 reduced aggressive social interactions and huddling behaviours and

123 spent time closer to the visitor viewing area, which were presumed

124 to be indicative of fear-responses to visitor presence during opening

125 hours (Sherwen et al., 2015). Other research has shown more

126 positive responses to humans. African penguins habituate to human

127 presence after prolonged exposure (Ozella, 2015). Furthermore,

128 controlling visitor behaviour and/or enabling penguins to have

129 control over the interaction led to positive behavioural change in

130 little penguins and African penguins. When visitors were 2m from

131 the penguin enclosure and they were unable to make loud noises or

132 threatening displays, fewer penguins were vigilant, huddling or

133 retreating and more penguins were close to the visitor viewing area

134 (Chiew et al., 2019). In programmes where African penguins have

135 control over their interactions with visitors, positive behavioural

136   indicators of welfare are observed, with penguins spending longer

137   interacting with the public than conspecifics (Saiyed et al., 2019).

138   The novelty of visitors and diversity in their behaviour may also

139   cause animals to seek out interactions (Hosey, 2005; Bloomfield et

140   al., 2015).

141

142   Whilst behavioural responses to zoo visitors differ or may be

143   dependent on the density of zoo visitors, animals may habituate to

144   human visitors (Sherwen & Hemsworth, 2019). However, the

145   prolonged absence of zoo visitors may lead to animals habituating

146   to a lack of visitors and a quieter environment. Interactions with zoo

147   visitors can be a source of enrichment or behavioural stimulation for

148   species and there are anecdotal reports which suggest that zoo

149   species engage in attention-seeking behaviours during zoo opening

150   hours (Sherwen & Hemsworth, 2019). There are no published

151   reports of either meerkats or penguins actively seeking interactions

152   with human visitors, but their high frequency of interactions with

153   visitors during 'animal encounters' makes them an excellent study

154   species for determining whether the COVID-19 zoo closures and the

155   consequential removal and reinstatement of visitors have impacted

156   on their behaviour. Whilst zoo staff have anecdotally highlighted

157   temporal behavioural shifts in animals (Colwill, pers comm) and

158   reports in the media have suggested some animals were 'seeking

159   out' interactions with zoo keepers during closure periods (Williams

160   & Rendle, 2020); to date no research has been undertaken which

161   investigates the impacts of zoo closures in a systematic and

162   repeatable manner.

163

164   The aim of this research was to systematically analyse data collected

165   opportunistically by zoo staff during this unique period. This paper is

166   presented as a case study, focusing on behaviour of two species

167   which are traditionally used in public interactions and visitor

168   encounters. The objective of this paper was to document

169   behavioural changes in slender-tailed meerkats and African

170   penguins between enforced closure periods and the first month of

171   facilities reopening. We hypothesised that animals would show

172   increased interest in public and would seek positive human-animal

173   interactions. We also hypothesised that animals of these species

174   would spend longer periods of time than were expected by chance

175   in areas of their enclosure that were closest to the public once

176   facilities reopened.

177

178   2. Methods

179   2.1. Subjects and study sites

180   Subjects were slender-tailed meerkats (n = 3 study sites, UK) and

181   African penguins (n = 1 study site, South Africa). The level of public

182   interaction pre COVID-19 facility closures varied across study sites

183   and was only partially reinstated when facilities reopened (Table 1).

184   Descriptions of the enclosures and visitor viewing areas are provided

185   in Table 2.

2.2. Data collection

2.2.1. Behavioural observations

Zoo staff collected data whilst their facility was still closed to the public and during the first month after visitors were allowed back on site (June to August 2020). Once the sites were open, visitor numbers varied according to their local government restrictions, however all facilities had a significant decrease in visitor numbers compared to pre-COVID times. Behavioural observations were undertaken 1 to 4 times per day, according to staff availability (Table 1). Each observation period lasted five minutes. Number of observations per site in open and closed conditions were: Site A - 86 closed, 83 open; Site B - 12 closed, 57 open; Site C - 6 closed, 12 open; Site D - 29 closed, 50 open.

Time of behavioural observations varied between facilities, but observations were split relatively evenly throughout the working day to ensure that observations covered periods of time when facilities were open to visitors (sites A, B and C: pre 11:00, 11:00 – 13:00, 13:00 – 17:00, site D: 06:00 – 09:00, 09:00 – 12:00, 12:00 – 15:00, 15:00 – 16:00) and were kept consistent within facilities. Observations were not taken during periods when keepers were interacting directly with the animals (e.g. for training or feeding). All observers were experienced with the study subjects and had extensive experience of behavioural observations as part of routine animal management protocols.

212   Table 1. Details of study sites, periods of data collection and

213   interactions with the public* at each facility

Study site	Species (number of individuals)	Period of data collection	Date of reopening	Frequency of observations	Number of observation days		Public interactions pre-facility closure	Public interactions post facility closure
					Closed	Open		
A	Meerkats (n=2, 1M 1 F)	June – August 2020	Mid July 2020	3 per day	29	28	No encounters	No encounters
B	Meerkats (n=7, 4M 3F)	June – July 2020	Mid-June 2020	2 – 4 per day	24	4	Public talks and encounters	Encounters commenced but no public talks
C	Meerkats (n=10, 10 M)	June – July 2020	Mid-June 2020	1 – 2 per day	8	5	Public talks and encounters	Encounters commenced but no public talks
D	African Penguins (n=58, 24M 34F)	August – September 2020	Late-August 2020	1 – 3 per day	19	12	Public talks No encounters	No public talks or encounters

214   *Public talks are sessions where zoo personnel (education staff

215   and/or keepers) interact with visitors at designated times and

216   locations to deliver relevant conservation education messages about

217   specific species or topics. Encounters are an opportunity for visitors

218   to pay for an exclusive experience whereby they safely meet, feed

219   and/or clean particular animals within the zoo's collection.

220

221   Table 2. Details of enclosures at the four study sites

Site	Enclosure size (approx.)	Description of enclosure boundary	Visitor viewing area (approx.)
A	25m^2	Wooden with glass window viewing areas	Two 2m glass viewing windows within the wooden boundary
B	258m^2	Wooden half rounds with 2ft of gravel and an electric fence on	32m of the 70m perimeter accessible to public

		the meerkat side, with two glass viewing areas	
C	176m^2	Stone wall with intermittent glass viewing panels. Wood and brick indoor/house with viewing window	Three 2m glass viewing windows within the stone boundary, one 1.5m viewing window within the indoor/house
D	83m^2 land, 155m^3 water	Stone wall around the land section, blue walls with glass viewing areas next to water areas.	21m of the 45m perimeter is around the water area. 10m of glass viewing windows including an underwater viewing window.

222

223   At each 5-minute sampling period, behaviours being performed by

224   the animals were recorded using instantaneous scan sampling with

225   a one-minute inter-scan interval. Due to the number of individuals

226   within the study groups the whole group was treated as one sample

227   point. All behaviours being performed by individuals within the

228   group were recorded which enabled identification of presence or

229   absence of behaviours within the study group, at each behavioural

230   scan. A sum total of frequency of behaviours at each five-minute

231   scan was then used to create a single observation period for

232   statistical analysis. Behaviours were recorded according to a pre-

233   defined ethogram (Table 3).

234

235   Table 3. Ethogram of behaviours for meerkats and penguins

236   recorded during the study period (adapted from Sherwen et al.,

237   2014 and Sherwen et al., 2015)

Behaviour	Description
Vigilant	Alert - showing a heightened awareness of their environment (including looking at visitors)
Human-animal interaction (positive)	Moving towards or seeking interaction from humans

Human-animal interaction (negative)	Avoiding, moving away from or showing fear of humans
Foraging/feeding	Locating and consuming foodstuffs
Comfort	Any self-maintenance or self-grooming behaviour
Social (positive)	Engaging in positive social behaviours (e.g. social play, grooming)
Social (negative)	Engaging in negative social behaviour (e.g. fighting, displaying)
Locomotion	Moving around the enclosure (on land or in water) in a non-repetitive pattern
Interaction with the environment	Investigating or interacting with things in the environment (other than food). For meerkats this also included digging behaviour.
Resting/sleeping	Sitting or lying motionless with eyes closed. No other behaviour is being performed.
Abnormal repetitive behaviour (ARBs)	Repetitive behaviour with no obvious function or purpose
Vocalising[P]	Production of a sound
Preening[P]	Using beak to peck, stroke, or comb feathers in any region of the body
Other	Any other behaviour not detailed in the ethogram
Out of sight	Animal out of sight of observer

238   [P] Behaviour only recorded for penguins

239

240   2.2.2.   Enclosure usage

241   Meerkat enclosures were split into approximately three equal zones

242   (closest third to visitors, middle third, third furthest away from

243   visitors). Penguin enclosure usage was split into six zones: three on

244   land (area 1: 49m^2, area 2: 24m^2, area 3: 10m^2) and three in the

245   water (62m^3, 35m^3, 58m^3). Locations with animals in were recorded

246   at the start of each observation period. All areas of the enclosure in

247   which individuals were in were recorded.

248

2.3. Data analysis

Data was split into two periods for analysis: (i) during COVID-19 closures, no visitors and skeletal staff (hereafter 'closed'), (ii) the first month post-reopening, visitors present but under local government social distancing restrictions i.e. reduced numbers compared to 'normal' (hereafter 'open'). To account for variation in data collection periods, differences in site/local government restrictions, and potential numbers of visitors entering different facilities, all statistical analysis was done 'within zoo'. Results are compared across facilities to aid in interpretation of findings. Significance values were set at 0.05, unless corrected for pairwise comparisons. Changes in frequency of behaviour when closed versus when open were assessed using R Studio Version 3.6.1 (R Core Team, 2019) using a Mann-Whitney U Test.

For meerkats inferential statistics were performed on vigilance, positive human-animal interactions, feeding, comfort, positive and negative social interactions, locomotion, interaction with the environment, resting, abnormal repetitive behaviours (ARBs) and out of sight. Negative HAI's were not analysed due to low frequency of occurrence (n = 7 observations at Zoo B). For penguins, inferential statistics were performed on preening, resting, vocalising, positive social interactions and locomotion. Vigilance (n=5 observations) and HAI's (n=1 observation) were not analysed due to low occurrence. ARBs were not observed during either open or closed periods.

275   Statistical analyses related to enclosure usage were undertaken

276   using SPSS Version 26 (SPSS Inc., Chicago, IL). The spread of

277   participation index (Dickens, 1955; Plowman, 2003) was used to

278   evaluate enclosure zone usage using the formula: SPI = (S | fo - fe |)

279   / *2 (N - fe $_{min}$) whereby f_o is the observed frequency of scans in each

280   zone, f_e is the expected frequency for each zone and $f_{e\,min}$ the

281   expected frequency in the smallest zone. A value of 0 suggests equal

282   use of all zones, whereas a value of 1 suggests exclusive use of one

283   zone. Differences in SPI values between closed and open periods

284   were analysed using a paired samples t-test. To determine how

285   enclosure use differed (in terms of use of enclosure zones) during

286   the two data collection periods (open and closed) a chi-square test

287   of independence with Bonferroni-corrected post hoc tests

288   (corrected significance value of $p < 0.008$) was applied.

289

290   2.4. Ethics statement

291   All research protocols were approved by Nottingham Trent

292   University, School of Animal, Rural and Environmental Sciences

293   School Ethics Group (reference number ARE192042) and meets the

294   ARRIVE guidelines where necessary. Permission to conduct the study

295   was granted by the participating zoos prior to commencement of

296   data collection.

297

298   3.   Results

299   The frequency of observations during closed and open periods

300   ranged across facilities (Site A: 86 closed, 83 open; Site B: 12 closed,

301   57 open; Site C: 6 closed, 12 open; Site D: 29 closed, 50 open).

302   Changes were observed in behaviour and enclosure usage, although

303   this varied across facilities. An overview of all meerkat behaviour is

304   detailed in Figure 1 and penguin behaviour in Figure 2. A breakdown

305   of meerkat and penguin behaviour per week after facility reopening

306   are provided in Tables 4a and b. Statistically significant changes in

307   frequency of behaviours are reported as mean observations per

308   observation period ± standard deviation throughout. Each behaviour

309   could have been recorded a maximum of six times per observation

310   period.
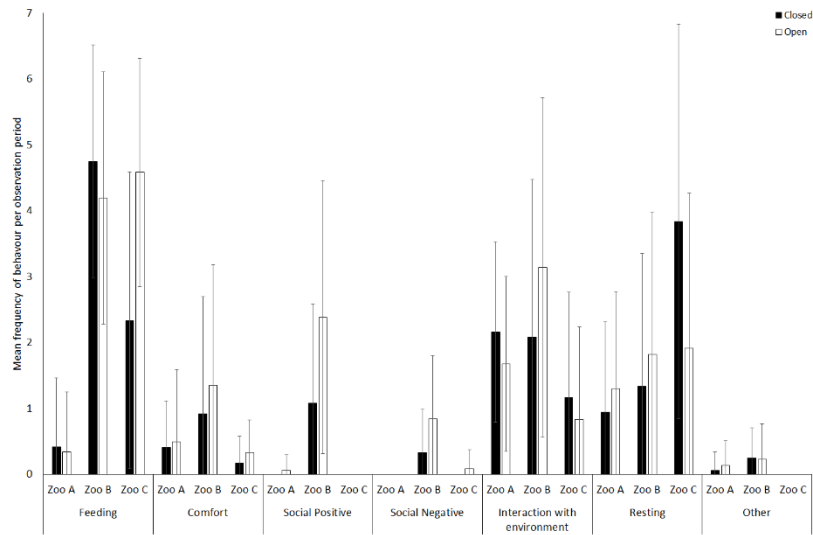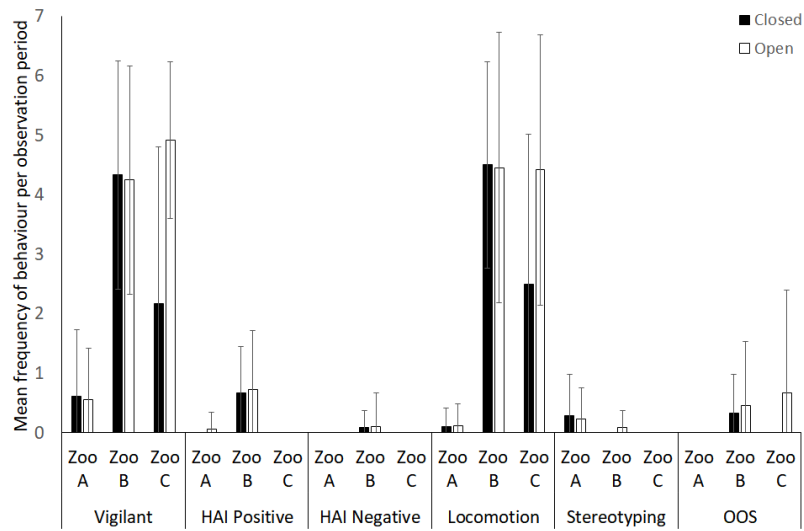
311

312

313

314

315

316

317

318

319

320

321

322 Figure 1a and b. An overview of slender-tailed meerkat behaviour

323 during facility closure and open periods. Mean values are based on

324 frequency of behaviour performed by the study group per five-

325 minute observation period (maximum frequency of observations

326 was six per five-minute period). Error bars represent standard
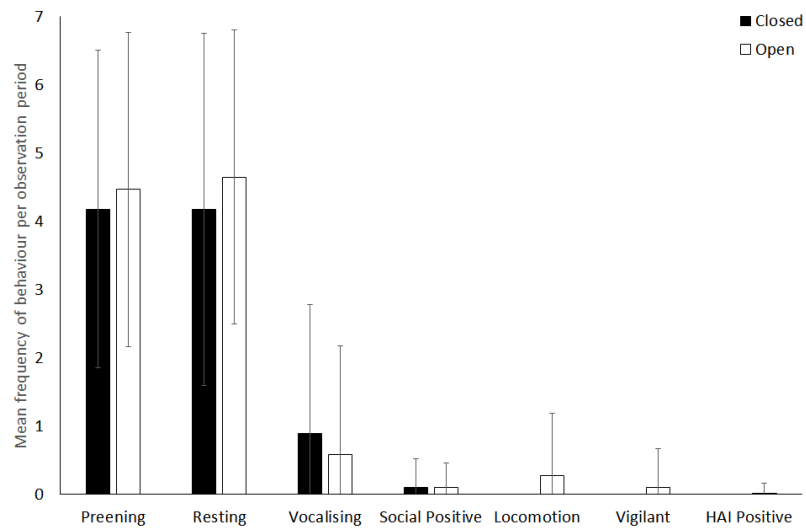
327 deviation.

328

329

330

331

332

333 Figure 2. An overview of African penguin behaviour during facility

334 closure and open periods. Mean values are based on frequency of

335 behaviour performed by for the study group per five-minute

336 observation period (maximum frequency of observations was six per

337 five-minute period). Error bars represent standard deviation.

338

339 Table 4a. Mean±SD frequency of behaviour performed by the study group per 5-minute observation (maximum 6 scans per behaviour) for meerkats at

340 Zoos A to C

Behaviour	Zoo and week since reopening															
	Zoo A						Zoo B						Zoo C			
	Closed	1	2	3	4	5	Closed	1	2	3	4	5	Closed	1	2	3
Vigilant	0.6±1.1	0.3±0.6	0.6±1	0.6±1	0.9±0.9	0.2±0.4	4.3±1.8	4±1.8	5.2±1.4	3.7±1.8	3.3±2.3	5.5±0.9	2.2±2.4	5.5±0.5	4±2	4.8±1.1
HAI positive	0	0	0	0	0.2±0.5	0	0.8±0.8	0.9±0.7	0.9±1.6	0.3±0.5	0.6±0.7	1.8±1.5	0	0	0	0
HAI negative	0	0	0	0	0	0	0.1±0.3	0.1±0.3	0	0	0	1±1.7	0	0	0	0
Feeding	0.4±1	0.1±0.3	0.1±0.5	0.1±0.3	1±1.5	0	4.8±1.7	4±2	4.9±1.4	5±1.2	3.3±1.9	3.5±2.2	2.3±2.1	5.3±0.8	2±1	5±1.4
Comfort	0.4±0.7	1.1±1.5	0.4±0.8	0.4±1.1	0.1±0.4	0.6±1.2	0.9±1.7	1.4±1.6	0.6±1.1	1.1±2.1	2.3±2.4	1.8±1.8	0.2±0.4	0	1±0	0.3±0.5
Positive social	0	0	0	0.1±0.2	0.1±0.3	0.1±0.3	1.1±1.4	1.9±1.7	2.4±1.8	1.9±2	3.1±2.2	4.5±2.6	0	0	0	0
Negative social	0	0	0	0	0	0	0.3±0.6	0.8±0.7	1.4±1.3	0.7±0.7	0.2±0.4	0.8±0.8	0	0.3±0.4	0	0
Locomotion	0.1±0.3	0	0.1±0.2	0.2±0.4	0.2±0.5	0	4.5±1.7	4.7±1.9	4.6±2.4	4.9±1.6	4.6±2	1.5±2.6	2.5±2.3	3.5±2.3	6±0	4.5±2.1
Interaction with the environment	2.2±1.4	1.9±1.3	1.6±1.2	1.3±1.2	1.4±1,1	2.5±1.6	2.1±2.3	2±2.2	4.6±2.4	3.9±2.2	3.6±2.4	2.3±2.5	1.2±1.5	2.3±1.5	0	0.2±0.4
Resting	0.9±1.4	1.3±1.2	1.6±1.6	1.9±1.5	0.4±0.8	1.5±1.7	1.3±1.9	1.8±2.4	1.1±1	1.4±2.1	3.1±2.1	2.5±1.7	3.8±2.7	1.5±2.6	5±1	1.2±1.2
Stereotyping	0.3±0.7	0.2±0.4	0.3±0.6	0.1±0.2	0.5±0.7	0.1±0.3	0	0.1±0.3	0.1±0.3	0	0	0	0	0	0	0
Other	0.1±0.3	0.1±0.3	0.1±0.3	0.2±0.5	0.1±0.3	0.1±0.3	0.3±0.4	0.3±0.6	0.1±0.5	0.3±0.7	0	0.3±0.4	0	0	0	0
OOS	0	0	0	0	0	0	0.3±0.6	0.3±0.7	0.7±1	0.6±0.9	0	1.5±2.6	0	0	0.5±0.5	1.2±2.2

Table 4b. Mean±SD frequency of behaviour performed by the study group per 5-minute observation (maximum 6 scans per behaviour) for African penguins at Zoo D

Behaviour	Weeks since reopening			
	Closed	1	2	3
Vigilant	0	0	0.2±0.9	0
HAI positive	0	0.1±0.2	0	0
Preening	4.2±2.3	4.1±2.6	4.6±2	5.1±1.9
Positive social	0.1±0.4	0	0.2±0.5	0
Locomotion	0	0.4±1.1	0.1±0.5	0.4±1.2
Resting	4.2±2.5	4.9±2.2	4.2±2.1	5.1±1.9
Vocalising	0.9±1.9	0.4±1.3	0.7±1.8	0.8±1.4

3.1. Behavioural change

3.1.1. Zoo A

Frequency of environmental interaction was higher during closed periods (2.2±1.4) than open periods (1.7±1.3) (W=4288.5, p=0.021).

Positive social interactions were higher when the facility was open (0.06±0.24), no positive social interactions were observed when closed (W=3354, p=0.022). Human-animal interactions (HAI) were also only performed when the zoo was open (0.06±0.29) (W=3397, p=0.04). No other significant behavioural changes were observed.

3.1.2. Zoo B

Positive social interactions were recorded more frequently when the facility was open (2.39±2.07) than closed (10.8±1.51) (W=214, p=0.039). No other significant behavioural changes were observed.

3.1.3. Zoo C

Meerkats displayed more vigilance behaviour when the zoo was open (4.92±1.31) than when it was closed (2.17±2.64) (W=14.5, p=0.043). No other significant behavioural changes were observed.

3.1.4. Zoo D

Penguins were only observed engaging in preening, resting, vocalising, locomotion and positive social behaviours. No behavioural differences were observed between observations undertaken when the site was closed or open (p>0.05).

3.2. Enclosure usage

On average, across all facilities, SPI values for enclosure usage were higher when facilities were closed (0.53+0.23) than when they were open (0.19±0.09) ($t_{(3)}$=-3.944, p=0.029) (Table 5).

Table 5. SPI values during open and closed periods at the study zoos

Facility	Spread of participation index	
	Open	Closed
A	0.09	0.50
B	0.20	0.57
C	0.31	0.79
D	0.15	0.24

3.2.1. Zoo A

Enclosure use differed for the meerkats at Zoo A between closed and open periods ($X_{(2)}$=30.166, p<0.001). All areas of the enclosure were used by meerkats during both observation periods. However, during closed periods, meerkats spent longer in the period closest to the public viewing area (Z=5.47, p<0.0001), and less time in the middle (Z=-4.27, p=0.00002) and furthest away zones (Z=-2.68, p=0.007362) than when the facility was open.

3.2.2. Zoo B

There was no difference from what would be expected by chance between enclosure use of meerkats at facility B when the site was closed or open (p>0.05). However, meerkats were only observed in zones furthest from the public when the zoo was open.

3.2.3. Zoo C

There was no difference from what would be expected by chance between enclosure use of meerkats at facility C when the site was closed or open (p>0.05). However, as with Zoo B, meerkats were only observed in zones furthest from the public during opening periods.

3.2.4. Zoo D

There was no difference from what would be expected by chance between enclosure use of penguins when Zoo D was closed or open

408 (p>0.05), and zone use remained relatively equal during both

409 observation periods.

410

411 ## 4. Discussion

412 The importance of understanding the impact of human-animal

413 interactions (HAIs) in animal welfare assessment has recently been

414 highlighted, and HAIs have been incorporated into the most recent

415 Five Domains model (Mellor et al., 2020). Yet traditional research

416 into the impact of zoo visitors on animal behaviour (Hosey, 2000;

417 Davey, 2007; Sherwen & Hemsworth, 2019) does not usually

418 encompass extended periods of time with 'no visitors'. This research

419 sought to investigate how enforced and extended facility closures

420 during the COVID-19 global pandemic affected behaviour and

421 enclosure usage of two popular zoo species; slender-tailed meerkats

422 and African penguins.

423

424 Anecdotal reports had described meerkats and penguins as being

425 among the species which were 'missing' zoo visitors (Roy, 2020;

426 Fahey, 2020) and these species are commonly used in animal

427 encounters. We thus anticipated that there would be high levels of

428 interaction seeking behaviour when zoo visitors returned to zoos.

429 Our results showed changes in behaviours performed and enclosure

430 usage. However behavioural responses were variable across species

431 and across collections and our findings were not as clear cut as we

432 had predicted.

433

4.1. Meerkat behaviour and enclosure usage

Meerkats reduced environmental interaction post opening and increased vigilance, positive social interactions and positive HAIs when facilities were open. Previous researchers have suggested that if visitors are having a positive effect on zoo animals then increases may be seen in affiliative behaviours or increased time spent near visitor viewing areas (Yeates and Main, 2008). If visitors are deemed more negative by the animals then avoidance of visitor behaviours may be performed, with individuals spending larger periods of observations out of sight or further from public viewing areas (Hosey et al., 2009). Scott (2014) reported reduced vigilance in meerkats when higher numbers of visitors were present at the enclosure, alongside increased faecal glucocorticoid metabolites.

Enclosure use was significantly reduced when facilities reopened to the public, and meerkats showed increased use of zones furthest from the public. The reasons for this are unclear but principally we propose three potential theories for this behavioural change: (i) meerkat behaviour during closures was being impacted by the range of enrichment techniques employed by facilities during closures, e.g. scattering of food, to minimise the impacts of reduced visitor presence and prevent boredom (ii) meerkats increased the use of the zones closest to the public during facility closures as they were 'looking for' humans as was anecdotally reported by a number of facilities, (iii) the return of visitors has made meerkats retreat to the rear of their enclosures as they are showing some level of fear of

460   visitors. Meerkat association networks can be affected by the size

461   and complexity of the enclosure (Pacheco Pacheco, 2017) and thus it

462   may be that individual enclosure usage is affected by social

463   relationships and proximity to conspecifics within the group. In

464   order to control for the impact of size and complexity of enclosures,

465   in addition to differences in visitor regulations, enclosure use has

466   been compared within facility for consistency.

467

468   Meerkats engage in sentinel behaviour as a form of coordinated

469   vigilance (Rauber & Manser, 2017). Whilst increases in vigilance

470   behaviour were observed there was not a significant increase in

471   period of time spent out of sight of observers. Vigilance behaviour

472   could be indicative of natural curiosity in meerkats. Given the long

473   period of absence of zoo visitors, their presence at enclosures may

474   have been stimulating and interesting (Sherwen & Hemsworth,

475   2019). The presence of indicators of positive welfare within the

476   group, including positive social interactions and engaging in positive

477   human-animal interactions, suggest the return of visitors was a

478   positive and engaging experience for the meerkats.

479

480   4.2. Penguin behaviour and enclosure usage

481   Penguins did not exhibit any significant behavioural changes, nor

482   was there any difference in their enclosure use or periods of time

483   spent out of sight between open and closed periods. Published

484   reports of penguin responses to visitors are highly variable, which

485   could be due to species differences or enclosure designs. The

486   majority of HAI in penguins is focused on investigating variation in

487   visitor number and behaviour, rather than looking at prolonged

488   periods of absence. Collins et al (2016) noted increased behavioural

489   diversity, including increased pool use, in a group of gentoo

490   penguins (*Pygoscelis papua*), in response to increased visitor

491   presence. Whilst in little penguins, covering a visitor window led to

492   behavioural changes indicative of improved welfare (e.g. reduced

493   vigilance, increased preening) and increased time spent in front of

494   the visitor viewing area (Chiew et al., 2020).

495

496   Visitor numbers were not reported for this study as facilities were

497   undergoing phased reopenings at the time of data collection; the

498   number of visitors on site and individuals at enclosures at any one

499   time were limited due to COVID-19 safety requirements (Rendle,

500   pers comm). Public access at facilities may have been variable due

501   to social distancing guidelines. While private encounters had

502   commenced for meerkats, the penguins studied did not engage in

503   private encounters, either before or after the closure periods.

504   Furthermore, the enclosure had not fully reopened to the public and

505   so the presence of members of the public near their enclosure may

506   not have been so apparent to them. Research into little penguins

507   has found Increasing the distance of zoo visitors from the enclosure

508   leads to reduced fear responses (Chiew et al., 2019).

4.3. Implications for animals, study limitations and areas for further research

The absence of behavioural indicators of negative affective state and in some instances absence of behavioural change, suggests that whilst animals changed how they used their enclosures and behavioural repertoire when visitors returned to facilities, the return of visitors was not necessarily negative for the species studied.

Public talks had not commenced at the study facilities and private encounters were only undertaken at two facilities. The absence of public talks and necessity for social distancing are likely to have led to a reduction in large groups of visitors at any one point in time, which could mitigate the negative effects of large groups of zoo visitors, which have been previously reported in the HAI literature (Davey, 2007). This theory is supported by the absence of behavioural change in the African penguins, whose enclosure was not fully open to the public, and who did not have any private encounters. However, in order to capture general behaviour and minimise potential bias from keeper interactions during feeding times, observations were not taken during feeding times, when there is the potential for slightly larger visitor groups to be at enclosures. The results reported here should be investigated further, to increase our understanding of 'the visitor effect' and to ascertain the impact of visitors (and number of visitors at enclosures) on animal behaviour and welfare throughout the day.

535

536   Collection of data a minimum of two months after facility closures

537   enabled the opportunity to understand impacts of visitor removal,

538   beyond immediate responses to the novel, quieter environments

539   that zoo animals were presented with immediately after site

540   closure. Analysis of animal behaviour immediately post reopening

541   was designed to capture initial reactions to the return of zoo

542   visitors, which may have been viewed by animals as a novel

543   environment. Unfortunately, due to the absence of data from pre-

544   facility closures it is not possible to state whether behaviours

545   changed during facility closures and indeed whether behaviour post-

546   opening replicates pre-closure behaviour. Future research should

547   seek to continue to monitor long-term changes in animal behaviour

548   in order to understand how animals habituate to human visitors

549   within zoological facilities, and to determine if there is an optimum

550   number of visitors for these popular species. If meerkats do not

551   return to 'during closure' enclosure usage then thoughts should be

552   given to enclosure design/visitor access to ensure animals continue

553   to use their enclosures widely, despite the presence of zoo visitors.

554   Work should also seek to understand whether other species, who

555   may have had differing levels of relationships with visitors pre-

556   closure periods, displayed more variable responses, as was

557   anecdotally reported by media outlets. Finally, due to group size and

558   difficulty in identifying individuals, study populations were treated

559   as a 'study group'. Future research should seek to investigate

560   whether individual differences are observed where possible, in

561   recognition of the impact of individual differences on animal

562   experiences within a zoo (Watters & Powell, 2012).

563

564   Due to the nature of this project and the need to quantify

565   behavioural responses of animals in an unprecedented situation,

566   observations had to be undertaken opportunistically. Facilities were

567   operating on minimal staffing due to being closed to visitors and this

568   meant that observations could not always be conducted multiple

569   times per day, and more importantly that different members of staff

570   were sometimes needed to undertake the observations. Inter-rater

571   reliability assessments could not be undertaken due to staffing

572   restrictions. Whilst there is the potential for observer discrepancy,

573   all observers were very experienced with the species they were

574   observing and were experienced in behavioural observations, which

575   they undertake as part of routine welfare assessments (BIAZA,

576   2021).

577

578   It is important to note that the methods employed were designed to

579   provide a snapshot assessment of behaviour and thus do not

580   represent 'full' activity budgets of the observed animals. Validation

581   of the accuracy of the sampling method would be required in order

582   to determine the representation of full daytime activity. However,

583   consistency of the observations and analysis 'within facility' enables

584   an opportunity to investigate accurately behavioural change within

585   these study populations, to determine impacts on group behaviour

586   of facilities closing for a prolonged period of time and reopening.

587

588 The limitations described here are inherent in zoo research and

589 where possible and appropriate, measures were put in place to

590 minimise the effect of them (e.g. conducting 'within zoo' analysis).

591 However, they must be borne in mind in interpretation of the

592 results. This study sought to use two popular zoo species as a case

593 study to explore the behavioural response of animals that had been

594 anecdotally reported to be 'missing' zoo visitors during the COVID-

595 19 global pandemic, when zoo visitors returned. Research such as

596 this is paramount in aiding evidence-based management of animals,

597 which ensures optimum welfare. Whilst this work is a case study

598 over a short period of time, it contributes significantly towards our

599 understanding of the impacts of zoo visitors (or absence of zoo

600 visitors) on animal behaviour. Further work should seek to build on

601 this research, over prolonged periods of time, and in a range of

602 species.

603

604 Conclusions

605 Meerkats and penguins are commonly used in animal encounters

606 and they are a popular species within zoos. The animal-visitor

607 relationship is complex and difficult to quantify, and research

608 typically does not incorporate observations during periods of time

609 when there are 'no visitors'. The aim of this research was to

610 document behavioural change in slender-tailed meerkats and

611 African penguins, when zoo visitors were absent during COVID-19

612 facility closures, and facility reopenings. The absence of changes in

613 behaviour or enclosure use for the penguins suggests that neither

614 lack of visitors during lockdown nor return of visitors post facility

615 closures had a negative effect. Meerkats increased the period of

616 time they spent in zones furthest from zoo visitors but there was not

617 a corresponding significant increase in out of sight behaviour.

618 Conversely, they also engaged in behaviours indicative of positive

619 valence; increased social interactions and positive HAIs. Due to the

620 mixed behavioural responses it is not possible to identify in this

621 instance whether visitor presence was 'stressful' or 'enriching' for

622 the meerkats after a long period of absence from visitors or whether

623 meerkats were showing naturally inquisitive behaviour on the return

624 of zoo visitors. It is advocated that this research is conducted over a

625 longer period of time, to begin to answer the fundamental question

626 of how animals habituate to zoo visitors. Whilst this work is only a

627 pilot study, it highlights the need to further understand the 'true'

628 nature of the potential effects of zoo visitors on animal behaviour.

629 Research such as this is extremely important in evidence-based

630 approaches to the management of zoo animals moving forwards,

631 including consideration of enclosure location and design, to ensure

632 positive visitor experiences which do not negatively impact on

633 animal behaviour and welfare.

634

646   Conflict of interest

647   The authors declare no conflict of interest.

648

649   References

650   BIAZA. 2021. BIAZA Welfare Toolkit.

651   https://biaza.org.uk/projects/detail/biaza-welfare-toolkit-2

652   (Accessed 10.01.2021)

653   Bloomfield, R.C., Gillespie, G., Kerswell, K.J., Butler, K., Hemsworth,

654   P.H. 2015. Effect of partial covering of the visitor viewing area

655   window on positioning and orientation of zoo orangutans: a

656   preference test. Zoo Biol. 34, 223 - 229

657   Carr, N. 2016. An analysis of zoo visitors' favourite and least

658   favourite animals. Tour. Manag. Perspect. 20, 70-76

659   Collins, C.K., Quirke, T., Overy, L., Flannery, K. O'Riordan, R.. 2016.

660   The effect of the zoo setting on the behavioural diversity of captive

661   gentoo penguins and the implications for their educational

662   potential. JZAR. 4, 85 - 90

663   Chiew, S.J., Butler, K.L., Sherwen, S.L., Coleman, G.J., Fanson, K.V.,

664   Hemsworth, P.H. 2019. Effects of regulating visitor viewing

665   proximity and the intensity of visitor behaviour on little penguin

666   (Eudyptula minor) behaviour and welfare. Animals. 9, 285

667   Chiew, S.J., Butler, K.L., Sherwen, S.L., Coleman, G.J., Melfi, V.,

668   Burns, A., Hemsworth, P.H. 2020. Effect of covering a visitor viewing

669   area window on the behaviour of zoo-housed little penguins

670   (Eudyptula minor). Animals. 10(7), 1224

671   Davey, G. 2007. Visitors' effects on the welfare of animals in the zoo:

672   A review. J. Appl. Anim. Welf. Sci. 10, 169-183

673   Dickens, M. 1995. A statistical formula to quantify the 'spread of

674   participation' in group discussion. Speech Monographs. 22, 28 - 31

675   Eckert, N. 2020. Animals notice something missing at the zoo -

676   people. The Wall Street Journal.

677   https://www.wsj.com/articles/animals-zoo-covid-closures-

678   lockdown-pandemic-los-angeles-phoenix-11596827024 (Accessed

679   24.10.2020)

680   Fahey, R. 2020. This is flipping fun! Penguins are given chance to

681   explore Singapore zoo after lack of human contact left them bored.

682   Mail Online. https://www.dailymail.co.uk/news/article-

683   8276909/Penguins-given-chance-explore-Singapore-zoo-lack-

684   human-contact-left-bored.html. (Accessed 24.10.2020)

685   Gandhiok, J. 2020. Call of the wild: quiet brings out animal instincts

686   at zoo. The times of India.

687   https://timesofindia.indiatimes.com/city/delhi/call-of-the-wild-

688   quiet-brings-out-animal-instincts-at-zoo/articleshow/75665638.cms

689   (Accessed 19.05.2020)

690 Hosey, G.R. 2000. Zoo animals and their human audiences: what is

691 the visitor effect? Anim. Welf. 9, 343-357

692 Hosey, G.R. 2005. How does the zoo environment affect the

693 behaviour of captive primates? Appl. Ani. Behav. Sci. 90, 107-129

694 Hosey, G., Pankhurst, S., Melfi, V.A. 2009. Zoo animals: behaviour,

695 management and welfare. Oxford University Press, UK

696 Mack, T. 2020. Animals at Twycross Zoo 'are missing visitors'.

697 Leicester Mercury. https://www.leicestermercury.co.uk/news/local-

698 news/animals-twycross-zoo-are-missing-4119435 (Accessed

699 19.05.2020)

700 Mellor, D.J., Neausoleil, N.J., Littlewood, K.E., McLean, A.N.,

701 McGreevy, P.D., Jones, B., Wilkins, C. 2020. The 2020 five domains

702 models: including human-animal interactions in assessment of

703 welfare. Animals. 10, 1870

704 Ozella, L., Favaro, L., Carnovale, I., Pessani, D. 2015. Pond use by

705 captive African penguins (Spheniscus demersus) in an immersive

706 exhibit adjacent to human bathers. J. Appl. Ani. Welf. Sci. 18(3), 303

707 - 309

708 Pacheco Pacheco, M.X. 2017. Social network structure and

709 personality in captive meerkat, *Suricata suricatta*, populations:

710 assessment, comparison between wild and captive meerkat

711 populations and captive management implications. PhD Thesis.

712 University of Exter.

713 Plowman, A. 2003. A note on modification of the spread of

714 participation index allowing for unequal zones. Appl. Ani. Behav. Sci.

715 83, 331-336

716   Powell, D.M., Kozlowski, C.P., Clark, J., Seyfried, A., Baskir, E.,

717   Franklin, A.D. 2020. Physical and physiological indicators of welfare

718   in guinea pigs (Cavia porcellus) serving as ambassador animals.

719   *Animals*. 10, 815

720   R Core Team. 2019. R: A language and environment for statistical

721   computing. R Foundation for Statistical Computing, Vienna, Austria.

722   https://www.R-project.org/.

723   Rauber, R., Manser, M.B. 2017. Discrete call types referring to

724   predation risk enhance the efficiency of the meerkat sentinel

725   system. Sci. Rep. 7, 44436

726   Roy, E.A. 2020. Animal tragic: New Zealand zoos strive to entertain

727   lonely inhabitants amid lockdown. The Guardian.

728   https://www.theguardian.com/world/2020/apr/02/new-zealand-

729   zoos-strive-to-entertain-lonely-inhabitants-amid-lockdown

730   (Accessed 24.10.2020)

731   Saiyed, S.T., Hopper, L.M., Cronin, K.A. 2019. Evaluating the

732   behaviour and temperament of African penguins in a non-contact

733   animal encounter program. Animals. 9, 326

734   Scott, K. 2014. Behaviour and Endocrinology of Meerkats in Zoos.

735   University of Exeter. PhD thesis.

736   Scott, K., Heistermann, M., Cant, M.A., Vitkainen, E.I.K. 2017. Group

737   size and visitor numbers predict faecal glucocorticoid concentrations

738   in zoo meerkats. R. Soc. Open Sci. 4, 161017

739   Sherwen, J., Hemsworth, P.H. 2019. The visitor effect on zoo

740   animals: implications and opportunities for zoo animal welfare.

741   Animals. 9(6), 366

742 Sherwen S,L., Magrath, M.J., Butler, K.L., Phillips, C.J.C., Hemsworth,

743 P.H. 2014. A multi-enclosure study investigating the behavioural

744 response of meerkats to zoo visitors. Appl. Ani. Behav. Sci. 156, 70-

745 77

746 Sherwen SL et al. 2015. Little penguins (Eudyptula minor) show

747 increased avoidance, aggression and vigilance in response to zoo

748 visitors. Applied Animal Behaviour Science. 168: 71 - 76

749 Steger I. 2020. A Japanese aquarium, under lockdown wants people

750 to video call its lonely eels. Quartz. Available at:

751 https://qz.com/1848528/japan-aquarium-asks-people-to-video-call-

752 eels-under-lockdown/ [Accessed on 19.05.2020]

753 Ward SJ & Hemsworth S. 2018. Zoo animals. In: Hosey G & Melfi V

754 (Eds), Anthrozoology: human animal interactions in domesticated

755 and wild animals. Oxford University Press, Oxford

756 Watters JV & Powell DM. 2012. Measuring animal personality for

757 use in population management in zoos: suggested methods and

758 rational. Zoo Biology. 31: 1 – 12

759 WAZA. 2020. World's leading zoos and aquariums. Available at:

760 https://www.waza.org/ [Accessed on 21.05.2020]

761 Whitehouse-Tedd, K.M., Spooner, S., Scott, L., Lozano-Martinez, J.

762 2018. Animal ambassador encounter programmes in zoos: current

763 status and future research needs. in: Berger,M., Corbett, S. (Eds) Zoo

764 Animals: Husbandry, Welfare and Public Interactions. Nova Science

765 Publishers.

766 Williams, E., Rendle, J. 2020. How captive animals are coping with

767 the sudden emptiness of the world's zoos and aquariums. The

768   Conversation. Available at: https://theconversation.com/how-

769   captive-animals-are-coping-with-the-sudden-emptiness-of-the-

770   worlds-zoos-and-aquariums-138668 [Accessed 24.10.2020]

771   Yeates, J., Main, D. 2008. Assessment of positive welfare: a review.

772   Vet. J. 175, 293-300

773   Zims. 2020. Species360 Zoological Information Management System

774   (ZIMS) (2020), www.zims.Species360.org.