The effect of visitor number on the behavior of zoo-housed macropods

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Abstract

Free-range exhibits are used by zoos to allow visitors to experience or interact with animals in a semi-natural setting; close interactions with animals have been shown to increase empathy and contribute to conservation outcomes, and as such zoos are increasingly implementing free-range style exhibits to facilitate this goal. We aimed to investigate whether this close proximity to zoo visitors impacted upon four species of macropod (red kangaroo *Macropus rufus*, red-necked wallaby *Macropus rufogriseus*, swamp wallaby *Wallabia bicolor* and quokka *Setonix brachyurus*) in a free-range exhibit in an Australian zoo. Specifically, we used instantaneous scan sampling to assess animal behavior, and examined whether visitor number affected the proportion of individuals that exhibited four target behaviors; visitor-directed vigilance, retreat, resting, and foraging behavior. We found that the proportion of individuals exhibiting visitor-directed vigilance significantly increased as pedestrian visitor number increased for three of the four species, and the proportion of individuals that were resting was significantly negatively related to visitor number for both wallaby species. The proportion of individuals of each species foraging or retreating was unrelated to visitor number. These data suggest that a visitor effect exists in a walk-through exhibit of macropods, and once visitor numbers go beyond a threshold, the behavior of more animals is impacted, likely compromising welfare. Interestingly, quokka do not appear to be affected by zoo visitors; which may be due to visitor pressure being perceived differently due to evolutionary differences, or that housing and husbandry ameliorate the visitor effect for this species but not others. Like many studies before, taking a species-specific approach to understanding zoo visitor-animal interactions has determined how the visitor effect likely impacts macropods differently.

Key words: Animal welfare, Macropod, Vigilance, Visitor effect, Zoo

Introduction

Zoos are increasingly focusing on positive and entertaining visitor interactions with animals in a naturalized setting to facilitate their conservation and education goals. Close interactions with animals in zoos are thought to promote empathy and lead to an increase in conservation-related behaviors (Clayton, Fraser, & Saunders, 2009). Walk-through exhibits, where visitors can view and/or interact with the animals with no physical or visual barriers, are one way in which zoos can facilitate human-animal interactions, without removing animals from their enclosure. These have existed since the 1920s (Olney, 1975), but the number of exhibits, and diversity of species presented have increased significantly in recent years (Hosey, 2005; Hosey, Melfi, & Pankhurst, 2013; Melfi, Bowkett, Plowman, & Pullen, 2005). Though interactions with free ranging animals have been shown to have positive effects on zoo visitors (Price, Ashmore, & McGivern, 1994), the effect on animals is less well studied (Melfi, et al., 2005). Determining how interactions with people affect the welfare of animals in zoos is fundamental to ensuring housing and husbandry standards are prioritizing the welfare of the animals in question.

Humans can be viewed by zoo animals as predators, inanimate objects, or heterospecific others (Hosey, 2008, 2013). Of these three ways, the perception of humans as predators is likely to lead to the highest level of stress, and therefore the possibility of reduced welfare. The behaviors expressed by animals that see humans as a predator include human directed aggression, hiding, high vigilance levels, alarm calls and flight or avoidance behavior, in which animals will maximize the distance between themselves and the perceived threat as much as possible (Hosey, 2013). The prolonged effects of constant visitor pressure may have lasting effects on those animals in captive environments.

There is a substantial amount of evidence that suggests that zoo animal behavior is affected by changes in visitor presence and density (Sherwen & Hemsworth, 2019). For example, decreased activity levels (Mallapur & Chellam, 2002); decreased visibility (Birke, 2002; Sellinger & Ha, 2005); and increased vigilance toward visitors (Mansour, Zakaria, & Fraser, 2000; Quadros, Goulart, Passos, Vecci, & Young, 2014) have been observed. It is unclear however, whether these behavioral changes ultimately result in reduced welfare (Hosey, 2013).

Macropods are a commonly chosen group of animals for free-range exhibits, particularly in Australia, however there has been little research to determine the effects of visitor activity and human-animal interactions on the behavior and welfare of macropods in captivity. One study on captive kangaroos suggested that natural history may play an important role in determining visitor effects, with increased visitor-directed vigilance in species with higher mammalian predation in the wild (Sherwen, Hemsworth, Butler, Fanson, & Magrath, 2015). Indeed, for wild macropods, increased risk of predation is generally coupled with increased vigilance behavior (Colagross & Cockburn, 1993; Edwards, Best, Blomberg, & Goldizen, 2013). Evolutionary history may therefore play a role in determining the level of vigilance behavior displayed, for example a comparative study of macropod species found a reduction in 'group-size effects' - a behavior where individuals devote less time to vigilance when in larger groups - in macropods that had been isolated on islands without mammalian predators (Blumstein & Daniel, 2005). Whether these effects hold for captive macropods, which likely have not experienced wild conditions, is of conservation importance. It has been suggested that preserving behaviors displayed in the wild, can have multiple positive ramifications, from supporting long-term reintroduction efforts, promoting cognitive function, and presenting a more meaningful educational display to the visiting public (Bryan, Bremner-Harrison, Price, & Wormell, 2017; McPhee & Carlstead, 2010).

The present study was designed to examine the effects of visitor number on the behavior of four macropod species (red kangaroo *Macropus rufus*; red-necked wallaby *Macropus rufogriseus;* swamp wallaby *Wallabia bicolor;* quokka *Setonix brachyurus*) housed together in a walk-through exhibit with two entry points for bidirectional flow of pedestrian traffic and a small section of overhead foot traffic from a high ropes course. We measured noise level, as a previous study has shown that visitor noise affected vigilance behavior in koalas (Larsen, Sherwen, & Rault, 2014). Four behaviors commonly recorded in studies of this type were included in the present study; visitor-directed vigilance (both on the ground and above), retreat behavior, resting behavior and foraging behavior. It was predicted that animals would perceive visitors as a potential threat, and thus vigilance, and retreat behavior would increase with increasing visitor numbers, and that resting and foraging behavior would decrease. In addition, it was predicted that differences in evolutionary history, particularly pertaining to predation risk, would affect the intensity of visitor-directed responses between species.

Methods

Study site and Subjects

Taronga Zoo (hereafter TZ) in Sydney, is a large urban zoo with a broad collection of native and exotic species. TZ attracts up to 1.4 million visitors per year (Taronga Conservation Society Australia, Annual Report 2015-16). This study took place in a mixed species walk-through exhibit of approximately 2600 m^2 (Figure 1). A high ropes obstacle course partially runs over a corner of the exhibit. A hay feeding station and a shelter is located directly under the rope course. Fresh grass and browse are placed throughout the exhibit daily, and pellets are placed in bowls or on the ground three times a day. The exhibit substrate is predominately mulch with patches of sand and scattered leaf litter. There are several trees, rocks, and a shallow

pond. Visitors enter and follow a path from one end of the exhibit to the other (in both directions), signs inform visitors that they must remain on the path and usually a uniformed volunteer is present to enforce this. The animals move freely throughout the enclosure and all animals have access to a retreat zone, which visitors are not allowed to enter and are unable to see into. The retreat zone has a sand substrate, a hay feeding station and two entry points.

The exhibit houses 20 macropods of four species: six red kangaroos (*Macropus rufus* 4 females, 1 male, 1 unknown sex); four red-necked wallabies (*Macropus rufogriseus*, 3 females, 1 male); seven swamp wallabies (*Wallabia bicolor*, 7 females); and three quokka (*Setonix brachyurus*, 3 females). Two emus (*Dromaius novaehollandiae*) and one cape barren goose (*Cereopsis novaehollandiae*) were also housed in the exhibit, but were not included in this study.

Data collection

This study was conducted from October – December 2015. Macropods were observed for a total of 18 days, including 10 week days when visitor activity was expected to be low and 8 weekend or holiday days when visitor activity was expected to be high. Data were collected via instantaneous scan samples (Martin & Bateson, 1993) every 15 minutes from 09:45-10:45, 11:30-12:45 and 14:00-14:45, a total of 15 scans per day. Each scan lasted for as long as it took to locate and record the behavior of the 20 individual macropods (never more than 15 minutes). During a scan, the species and behavior of each of the 20 animals was recorded during a single pass along the access path. Individuals of each species could not be individually identified.

Behaviors of interest for this study included; (1) vigilance, either directed at pedestrian visitors or at visitors on the wild ropes course (hereafter visitor-directed vigilance (ropes) and visitor-directed vigilance (pedestrian)), this was defined as animals having an erect posture with a

fixed gaze towards the visitor pathway or rope course (Sherwen, et al., 2015) (2) using the retreat zone or positioning themselves under rocks (quokka); hereafter retreat behavior, this included animals that were not visible, and assumed to be in the retreat zone or otherwise hidden from view, (3) resting which was defined as animals lying on their sides or backs with their heads down (Sherwen, et al., 2015), (4) foraging, defined as manipulation of food by paws or mouth, ingestion of food or water or sharing food with conspecific. For each scan sample the proportion of individual animals displaying each behavior was calculated for each species separately.

The number of pedestrian visitors inside the exhibit was counted at the beginning of each 15-minute sample period. The number of visitors using the high rope obstacle course, above the enclosure, varied largely during this period therefore the total number of visitors on the wild ropes during the whole 15-minute sample period was recorded using a clicker. Sound levels (dB) were measured using a hand held Digitech sound level meter (QM1591) at the beginning of each 15-minute sample period). These data were collected from the path directly under the rope course to best capture both types of visitor noise (if present).

Data management and statistical analysis

To examine which factors influenced the four behaviors of interest binomial candidate generalized linear models were constructed for each species separately. The proportion of individuals displaying the behavior of interest per scan was the response variable. Global models included the additive effects of: visitor number (pedestrian); visitor number (ropes); sound (dB); time (recorded as a factor); and date (to account for repeated measures; Bolker et al., 2009). Continuous explanatory variables were standardized following Gelman (2008). Backwards selection was used to obtain the minimum adequate model (Crawley, 2012), though

date was retained in all cases to account for repeated measurements on the same day (Bolker, et al., 2009). Models were fitted using the 'glm' function in the R package 'stats'. All models were checked for over dispersion and if necessary a quasibinomial model was fitted. Model residuals were visually inspected for normality of errors. It is important to note that during our study, on only two of 18 observation days did pedestrian visitor number at the beginning of a scan sample exceed 45 visitors, and models fitted including these two extreme days tended not to fulfil model assumptions, therefore the two days where visitor numbers exceeded 45 (for frequency histograms of these variables see Online Supplemental Figure 1) were excluded, and instead the observations on very high visitor pressure days are discussed anecdotally. All analyses were conducted in the 'stats' package within the R environment for statistical computing (R Core Team, 2017).

Ethical approval

This study was approved by Taronga Conservation Society Australia, took place under standard housing and husbandry conditions, and was conducted in accordance with the Exhibited Animals Protection Act 1986.

Results

Visitor-directed vigilance behavior

Minimum adequate models included visitor number (pedestrian) for all species except quokka (Red kangaroo: estimate = 1.37, deviance = 22.61, $p < 0.001$; Red-necked wallaby: estimate = 0.53, deviance = 8.46, $p = 0.008$; Swamp wallaby: estimate = 0.59, deviance = 27.42, $p < 0.001$; Table 1; Figure 2). Minimum adequate models included visitor number (ropes) for quokka only (estimate = -0.98, deviance = 5.03, $p = 0.018$; Table 1; Figure 2). Minimum adequate models did not include sound for any species. Minimum adequate models included time (as a factor)

for quokka, red kangaroos and red-necked wallabies (Quokka: deviance = 28.61, $p = 0.007$; Red kangaroo: deviance = 24.51, $p = 0.040$; Red-necked wallaby: deviance = 45.17, $p < 0.001$; Table 1; Figure 2).

Retreat behavior

Minimum adequate models did not include visitor number (pedestrian) or visitor number (ropes) for any species. Minimum adequate models included sound for red kangaroos (estimate = 0.41, deviance = 4.56, p = 0.033; Table 1). Minimum adequate models included time (as a factor) for red kangaroos, red-necked wallabies and swamp wallabies (Red kangaroo: deviance = 56.28, $p < 0.001$; Red-necked wallaby: deviance = 84.33, $p < 0.001$; Swamp wallaby: deviance = 107.89, $p < 0.001$; Table 1).

Resting behavior

Minimum adequate models included visitor number (pedestrian) for red-necked wallabies and swamp wallabies (Red-necked wallaby: estimate = -1.48, deviance = 18.04, $p < 0.001$; Swamp wallaby: estimate: -0.934, deviance = 21.07, $p < 0.001$; Table 1; Figure 3). Minimum adequate models did not include visitor number (ropes) for any species. Minimum adequate models included sound for swamp wallabies only (Swamp wallaby: estimate: -0.56, deviance = 10.35, $p = 0.003$; Table 1; Figure 3). Minimum adequate models included time (as a factor) for all species (Quokka: deviance = 83.97, p < 0.001; Red kangaroo: deviance = 135.16, $p < 0.001$; Red-necked wallaby: deviance = 35.56, $p < 0.001$; Swamp wallaby: deviance = 31.53, $p = 0.002$; Table 1; Figure 3).

Foraging behavior

Minimum adequate models did not include visitor number (pedestrian), visitor number (ropes) or sound for any species. Minimum adequate models included time (as a factor) for quokka (deviance = 74.36, $p < 0.001$; Table 1).

Discussion

Increasing pedestrian visitor number significantly affected the behavior of four different species of macropod housed in a walk-through exhibit. Of the four targeted behavioral measures (visitor-directed vigilance, retreat, resting and foraging behavior), increasing numbers of pedestrian visitors significantly increased visitor-directed vigilance in three of four species, and resting behavior was reduced as pedestrian visitor number increased in two of the four species. Pedestrian visitor number had no effect on either retreat or foraging behavior. As expected, effects were species-specific, highlighting the need for species-specific approaches to examine visitor effects.

Red kangaroos, red-necked wallabies and swamp wallabies showed significantly greater visitor-directed vigilance as visitor numbers increased. The response was very similar for the two wallaby species, but was less pronounced for red kangaroos. Though increased visitor-directed vigilance has been reported in a number of studies, it has been interpreted as neutral (Cooke & Schillaci, 2007; Sherwen, et al., 2015), negative (Birke, 2002; Carder & Semple, 2008; Mansour, et al., 2000), or in the case of some ungulate species, positive (Thompson, 1989), again underscoring the need for a species-specific approach to understanding welfare. It is important to note that during our study, on two of the observation days (at Chinese new year) pedestrian visitor number at the beginning of a scan sample reached approximately 140 visitors. At this time the proportion of individuals displaying visitor-directed vigilance approached 100% for kangaroos and both wallaby species, and 43% for quokka. Whereas when

approximately 40 visitors were present the proportion of animals displaying visitor-directed vigilance was 20% for kangaroos, 57% and 40% for red-necked and swamp wallabies respectively, and 12% for quokka. The ambiguity in how visitor-directed vigilance relates to animal welfare (Sherwen & Hemsworth, 2019), is reflected in widespread concern about how vigilance should be interpreted and whether it reflects fear or curiosity is unclear (Beauchamp, 2017). Visitor-directed vigilance may reflect fear or interest in the visitor (Hosey, 2013) and thus result in a negative or positive animal welfare outcome. Interpreting the animals' perception of the visitors is difficult, whilst considering the energetic demands of performing the behavior is not. In the current study individuals spending the majority of their time performing a single behavior, will likely experience negative welfare as a consequence of having limited time left within their activity budget to perform other essential behaviors such as foraging and resting (Bubier, 1996). Described by Dawkins (1988) as an inelastic demand which was associated with poor welfare, she later went on to suggest that zoo animal welfare could be improved by preventing situations which led to activity budgets being monopolized by these 'costly' behaviors (Dawkins, 1990). It is therefore worth considering whether a management decision such as restricting the total number of visitors entering the enclosure at one time could be implemented to mitigate the high level of visitor-directed vigilance behavior that we observed, and therefore any related welfare issues.

It is interesting to note that noise was rarely a significant factor in any of the models (Table 1). A previous study demonstrated that vigilance behavior in koalas was linked to visitor number and also to visitor noise (Larsen, et al., 2014), but this study was experimental and directly manipulated visitor noise. In our study we recorded ambient sound that may or may not have included noise from visitors. In order to examine in more detail what aspect of visitor presence animals are reacting to an experimental study would be extremely useful. Playback of visitor

sound could be used, ideally in conjunction with varying numbers of silent volunteers acting as visitors.

Our results seem to suggest the macropod species identify visitors as potential predators, since the observed responses here broadly fit with what would be expected based on predation pressure in the wild. Wallabies might be expected to exhibit the greatest level of visitor-directed vigilance as wallabies face higher predation pressure from dingoes and European foxes than kangaroos (Jarman & Coulson, 1989; Robertshaw & Harden, 1986, 1989; Shepherd, 1981), and these species were observed to have the highest visitor-directed vigilance behavior. Rottnest Island quokka have been isolated from predators for approximately 7000 years (Playford, 1983), and though research suggests that they have retained some apparent anti-predator behavior (Blumstein, Daniel, & McLean, 2001), it might be expected that this species exhibit the lowest visitor-directed vigilance behavior of the four species studied. Quokka were also the only species to exhibit a behavioral response to the number of visitors on a rope walkway passing over the exhibit. Quokka are likely to be the only one of the four species studied to have any avian predators (Blumstein, et al., 2001) which may explain this result. The association between behavioral response to visitors and evolutionary history could be considered to suggest that the increased vigilance directed at visitors reflects an anti-predator response indicative of fear and anxiety (Sherwen & Hemsworth, 2019), rather than an interest in visitors which could be considered positive.

Resting behavior was significantly lower as visitor number increased for the two wallaby species. It is important to note however, that resting behavior in red-necked and swamp wallabies was very low (<20% of individuals) even when there were no visitors present. By contrast on average >60% of quokka and red kangaroo individuals rested when no visitors were

present. It is difficult to interpret changes in resting behavior in terms of welfare *per se*, as these changes could be due to either fear or curiosity of the visitors themselves. Previous studies have interpreted the time needed for resting behavior to elastic behavior (Bubier, 1996), where time spent performing the behavior increases or decreases depending on whether energetic outcomes have been achieved by the performance of other inelastic behaviors. As the activity budgets generated in this study resulted from daytime observations, it is acknowledged that it is likely a large amount of time was spent resting outside of the study period. Consequently, time spent resting and changes in this, appear to be an artefact of the time spent in other inelastic behavior i.e. vigilance.

Avoidance behavior has been used as a measure of fear of humans, and linked to physiological indicators of stress in the livestock industry (Hemsworth & Coleman, 2010). Retreat behavior was not significantly related to visitor number for any species. It is possible that use of the retreat zone may be driven by other factors such as competition between species for a resource, but future work would be necessary to investigate this, for example data could be recorded outside of zoo opening hours to examine how retreat zones were used by the different species when no visitors were present, and/or further data documenting any aggressive interactions between the different species in relation to the retreat zone could be collected.

In our study sample there were varying numbers of each species (red kangaroo n = 6; red-necked wallaby n = 4, swamp wallaby n = 7, quokka n = 3). This in theory could affect the proportion of individuals displaying visitor-directed vigilance, as due to group size effects, fewer individuals would be expected to be vigilant when the group size is larger (Blumstein & Daniel, 2005; Blumstein, et al., 2001). However, given the similarity in response to visitors between the two wallaby species despite the difference in number of individuals, and the lowest

pedestrian visitor-directed vigilance response of quokka despite having the smallest group size, it seems likely that the observed response is due to species differences, rather than differences in group size. More research would be necessary to confirm whether there is indeed a collective vigilance effect, whereby individuals reduce their per capita risk by effectively sharing the role of sentinel. It is also possible that individuals of different species include heterospecifics in their estimates of group-size.

It is acknowledged that a better understanding of human-animal interactions in zoos is needed (Ward, Sherwen, & Clark, 2018), and factors which impact our understanding of these interactions have been identified (Cole & Fraser, 2018). However, a change of focus is needed which incorporates metrics which can more equivocally be allied with the evaluation of animal welfare, notably those which help inform us about animal emotion. Interpreting activity budgets has its limitations (Howell & Cheyne, 2019), despite its widespread use in zoo biology, not least because it is cost-effective and non-invasive. Working towards innovative methods of assessing zoo animal welfare (Whitham & Miller, 2016), and animal emotion in zoos is invaluable in determining if an animal is curious or fearful, both emotions share physiological processes. Initial studies of curiosity in zoo animals, has found individual and species differences (Hall, Melfi, Burns, McGill, & Doyle, 2018), suggesting that the impact of the zoo visitor effect is not simple.

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