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Is passive observation of habituated animals truly passive?

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Abstract The term "habituated" is sometimes used to imply that animals no longer respond to the presence of a human observer. There is an accumulating body of evidence, however, suggesting that habituated animals that no longer perceive humans as a direct threat nevertheless continue to respond to their presence in other ways. Data were collected from a troop of free-ranging vervet monkeys in the Klein Karoo of South Africa for months 5–12 of their habituation period to determine how self-directed behaviour (SDB) was affected by human presence across time. SDB decreased across the 8 month period, indicating that habituation was ongoing. The human observer's location in relation to the focal animal had a significant effect on SDB. Furthermore, when the habituation period was divided into an early and a late phase this pattern did not arise until the later habituation period (9–12 months). This evidence suggests that animals continue to respond to human presence as they become habituated, although the observed responses change.

Keywords Habituation - Self-directed behaviour - Vervet monkey · Passive observation · Human presence · Spatial location

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Introduction

The presence of humans is known to affect the behaviour of wild animals in a variety of ways (Jack et al. [2008](#page-4-0); Taylor and Knight [2008;](#page-4-0) Walker et al. [2006](#page-4-0); Webb and Blumstein [2005\)](#page-4-0) that can be classified into three response types: attraction, habituation, and avoidance (Whittaker and Knight [1998](#page-4-0)). Much scientific research on the behaviour of wild animals, particularly with primates, requires habituation of subjects before recording observational data (Williamson and Feistner [2003](#page-4-0)). Habituation is the reduction of a response to a repeated stimulus that is neither aversive nor beneficial (Bejder et al. [2009](#page-4-0); Thorpe [1963](#page-4-0); Whittaker and Knight [1998\)](#page-4-0) and it is implemented in observational studies such that natural behaviour may be recorded with minimum effect of the observer. However, behaviour can be affected in ways that are not directly related to the perception of a human observer as either a threat or an attractive stimulus.

Although it is convenient to assume that observers of habituated animals are no longer influencing their behaviour, this may not be a valid assumption. For example, the presence of humans has been documented to reduce predation on a group of vervet monkeys in Kenya (Isbell and Young [1993](#page-4-0)). This reduction in predation was attributed to different levels of habituation of vervets and their leopard predators (Isbell and Young [1993\)](#page-4-0). It is conceivable that avoidance of humans by unhabituated predators could result in reduction in vigilance/predator scanning behaviour in habituated animals over time owing to a decrease in predation risk because of human observers. Natural rates of vigilance and predation may, therefore, not be found for habituated animals. Although habituation may reduce or eliminate an animal's perception of a human as a threat, it may not be possible to completely eliminate any effect on

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their behaviour. Observers of habituated animals should thus take into account all of the ways in which they may affect the behaviour of their subjects, and consider whether their presence may be confounding their data in any way.

In this study, I assessed whether the extent of arousal experienced by vervet monkeys (Chlorocebus aethiops) was affected by the spatial location of the human observer (i.e. whether the observer was located to the front, back, left, or right of the focal animal) and whether any observed effect changed across time as a result of increasing habituation. I predicted that observer presence will continue to affect vervet monkey behaviour irrespective of the level of habituation, thereby demonstrating that truly "passive" observation may not exist (i.e., a human observer could not be regarded as a neutral stimulus).

Methods

Study site

The study site is situated in the semi-arid Klein Karoo of South Africa (32 \degree 22'S, 24 \degree 52'E) at an altitude of 846 m. With a mean annual rainfall of 330 mm, most of the surrounding area is uninhabitable by vervets apart from the woodland surrounding drainage-line riverbeds. These riverbeds only flow in times of heavy rain in their catchment area, but nonetheless contain fairly permanent pools of water throughout most of the year (McDougall et al. [2010](#page-4-0)). The woodland surrounding the Milk River, where the focal study troop resides, is dominated by acacia (Acacia karoo), Karee (Rhus lancea), and Peruvian pepper (Schinus molle), all of which are primary food sources.

Subjects

Data were collected from October 2008 to June 2009 for a single troop of free-ranging vervet monkeys. Individual identification of subjects was possible by use of a combination of characteristic facial features, coat colour, body size, tail posture/length, and scars/wounds to the face, ears, body and/or tail. Troop size was approximately 70 individuals. This included 22–24 adult and sub-adult females and 13–18 adult and sub-adult males. Thirteen infants were born between October and November 2008. Sub-adults were counted as those who participated in the 2009 breeding season but, in the case of females, did not yet have elongated nipples (indicative of nursing offspring), and in the case of males, were larger than adult females, but not yet adult size.

Eleven females in the troop were chosen as focal subjects. The entire troop received approximately 4 months of habituation time before the start of the study period, and data collection from each female began once they were easily followed within 10 m and no longer showed fearful responses to being followed (e.g., they did not run from the observer or attempt to hide in trees or shrubs). A minimum of 40 h of focal data were collected from each test female.

Data collection

The monkeys were followed on foot for 10 h per day. Daylight hours were divided into four equal time blocks and focal samples from each female were distributed evenly across the time blocks. Data were not collected from the same focal subject more than once per day in each time block. The length of each time block fluctuated between 2.5 and 3.5 h depending on the seasonal photoperiod. Focal samples were 20 min in length from October 2008 through to March 2009, and were 30 min in length after that. A focal sample was terminated if an individual went out of sight for more than 5 min.

Data were collected on a Palm TungstenTM E2 Handheld computer using Pendragon 5.1 (2005–2007) software. An instantaneous ''scan'' sample was collected when following of each focal animal was started and then every 2 min throughout. Scan samples included a record of the focal animal's activity (classified as resting, foraging, travelling, or interacting socially), the distance and location of the human observer in relation to the focal animal (scored as $\langle 2, 2-5, 5-10, \text{ or } >10 \text{ m} \rangle$, and the ID and location of every conspecific adult/sub-adult neighbour within a 5-m radius of the focal animal. This region of space was divided equally into four mutually exclusive areas (front, back, left, and right) in respect of the perspective of the focal animal. These spatial locations projected in a triangular fashion away from the focal individual such that they filled the five metre region of space around the monkey. Because the observer was unable to manoeuvre effectively throughout the vervets' three-dimensional habitat, only the twodimensional plane was examined in this investigation. Thus, data from when the focal animal was located directly above the observer were excluded from analysis.

Self-directed behaviour (SDB) was recorded continuously during following of focal animals according to the following categories:

- 1. Scratch—the fingertips of the hand or foot are repeatedly drawn across the fur/skin of the body.
- 2. Self-groom—examining various body parts or slowly brushing through the hair and picking at the skin with one or both hands.
- 3. Body/head shake—shaking of the head and neck, sometimes followed by shaking of the entire body.
- 4. Yawn—tilting the head back with gaping of the mouth.

A new SDB was recorded any time an individual switched to a new class of SDB or if there was a break of >5 s between bouts (for scratching and self-grooming). Each time a SDB was scored, the animal's activity, and the distance and location of the observer and all conspecific neighbours were recorded in the same fashion as for the instantaneous samples.

Analysis

Incidence of SDB was determined for 4 different observer locations (front, back, left, and right) within a 5-m radius of the focal animal. This was done by dividing the total number of SDB that occurred when only the human observer was located in each of the spatial locations (i.e., no conspecific neighbours within 5 m) by twice the number of scan samples recorded for the corresponding condition (for example, under condition x: $SDB_x/(scan samples_x \times 2)$.

The side condition (i.e. when the human observer was $<$ m to the left or right of the focal female) was divided into its corresponding left and right components and these were compared using the Wilcoxon signed-ranks test. Also, because incidence of SDB may differ between activities, it is important to ensure that the observer was in each spatial location for similar proportions of time during each activity. I thus compared the proportion of time the observer spent in each spatial location between activities using the Wilcoxon signed-ranks test. To keep the comparisons conservative and prevent pooling of potentially different data sets, no α -level correction (e.g., Bonferroni) was applied. The incidence of SDB for each spatial location (front, back, and side) were then compared using Friedman's repeated measures ANOVA. Post-hoc analyses for pairwise comparisons were performed using Wilcoxon signed-ranks tests with a Bonferroni correction applied to the p values.

Finally, an investigation into whether increasing habituation would result in a decreasing response to human presence was conducted. This analysis included temporal comparison of incidence of SDB across the 8-month datacollection period when only the human observer was within 5 m of the focal animal. Linear regression analysis was used to determine whether the incidence of SDB declined or remained stable during this time. Next, the study period was divided into 4-month periods and Friedman's ANOVA was used to test whether observer location had an effect on the incidence of SDB in both the first and second periods. The incidence of SDB in the first and second period was also compared for each observer location by use of the Wilcoxon signed-ranks test with a Bonferroni correction applied to the p values.

Results

The mean $(\pm$ SEM) incidence of SDB for each of the four observer locations is given in Table 1. Comparison of the

Table 1 Mean \pm SEM incidence of self-directed behaviour (SDB) for the 11 focal females when a human observer was located in each of the four locations

Mean incidence of SDB	SEM	
0.37	0.02	
0.24	0.02	
0.33	0.04	
0.31	0.02	

Incidence of SDB when the focal animal was ''travelling'' was not included in calculation of the mean

two components of the side condition (observer located on the left or right) indicated that the incidence of SDB did not differ between these two conditions (Wilcoxon signedranks test: $n = 11$, $z = 0.533$, $p = 0.594$), therefore these data were pooled into the ''side'' location for further analysis. The proportion of time spent by the observer in each location differed only in the ''traveling'' condition (Fig. [1\)](#page-3-0). Data from when the focal individual was travelling was thus excluded from subsequent analysis.

Observer location had a significant effect on the incidence of SDB (Friedman's ANOVA: $n = 11$, $\chi^2(2) =$ 8.909, $p = 0.012$). Post hoc pairwise comparisons indicated that the incidence of SDB was significantly lower when the observer was located behind the focal animal rather than to the front or side (behind vs. front: $n = 11$, $z = 2.667$, $p = 0.024$; behind vs. side: $z = 2.756$, $p =$ 0.018). The incidence of SDB did not differ when the observer was located to the front or side of the focal female (front vs. side: $n = 11$, $z = 1.245$, $p = 0.639$).

Linear regression analysis revealed that the incidence of SDB decreased across the duration of the study $(r^2 = 0.082, B = -0.012, \beta = -0.287, p = 0.007)$ $(r^2 = 0.082, B = -0.012, \beta = -0.287, p = 0.007)$ $(r^2 = 0.082, B = -0.012, \beta = -0.287, p = 0.007)$ (Fig. 2). The data-collection period was therefore divided into two 4-month periods for further analysis. The incidence of SDB for each observer location was not found to differ in the first 4-month period (Friedman's ANOVA: $n = 11$, $\chi^2(2) = 4.545$, $p = 0.103$), whereas observer location had a significant effect on incidence of SDB in the second 4 month period $(n = 11, \chi^2(2) = 13.818, p = 0.001)$. Post-hoc analysis showed, once again, that the ''observer behind'' condition differed from both the front and side conditions (behind vs. side: $n = 11$, $z = 2.934$, $p = 0.009$; behind vs. front: $n = 11$, $z = 2.845$, $p = 0.012$) whereas the last two conditions did not differ $(n = 11, z = 1.689, z = 1.689)$ $p = 0.273$). Incidence of SDB when the observer was located to the front or side of the focal animal did not differ between the first and second data-collection periods (front: $n = 11$, $z = 0.267$, $p = 1.00$; side: $n = 11$, $z = 1.334$, $p = 0.546$; however, the incidence of SDB when the observer was located behind the focal animal decreased 0.60

 0.50

 0.30

 0.20

 0.10

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SDB_{rate}

8 0.40

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Fig. 1 Mean \pm SEM incidence of self-directed behaviour (SDB) when the observer was located to the front, side, or back of the focal female $(n = 11)$ for each of the four different activities that the females engaged in. *Significantly differs $(p = 0.003)$ from the other three activities within the same observer location. **Significantly differs from resting ($p = 0.033$) and foraging ($p = 0.016$) within the same observer location, but not social ($p = 0.424$)

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Fig. 2 Open circles indicate the mean monthly incidence of selfdirected behaviour (SDB) for each of the 11 focal animals when only the observer was present within a 5-m radius. The solid line represents declining incidence of SDB across time (average monthly decrease of 0.01 SDB/min). Dotted lines indicate the 95% confidence interval

significantly in the second data-collection period ($n = 11$, $z = 2.756$, $p = 0.018$) (Fig. 3).

Discussion

Observer location had a significant effect on the incidence of vervet monkey SDB. Incidence of SDB was lower when the observer was located behind the focal animal, whereas the other locations did not differ. A decrease in the incidence of SDB was observed for the focal subjects during the study period, suggesting that habituation was ongoing. Furthermore, when the data-collection period was divided into early and late phases, the pattern of decreased SDB

Fig. 3 Comparison of incidence of self-directed behaviour (SDB) in the first and second habituation periods for each of the human observer's spatial locations. A non-significant declining trend in the incidence of SDB was observed for the front and side conditions. Significantly reduced incidence of SDB was observed for the back condition in the second data-collection period (corresponding to months 9–12 of habituation)

Observer position in relation to the focal animal

when the observer was located behind the focal animal was not evident until the later phase, suggesting that the pattern may be related to the vervets' changing perception of a human observer during the habituation period.

The overall incidence of SDB when only the observer was present within a 5-m radius of the focal animal decreased during the 8 months of data collection. Thus, although the 4 months of habituation before the start of data collection resulted in large-scale behavioural changes in the monkeys (e.g., no longer threatening, running from, or hiding from human observers), continued habituation was evident from small behavioural changes (i.e., SDB) for

at least a year, although at a slower rate of decline (SDB incidence decreased by only 0.01 per month in the 8 month data-collection period). Jack et al. (2008) also noted evidence of continued habituation, in the form of decreasing cortisol levels, of a group of capuchins in Costa Rica after the conclusion of an 18 month behavioural study. Thus, although large-scale behavioural changes may occur fairly quickly, less overtly noticeable indicators of habituation (e.g., cortisol, SDB) may decrease over a longer period than previously estimated (Williamson and Feistner 2003).

Dividing the study period into the early and late phases of habituation revealed an interesting effect: specifically, that differences in incidence of SDB associated with the observer's spatial location did not become evident until the late phase of habituation (i.e., months 9–12). This finding suggests that particular behavioural responses to human observers may only appear when animals are sufficiently habituated and no longer perceive humans as a potential predator or threat. At field sites involving long-term projects (up to 24 years), observer-directed behaviour such as threats, play solicitation, watching, and throwing objects at observers, has been observed for chimpanzees (Pan troglodytes) and capuchins (Cebus capucinus) (Jack et al. 2008; Nishida et al. 2009). Domestic livestock also respond to direct gaze from human observers by watching them more frequently, but no increase in fear-related behaviour is observed, demonstrating that although human observers do not represent a direct threat, altered behavioural patterns are still evident (Beausoleil et al. 2006). The term "habituation" may therefore be better suited to imply that animals will no longer perceive humans as a direct threat, rather than indicating that animals no longer respond to our presence (Knight 2009). This is an important distinction, because it may not be possible to completely ignore the presence of another animate being moving amongst a group. Indeed, Rasmussen (1991) found that the ranging patterns of stumptail macaques (Macaca arctoides) were still affected by human presence after 14 years of observation. Moreover, other non-threatening animate beings (e.g. other prey species occupying the same habitat) may not be neutral stimuli either. Other non-predator species, for example buffalo (Syncerus caffer) and kudu (Tragelaphus strepsiceros), regularly forage alongside the vervets in this region; however, whether the vervets also respond to these animals in a similar manner to the way they respond to human observers has yet to be determined.

In conclusion, in addition to intraspecific effects, behavioural studies may also need to account for interspecific effects on behavioural patterns. Furthermore, some human-induced behavioural responses may only appear

when individuals reach a specific level of habituation. Researchers should therefore be cautious about what they are implying when stating that their animals were habituated to human presence and consideration should be given to all of the ways that behaviour may be affected by observation in close proximity.

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