Effects of visitor numbers on captive European red squirrels (*Sciurus vulgaris*) and impacts on visitor experience

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[Running head: Visitor effects on red squirrel behavior]

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ABSTRACT

Visitors to zoological collections can have substantial effects on captive animals that vary according to species, enclosure design, visitor proximity and husbandry methods. One particularly intense form of visitor interaction occurs in immersive exhibits such as walk-through enclosures. Such enclosures are increasingly common but effects on animal behavior are currently understudied. Here, the behavior of captive European red squirrels (*Sciurus vulgaris*) is studied in relation to visitor numbers in a walk-through enclosure. We also quantify the correlation between squirrel encounters and visitor experience. Interaction with humans increased significantly as the number of visitors inside the enclosure increased. The number of children present significantly increased locomotion and decreased eating, possibly due to disturbance and squirrels moving away from busy areas. By contrast, the number of adults significantly increased eating and decreased inactivity due to squirrels approaching visitors. The positive reinforcement training used by the keepers (offering food rewards to the squirrels for coming to them to allow routine medical checks) meant that squirrels associated adults with food opportunities. Squirrel encounter rate (number of squirrels seen by each group of visitors) was significantly affected by the number of adults and visitor duration (positive relationships) and noise as perceived by visitors (negative relationship). Encounter rate was positively correlated with overall visitor experience. Our results indicate that visitors affect behavior but this effect is influenced by husbandry methods. It is vital that visitors, especially children, minimize noise and move slowly in the enclosure, both for the sake of the animals and their own experience.

Keywords: animal behavior, activity budget, visitor effects, walk-through enclosure, zoo animals

INTRODUCTION

With over 700 million people visiting zoos and aquaria worldwide annually (Gusset and Dick, 2011), public animal collections provide an important bridge between public knowledge and scientific research. Zoos have a vital role in science communication as information can be conveyed in many different ways, often through engaging and immersive exhibits. Previous research shows that the majority of visitors arrive with an educational agenda (Roe and McConney, 2015) and that teaching visitors about different species, and threats to those species, can profoundly affect conservation awareness, attitudes, and behavior (Jacobson, 2010).

However, although a large part of the remit of the modern zoo is education oriented, and most zoos rely on paying visitors for a large part of their income, the presence of visitors, especially in large numbers, can have a substantial effect on captive animals (e.g. Amrein *et al*., 2014; Farrand *et al.*, 2014; Maia *et al.*, 2012). This is known as the "visitor effect" (Hosey, 2000). In some cases, visitor presence can initiate aggressive or stereotypical patterns of animal behavior and thus be a stressor (e.g. Fernandez *et al*., 2009; Hosey, 2000; Hosey, 2008), while at other times they can stimulate cognition and social interaction and thus effectively act as a form of enrichment (e.g. Chamove et al., 1988; Davey. 2007; Owen 2004); there are also situations where visitor presence has no discernible effect on behavior (Jones *et al.*, 2016; Margulis *et al.*, 2003). Effects can vary by species (Collins and Marples, 2015), time of day (Maia *et al.*, 2012) and existing levels of enrichment within the enclosure (Carder and Semple, 2008). The visitor effect can thus be very situation specific such that the findings of one study will not necessarily be directly transferable to other situations or species.

One particularly intense form of visitor interaction with captive animals occurs in immersive exhibits such as walk-through enclosures, which are becoming increasingly common in zoos (Shani and Pizam, 2011). Such enclosures can be larger than traditional enclosures as the viewing area is incorporated within the exhibit rather than being adjacent to it (Moss et al., 2008); there can also be fewer conflicts between public requirements and maintaining good welfare. For example, bats (Chiroptera) require a dark environment that can conflict with external viewing. Dark walk-through bat enclosures can simultaneously allow superior husbandry and public viewing opportunities (Fascione, 1996).

Walk-through enclosures tend to be very popular with the public as they allow visitors to observe animals in close proximity without barriers in a way that many people find more enriching. Although many things affect visitor experience in zoos, educational opportunities and the extent to which exhibits and enclosures facilitate “special moments” and allow visitors to engage with animals are paramount (Lee, 2012; Morgan and Hodgkinson, 1999; Sickler and Fraser, 2009). The direct animal encounters that are possible in walk-through enclosures can be a powerful way of maximizing both education and memorable experiences (Fernandez *et al.*, 2009; Moss and Esson, 2013). This is particularly true for young children who generally experience the world through kinetic and visual stimuli (Corbetta and Snapp-Childs, 2009). Such experiences can therefore be important in child development and provide a perfect opportunity to spark interest in children about animals and the environment.

Despite their increasing popularity with both visitors and zoos, very few behavioral studies have been conducted specifically on animals housed in walk-through enclosures (Sherwen *et al.*, 2015). This is concerning because, for some species, having visitors in such close proximity might increase anxiety and alter behavior in non-desirable ways. For example, in one of the few studies on walk-through enclosures, Larsen *et al.* (2014) found that koalas *(Phascolarctos cinereus)* responded to large numbers of visitors and high noise levels by increasing vigilance behavior. Similarly, Sherwen *et al.* (2015) found that visitor-directed vigilance increased with visitor number in western grey kangaroos (*Macropus fuliginosus fuliginosus*) and red kangaroos (*Macropus rufus*) housed in walk-through enclosures. Changes such as these, especially when they involve non-natural behavior, can not only be detrimental to welfare per se (Montaudouin and Le Pape, 2005) but potentially also to visitor numbers and income as the appearance of poor welfare can negatively affect public support (Miller, 2012). However, negative effects are far from inevitable. In a study of captive crowned lemurs (*Eulemur coronatus*) Jones et al. (2016) found that allowing visitors into the lemur exhibit had a positive effect by decreasing lemur aggression. It is thus in the best interests of zoos to research visitor effects, especially for walk-through enclosures, to maintain high standards of welfare, reputation and income.

This study focuses on quantifying any effect of visitors on the behavior of European red squirrels (*Sciurus vulgaris*) at the largest walk-through enclosure in the UK. It also examines the effect of visitors on squirrel encounters and, in turn, quantifies the correlation between squirrel encounters and visitor experience. This is the first ever study on captive red squirrel behavior or on visitor effects on the red squirrels, and is unusual in examining the effect of the number of adults and the number of children on animal behavior separately. It will thus inform husbandry decisions and, where appropriate, allow optimization of visitor experience.

MATERIALS/METHOD

Study species

The European red squirrel (*Sciurus vulgaris*) is an arboreal omnivorous rodent, preferring woodland but is also found in parks, gardens and subalpine environments. The species is rare and declining in parts of its European range, primarily the UK and Italy (Shar et al., 2008), and is thus protected under Appendix 3 of The Convention on the Conservation of European Wildlife and Natural Habitats 1982 (The Bern Convention). Participating parties undertake necessary actions to conserve the species listed, including, but not limited to, the education of the public in the aim of conservation.

Study site

Wildwood Escot Estate is located near Ottery St Mary, Devon, UK (centered on 50.773795N, -3.304410E). Their red squirrel enclosure was built in the summer of 2011 and is enclosed by a 185cm high fence and covers approximately 2100m^2 (Fig. 1). It contains a wooden raised boardwalk, a wooden viewing platform measuring 5m x 6m and two feeding platforms where food is placed at the start and end of the day. Visitors are encouraged to enter the enclosure and experience the squirrels in close proximity. In July and August 2015, when this study was conducted, there were six females occupying the enclosure (three aged 12 months, two aged 3 years, and one aged 4 years). This group structure had been consistent for around one year.

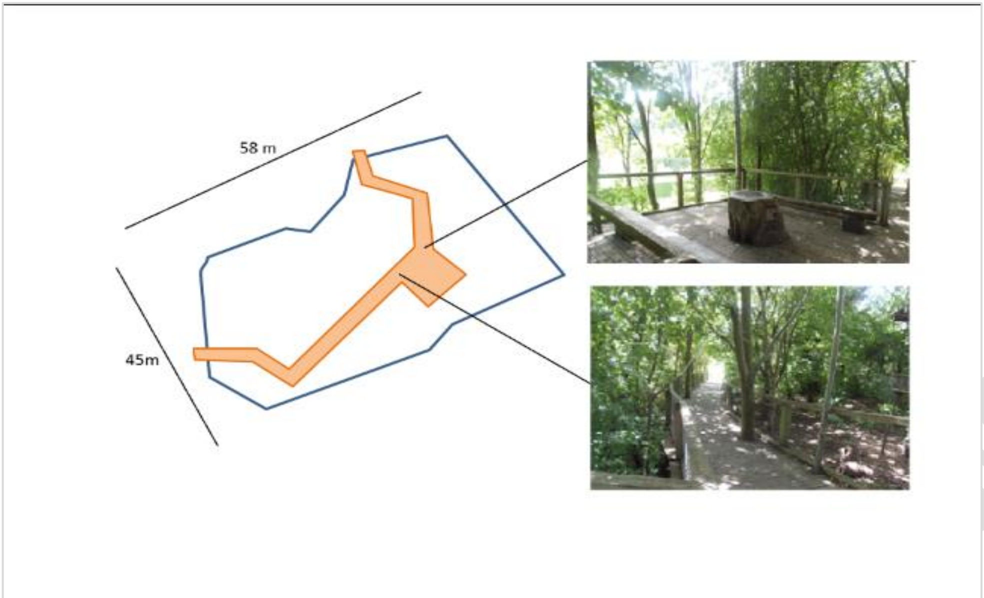

Figure 1: Schematic of enclosure, showing external fence line and raised boardwalk (shaded area), with photographs of the viewing platform (top) and boardwalk (bottom).

Squirrel behavior

To assess the effect of visitor numbers on squirrel behavior, an ethogram was used in conjunction with counts of the number of visitors in the enclosure. This ethogram was constructed based on initial observations of the squirrel group, and is shown in Table 1. Each squirrel could be recognized individually through differences in coloration and size. Behavioral data were collected using focal sampling (Martin and Bateson, 2007) whereby a specific squirrel was identified and followed, with its behavior recorded at one minute intervals. Recording continued for a 20 minute period or until the focal squirrel was lost from view. At this point a different individual was located and identified, and the same recording protocol was followed. In total, data were collected over a period of 30 hours. To ensure that all squirrels were studied for approximately the same amount of time each day (and thus the overall study), when multiple individuals were in view, such that there was a choice of potential focal squirrels, the squirrel that had been observed the least was chosen. This avoided the group data being skewed by inadvertent overrepresentation of one or two individuals. As the study was undertaken in a walk-through enclosure, the squirrels were in view for a higher percentage of the time than might otherwise have been the case; behaviors were also easier to interpret as observation was possible from multiple viewing angles.

Table 1: Ethogram used to categorize behaviors during data collection and their descriptions.

Behavior	Description
Aggression	The chasing or physical fighting between squirrels
Digging	The act of moving soil for the purpose of retrieving or burying a food item
Drinking	The consumption of water
Eating	The consumption of food items
Grooming	Licking or scratching self
Inactive	Standing or sitting calmly for no obvious purpose in a non-alert manner
Interaction (with humans)	Behaviors related to visitors including but not limited to: sniffing hands or feet, physical contact or inquisitiveness towards the visitor
Locomotion	Movement from one area of the enclosure to another, at any speed
Scent Marking	Rubbing facial or anal glands on a substrate
Sniffing	Travelling slowly across the ground with nose lowered

Visitor experience

To collect information on the visitor experience, visitors leaving the enclosure were asked to complete a short, closed-question questionnaire. This highly-structured and simple method was chosen for its speed of completion to maximize visitor participation. The questionnaire asked groups of visitors to record: (1) number of adults; (2) number of children; (3) duration of visit in minutes; (4) group noise level; (5) how many squirrels were seen; and (6) overall experience. The noise level of the group was based on visitor perception, whereby visitors were asked to record their noise level using a Likert scale from 1 (silent) to 10 (extremely noisy). Overall experience was also recorded using a Likert scale from 1 (extremely poor) to 10 (excellent). In total, 317 visitors were surveyed.

It is recognized that asking visitors to record perceived noise was less accurate than using a decibel meter to quantify the noise pressure objectively and could have introduced inter-individual variability. However, the only alternative was to ask each group of visitors entering the enclosure for permission to follow them around the enclosure to record their noise level, which would likely have altered visitor behavior patterns. Enclosure-wide noise monitoring was not feasible given the size of the enclosure. The strategy adopted – asking visitors to record their own perception of their noise level at the *end* of the visit – reduced the chances of the study itself affecting the behavior of the participants.

Data analysis

To quantify any relationship between the number of visitors and the incidence of specific squirrel behaviors, a series of multiple binary logistic regression analyses was used. Each analysis used the presence (1) or absence (0) of a given behavior as the dependent variable, while the number of adults and the number of children were entered as separate predictor variables. Multicollinearity between the predictor variables was within acceptable limits (variance inflation factor <10 in both cases: Ho, 2006). However, because the number of instances where a specific behavior occurred (1) was low compared to instances where that same behavior did not occur (0), the data were zero-inflated. As a result, the *apriori* classification power of the full models was extremely high such that the effect of visitor numbers was hard to quantify in terms of effect size (R^2 or classification accuracy), even when models were significant. Accordingly, subsampling was undertaken whereby each model was rerun on a restricted dataset that included all instances of the focal behavior and the same number of instances where the behavior did not occur selected at random. This random undersampling of the majority class is similar to subsampling to circumvent spatial autocorrelation in data prior to analyzing with logistic regression (Dale and Fortin, 2002) and is recommended for, and efficient at resolving issues with analyzing, strongly unbalanced binary datasets (Japkowicz, 2000; Kubat and Matwin, 1997). In this case, the process provided a balanced dataset and reduced the *apriori* classification power to 50% such that any added effect of entering the predictor variables could be determined.

To quantify any relationships between the number of squirrels seen (henceforth referred to as squirrel encounters) and visitor numbers, noise as perceived by visitors, and duration of visit as determined by the questionnaire data, multiple linear regression analysis was used. The potential relationship between squirrel encounters and visitor experience score was analyzed using binary regression. The assumptions of normality, linearity and homoscedasticity were assessed by visual examination of p-p plots and residual plots, while the assumption of orthogonality was assessed using the variance inflation factor. All assumptions were met.

When significant models were produced after the full suite of predictor variables was entered, additional analysis was undertaken whereby the predictor variables were entered using a stepwise approach (entry criterion $\alpha = 0.05$; subsequent removal criterion $\alpha = 0.10$: Field, 2010). This allowed identification of those predictor variables significantly associated with the dependent variable.

RESULTS

Squirrel behavior

The most frequent behaviors recorded were, in order, locomotion (28%), digging (24%), eating (19%) and sniffing (14%). The remaining 15% of observations were split between inactivity, grooming, drinking, interaction with humans, scent marking, and aggression (Fig. 2).

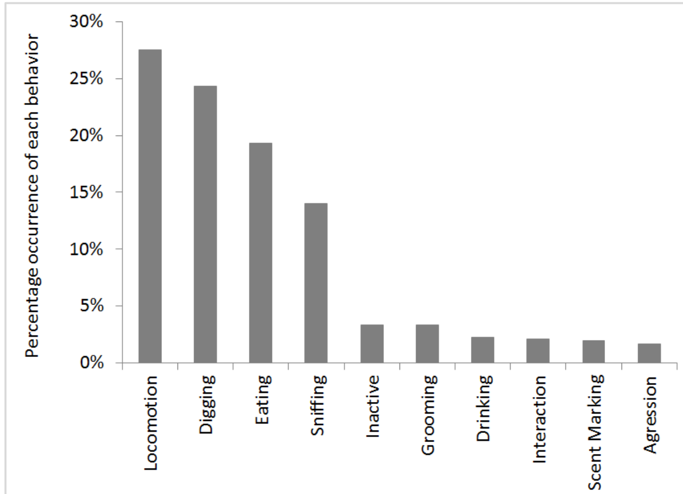

Figure 2: Activity budget showing the percentage occurrence of each behavior for all squirrels in the enclosure.

Multiple logistic regression analysis demonstrated that four of the behaviors were significantly correlated with the number of visitors: locomotion, eating, inactivity, and interaction with humans. As noted in the methods, two models were created for each behavior, one using the full (zero-inflated) dataset and the other using a restricted (balanced) dataset. Both models are given in Table 2 for each behavior, but model fit parameters are provided for models on the restricted dataset only so that zero-inflation did not affect their estimation. There was no change in whether models were significant or not between the two approaches for any behavior (Table 2).

Table 2: Multiple logistic regression analyses showing the effects of the number of visitors (separated into adults and children) on the occurrence of each behavior.

Behavior	Full (zero-inflated) dataset (n = 720)		Restricted (balanced) dataset					
	Chi-square	P value	Classification accuracy	Number of adults (direction of relationship)	Number of children (direction of relationship)	Chi-square	N	P value
Locomotion	19.827	**<0.001**	56.3%	-	+	15.608	376	**<0.001**
Eating	20.762	**<0.001**	60.4%	+	-	22.326	278	**<0.001**
Inactive	11.062	**0.004**	70.8%	-	-	13.294	48	**0.001**
Interaction with humans	10.286	**0.006**	93.3%	+	-	12.970	30	**0.002**
Drinking	0.379	0.827	56.3%	-	+	1.850	32	0.397
Digging	3.160	0.206	50.0%	+	-	1.708	350	0.426
Aggression	4.345	0.114	54.2%	+	-	1.527	24	0.466
Grooming	1.544	0.462	52.1%	+	-	1.298	48	0.523
Scent marking	2.475	0.290	57.1%	-	+	2.753	28	0.253
Sniffing	0.694	0.707	53.5%	-	-	3.298	202	0.192

Footnote: Analyses on the full (zero-inflated) data set the restricted (balanced) dataset are shown. The apriori classification probability was 50%. Emboldened P values show significance at $\alpha = 0.05$.

For the four behaviors that were significantly related to total group size, analyses were re-run using stepwise entry as detailed in the methods to determine whether it was the number of adults or the number of children (or both) that caused the change in behavior (Table 3). The stepwise analysis showed that the number of children was the most influential variable on squirrel locomotion; this was a positive relationship. Adding the number of adults into the model increased the classification accuracy to 56.3% but, interestingly, this relationship was negative. This pattern was entirely reversed for squirrel eating behavior, as the number of adults was entered into the model first, and was positive, while the number of children was added second, and was negative. The combined classification accuracy was 60.4%. For inactivity and interaction with humans, adults alone were entered into the model under stepwise entry, however the direction of the relationship differed (inactivity = negative; interaction = positive). The classification accuracy of the final models was 72.9% and 53.3%, respectively. Full details of model fit and significance is given in Table 3.

Table 3: Stepwise logistic regression models of those behaviors exhibited by squirrels that were significantly related to visitor numbers (both number of adults and number of children) in the forced entry models shown in Table 2.

Behavior and sample size	Model	Variables in model	Direction of relationship	Classification accuracy	P value
Locomotion (n = 376)	1	Number of children	+	48.5%	0.013
	2	Number of children Number of adults	+ -	56.3%	<0.001
Eating (n = 278)	1	Number of adults	+	53.6%	0.005
	2	Number of adults Number of children	+ -	60.4%	<0.001
Inactive (n = 48)	1	Number of adults	-	72.9%	0.001
Interaction with humans (n=30)	1	Number of adults	+	53.3%	0.014

Footnote: See Methods for details of stepwise criteria.

Visitor experience

The mean number of adults per group was 1.84 (min = 0; max = 5) and the mean number of children per group was 1.41 (min = 0; max = 8). The mean overall group size (i.e. adults and children combined) was 3.26 (min = 1; max = 12). There was considerable variation in visit duration, with some groups staying in the exhibit for just one or two minutes and others up to 40 minutes; mean visit duration was 7 mins. The mean number of squirrel encounters was 1.38 ± 1.25 sd. People generally seemed to enjoy their experience, with a mean experience score of 6.73/10, although 6% of respondents rated the experience ≤ 3/10.

There was a significant relationship between squirrel encounters and the suite of predictor variables, which included group size, noise as perceived by visitors, and visit duration (MLR: $F_{6,93} = 3.546$, $P = 0.010$). The adjusted R^2 was 0.240, implying that 24% of the variability in squirrel encounters could be explained by the suite of predictor variables. Re-running this analysis using stepwise entry allowed the relative importance of the three variables to be identified. The first model included number of adults (positive correlation), the second added visit duration (positive correlation) and the third added the noise level of the group as perceived by that group (negative correlation) (Table 4). The adjusted R^2 of the final stepwise model was higher than the full model at 0.265.

Table 4: Stepwise regression model of the number of squirrels encountered by visitors to the walk-through in relation to visitor numbers and behavior.

Footnote: The full suite of possible predictor variables was: number of adults, number of children, visit duration, and noise as perceived by visitors. See Methods for details of stepwise criteria; n = 100 in all cases.

Model	Variables in model	Direction of relationship	Classification accuracy	P value
1	Number of adults	+	48.5%	<0.001
2	Number of adults Visit duration	+ +	56.3%	<0.001
3	Number of adults Visit duration Noise as perceived by visitors	+ + +	53.6%	<0.001

Finally, a univariate regression showed that enjoyment of the visitors was significantly and positively related to the number of squirrel encounters (regression: $F_{1,98} = 37.761$, $P < 0.001$, $R^2 = 0.278$).

DISCUSSION

Baseline squirrel behavior

The most frequent behaviors were locomotion, eating, digging and sniffing; these totaled 85% of activity. This is very similar to the 82% of the activity budget taken up by foraging, eating and hording combined in a study of free-ranging red squirrels studied using radio tracking, when digging and sniffing (and, to a large extent, locomotion) were primary components of foraging and hording (Tonkin, 1983). It should, however, be noted that because squirrels came to fixed resources within the enclosure to feed, this behavior might have been over-recorded relative to behaviors such as grooming, which could take place anywhere in the enclosure including areas that were out of sight of the observer.

Visitor impacts on squirrel behavior

The number of visitors in the enclosure was significantly related to the expression of several different behaviors. The most intuitive relationship was the positive correlation between the number of visitors and the amount of time the squirrels spent interacting with visitors. This is likely to have been driven in part simply by there being more opportunities for interaction when more visitors were in the enclosure. However, the fact that the interaction behavior was related to the number of adults, and not the number of children, is interesting. One likely explanation is that the positive reinforcement training method used by the keepers (offering food rewards to the squirrels for coming to them for routine medical checks) means squirrels associate the presence of adults with food opportunities (Carlstead, 2009). It was often noted during data collection that the squirrels would engage with adult visitors (not children) apparently seeking food. In this way, the pre-existing animal:keeper relationship seems to influence squirrel behavior around other adults. Ward and Melfi (2015) have previously found that change in behavior can be driven by keeper-animal relationships. This would be an interesting area for future study in other species; it might also be interesting to compare visitor interaction levels between individuals that have been hand reared with those that had not.

The effects of visitor number on locomotion behavior were rather more complex. The positive relationship between number of children and locomotion may be due to increased stress or anxiety causing animals to move from the boardwalk. It was noted anecdotally by the researchers during data collection that noise levels increased with the number of children present, which might have been the driving factor here, especially considering the timidity and shyness of the squirrels. Such effects have been shown previously in a study of white handed gibbons (*Hylobates lar*) when bipedal walking and brachiation (arboreal locomotion) increased with the presence and number of children (Cooke and Schillaci, 2007). In contrast, the presence of more adults in the enclosure was associated with a reduction in squirrel movement. There are several possibilities for why this might have occurred. Firstly, it is possible that the presence of more adults acts to reduce noise levels of children as more control and influence is exerted over child behavior. Alternatively, the aforementioned interaction between adults and squirrels (which is largely static) might have meant that squirrels were less likely to move when adults were in the enclosure. The effects of visitors on locomotion has been seen previously in captive kangaroos whom have displayed increased locomotion as visitor numbers increase (Sherwen et al. 2015). While Sherwen's study did not distinguish between adult and child visitors on locomotion, the different – sometimes opposing – effects of adults and children on locomotion (and other behaviors) highlighted in our study clearly demonstrates the need for this distinction to be made in future studies of the visitor effect.

An increase in the number of adults was associated with a reduction in inactivity. Given that the behaviors as recorded in this study were mutually exclusive, this might again be linked to the interaction between adult visitors and squirrels or alternatively might be the result of an increase in eating when adult visitors were in the enclosure. In terms of eating, it was notable that this activity was less likely to occur when there were a lot of children in the enclosure. This has been seen previously (e.g. in a study on captive Mexican wolves *(Canis lupus baileyi)* that showed high visitor disturbance decreased eating levels: Pifarre et al., 2012).

Influences on squirrel encounter rate

The number of adults, the visit duration, and noise (as perceived by visitors) all significantly influenced the number of squirrel encounters. To take these in turn, squirrel encounter frequency increased as the number of adults increased. This is likely to be partly explained by squirrels engaging with adult visitors when seeking food due to positive reinforcement training by keepers (see above). It is also likely that having more adults in a group allowed that group to see more squirrels because primary observations showed that children generally are inefficient at spotting the squirrels and relied on adults locating them. In addition, an increase in visitors allows more viewing angles to be covered, thus the number of squirrel encounters rises. Visit duration proved a positive influence on sighting frequency; this is entirely logical as there is more effort spent in observation. The negative relationship between perceived noise and sighting frequency can be explained by the fight or flight response: when faced with danger squirrels flee (Randler, 2006). An increase in noise level may invoke fleeing or the avoidance of noisy areas. Conversely, a study on captive born meerkats *(Suricata suricatta*) – who also flee when faced with danger - showed no change in behavior with a decrease in visitor noise of approximately 30% (Sherwen *et al*., 2014). This underlines the fact that visitor effects are often species- and/or situation-specific.

Effects of squirrel encounters on visitor experience

The difficulty in balancing natural animal behavior, welfare, enclosure design and visitor experience is well known (Kuhar et al., 2010). If this balance is wrong, visitors will not receive the intended conservation and education messages and/or husbandry will not be optimal. In this study the overall rating given by visitors significantly increased with an increase in squirrel encounter frequency. These results are as expected as the purpose of the enclosure is for visitors to experience the squirrels up close so when this is not achieved the rating drops.

CONCLUSIONS

1. Squirrel encounter rate positively affected visitor experience. In turn, the number of squirrels seen was affected by visit duration (positive) and noise (negative). Visitors should be encouraged to spend more time in the enclosure, either through direct advice or strategies to encourage visitors to stay longer (e.g. large viewing areas: Moss et al., 2008).
2. The amount of squirrel interaction with humans increased as the number of adult visitors increased. This can be partly attributed to more opportunities for engagement and partly to a positive squirrel-keeper relationship gained via positive reinforcement. The amount of time that squirrels spent eating was also positively related to the number of adult visitors. Again this might link to positive reinforcement training (which used food as rewards) with squirrels feeling comfortable eating with adults in the enclosure. This also highlights the fact that positive animal-keeper relationships not only affect animal welfare but potentially also visitor experience. The amount of time that squirrels spent moving was inversely correlated with the number of adults, possibly as a direct result of spending more time undertaking feeding and interaction activities.
3. The number of child visitors correlated with locomotion (positive) and eating (negative) possibly as the squirrels became more cautious and moved away from visitor disturbance. In addition to being less likely to eat when vigilance was high, the position of the feeders was such that as squirrels moved away from visitors they also moved away from the feeders. It is recommended, therefore, for at least one feeder to be placed away from visitor-accessible areas to ensure that food is always available. This might be worthy of consideration in other walk-through enclosures for other species too.
4. The need for visitors to be made aware of the importance of being quiet and moving slowly in the enclosure, both for the sake of the squirrels and their own experience, cannot be overstated.
5. This study accords with previous work on the value of walk-through enclosures on providing visitors with memorable experiences, which in turn often results in repeat business and the delivery of stronger conservation messages.

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