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JZAR Research article

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Are "visitor effects" overestimated? Behaviour in captive lemurs is mainly driven by co-variation with time and weather

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Keywords: Activity budget, captivity, Lemur catta, time of day, zoo animals

Article history:
Received: 25 Oct 2017
Accepted: 19 Mar 2019
Published online: 30 Apr 2019

Abstract
The potential influence of visitors on behaviour of captive animals is well known. However, little research on "visitor effects" has also evaluated time of day and weather, which can affect behaviour directly and often also co-vary with visitor numbers. Here, visitor effects on captive ring-tailed lemurs (*Lemur catta*) are examined in a walk-through enclosure, where potential for visitor effects is especially high, while specifically considering weather and time of day (between 10:00 hr when lemurs were released into their outdoor enclosure and 16:00 hr when then returned to overnight accommodation). Time, weather and visitor variables interacted in complex ways, but time and weather exerted the strongest effect on behaviour. Weather strongly affected resting, feeding/foraging, and locomotion. Sunbathing was highest in mornings; locomotion increased in afternoons. Visitor numbers were negatively associated with feeding/foraging and sunbathing; visitor activity was positively associated with locomotion and alertness. Crucially, however, visitor effects were small both overall and in relation to underlying effects of time/weather. Univariate models suggested visitors accounted for ~20% of behavioural variation; after time/weather had been included this dropped to ~6–8%. The study concludes that underlying visitor:time and visitor:weather correlations can lead to overestimation of visitor effects and offers recommendations for future work.

Introduction

The last 20 years has seen considerable focus on making zoo enclosures larger and more naturalistic both to improve the husbandry of the animals housed within them and the experience of the viewing public. For some species, particularly in Europe, there has also been an increasing trend towards walk-through enclosures, which allow visitors to enter the exhibit to get closer to the animals. Walk-through enclosures usually have separate entrance and exit doors linked by a path to guide visitors while they are inside the enclosure; there can be additional features such as viewing areas or elevated platforms. Such exhibits can be larger than traditional enclosures as the viewing area is incorporated within the enclosure rather than being adjacent to it and animals are often more visible, both of which increase visit length (Moss et al. 2008; Moss and Esson 2013; Kirchgessner and Sewall 2015). Although many things affect zoo visitor experience, the ability to engage with animals is paramount (Morgan and Hodgkinson 1999; Sickler and Fraser 2009; Lee 2012). Direct animal encounters, such as those facilitated by walk-through enclosures and other immersive exhibits, are thus a powerful way of maximising visitor experience (Woods 2002; Lee 2012; Luebke and Matiasek 2013; Woolway and Goodenough 2017). This potentially increases subsequent pro-conservation behaviour (Skibins and Powell 2013).

However, the very aspect of immersive walk-through enclosures that makes them so advantageous to visitor experience—bringing people closer to the animals—could potentially have negative effects on the behaviour of the animals involved (see review by Fernandez et al. 2009). The possible effect of visitors on animal behaviour in zoos is not a new idea, being suggested initially in the 1960s (Morris 1964; Heidger 1969). Since then, there has been considerable research interest in this "visitor effect", as reviewed by Hosey (2000) and Davey (2007). Studies have been conducted on numerous taxa including mustelids (Owen 2004), marsupials (Larsen et al. 2014; Sherwen et al. 2015), felids (e.g. Margulis et al. 2003; Sellinger and Ha 2005; Maia et al. 2012) and primates (e.g. Nimon and Dalziel 1992; Birke 2002; Jones et al. 2016).

In some situations, visitor presence has no discernible effect on behaviour. For example, Margulis et al. (2003) found that visitor presence did not influence the behaviour of several big cat species, including lion (*Panthera leo*), Amur tiger (*Panthera tigris altaica*), and snow leopard (*Panthera uncia*), housed in outdoor enclosures with viewing windows. Sometimes, visitors are deemed to have a positive effect on species, for example between-individual aggression in crowned lemurs (*Eulemur coronatus*) decreased when visitors were allowed into the enclosure at feeding time (Jones et al. 2016) or acting as a form of enrichment via food solicitation in captive orangutans (*Pongo pygmaeus*) in treetop free-ranging exhibits in Singapore (Choo et al. 2001). However, visitor presence can cause non-desirable behaviours. Primates seem particularly susceptible to adverse effects, with visitor numbers previously being shown to correlate with: (1) increased hiding or escape-preparation behaviours (e.g. orangutan: Birke 2002); (2) increased aggression (e.g. Diana monkey, *Cercopithecus diana*: Chamove et al. 1988 and gorilla, *Gorilla gorilla*: Blaney and Wells 2004; Kuhar 2008); (3) decreased maintenance behaviours such as foraging and grooming (e.g. chimpanzee, *Pan troglodytes*: Wood 1998); and (4) decreased social behaviours (e.g. cotton top tamarins, *Saguinus oedipus oedipus*: Chamove et al. 1988).

Despite a recent focus on visitor effects and the increasing popularity of walk-through enclosures, few studies have been conducted specifically on walk-through enclosures (Sherwen et al. 2015). Of the few studies conducted, high visitor numbers have been found to increase vigilance behaviour in koalas (*Phascolarctos cinereus*) and western grey kangaroos (*Macropus fuliginosus fuliginosus*) housed in walk-through enclosures (Larsen et al. 2014; Sherwen et al. 2015). In both cases, this was deemed to be a negative effect because it reduced time spent resting; for koalas it also decreased time spent feeding and foraging. As visitor effects can vary not only by species, but also by sex (Sellinger and Ha 2005; Kuhar 2008), time of day (Maia et al. 2012), enrichment levels (Carder and Semple 2008) and even social group (Kuhar 2008), impacts can be very situation-specific such that the findings of one study will not necessarily be transferable to other situations or species, as recently highlighted by Collins et al. (2017).

The ring-tailed lemur (Lemur catta) is a popular species to house in walk-through enclosures (Webster 2000; Jens et al. 2012; Mun et al. 2013). Some research has been carried out previously on the behaviour of captive ring-tailed lemurs and potential visitor effects, but this has typically involved traditional enclosures (e.g. Hosey and Druck 1987; Mitchell et al. 1992; Hutchings et al. 2003; Fleming 2008; Shire 2012) or lemurs that are free-ranging across an entire site (Collins et al. 2017). These have shown that visitor numbers can be positively correlated with locomotion (Fleming 2008; Collins et al. 2017), while visitor behaviour can affect lemur locomotion and aggression (Hosey and Druck 1987; Mitchell et al. 1992). In the only two studies to consider ring-tailed lemurs specifically in walk-through enclosures, Hosey et al. (2016) showed that levels of lemur–lemur wounding did not correlate with the number of people in the zoo that day, while Farhall and Litten-Brown (2010) showed that the feeding behaviour in a walk-through enclosure was similar to that seen in the wild. It is not only visitors that are important modifiers of lemur behaviour: time of day and weather are also important (Ramsay 1995; Hutchings et al. 2003; Farhall and Litten-Brown 2010). However, these variables are cross-correlated making causality hard to determine. For example, visitor numbers are not independent of time or weather: people are more likely to visit towards the middle of the day and in good weather conditions.

In this study, the behaviour of ring-tailed lemurs is examined in the largest walk-through enclosure in the UK in relation to visitor numbers and behaviour (active or passive) over two years. Crucially, the possible effects of weather and time are explicitly factored into the analysis. This builds on recent seminal work by Collins et al. (2017) who studied the combined effect of time of day (and seasonality), weather and visitor parameters on lemur behaviour in an entirely free-ranging group of lemurs by: (1) examining the situation for enclosure-housed lemurs, which is more typical of husbandry in captive collections and where the opportunity for lemurs to move away from visitors is arguably more constrained; and (2) quantifying the relative importance of time/weather/visitors on lemur behaviour in terms of effect size to determine any additive effect of visitors over-and-above time and weather influences. In this study, three specific hypotheses are tested: (1) there will be a relationship between visitor numbers and lemur behaviour such that a "visitor effect" is evident; (2) time and weather will affect lemur behaviour; and (3) a large part of the relationship between visitor numbers and lemur behaviour will be explained by underlying relationships between visitors and both time and weather such that the "visitor effect" is either reduced or disappears completely. Recommendations are made for the management of visitors within lemur enclosures and the study highlights the importance of allowing for time and weather in studies of visitor effects in all species.

Methods

Study population and enclosure

This study was conducted on a troop of adult ring-tailed lemurs at West Midlands Safari Park, Worcestershire, UK, which is part of a European Endangered Species Programme. There were 19 individuals, which is fairly typical of troop size in the wild (Jolly and Pride 1999), with 12 adult females and seven adult males. The lemurs were housed during the day in the UK's largest walk-through enclosure (approx. 5,600 m^2). This outdoor enclosure is naturally bordered on one side by a lake, with the remaining perimeter being secured by an electrified chain-link fence. The enclosure contains fairly complex habitat comprising mixed mature woodland. As well as replicating the lemurs' natural environment as far as possible, this provided foraging opportunities as well as shelter and retreat areas. There is also an open area to allow lemurs to forage on the ground or sunbathe and three heated shelters provided additional warmth. Two other species of lemur were housed in the same enclosure: white-fronted brown lemurs (*Eulemur albifrons*) (n=3) and red-bellied lemurs (*Eulemur rubriventer*) (n=2). The three species were not observed to interact and only came into contact when entering or leaving their separate indoor areas at night.

Visitors entered through a double-gated entrance and walked along a visitor pathway, which was bordered by a low wooden fence to encourage visitors to keep to the path. A keeper remained in the enclosure at all times to ensure that visitor guidelines (keeping to the path; no touching or feeding; no chasing) were observed. This is fairly typical for walk-through enclosures, especially for primates (e.g. Jens et al. 2012).

Data collection

Data on lemur behaviour were collected in Autumn 2013 and Autumn 2014. Year 1 was regarded as a pilot year to provide baseline data and enable basic analysis to be undertaken to

Table 1. Ethogram used to record individual lemur behaviour including a short description of each behaviour. Behaviours are grouped into active or inactive using Shire (2012). * = only used in Year 2 of the study (classified as resting in Year 1)

Type	Behaviour	Description
Active	Feeding/Foraging	Searching for food items or consuming them
	Locomotion	Walking, running or climbing
	Playing	Engaging in an activity for entertainment; usually with other lemur(s) but occasionally alone when interacting with an enrichment item
Inactive	Alert	Still but alert/vigilant (not relaxed as in resting)
	Allogrooming	Cleaning another individual
	Autogrooming	Self-cleaning
	Resting (R)	Sleeping or otherwise motionless with a relaxed body posture
	*Sunbathing (S)	Sunbathing stance, reclining with limbs facing forwards and upwards
Not classified	Out of sight	Cannot be seen

inform more detailed data collection in Year 2 for robust scientific analysis. In both years, ethogram-based scan sampling was undertaken whereby the number of individuals undertaking each pre-determined behaviour was recorded. The ethogram was based on keeper input and scientific literature (Shire 2012). In Year 1, the ethogram comprised seven mutually-exclusive behaviours, plus “out of sight” (Table 1). In Year 2, sunbathing was added as an eighth behaviour as per Keith-Lucas et al. (1999); this behaviour was classified within “resting” during in Year 1. The ethogram differentiated allogrooming and autogrooming because the former is an important social behaviour whereas the latter is a maintenance behaviour that can, in rare cases, become a non-desirable stereotypic behaviour (Hosey and Skyner 2007). To allow comparison of activity budgets with other published work (e.g. Jolly 1966; Keith-Lucas et al. 1999; Shire 2012), each behaviour was designated either as active or inactive (Table 1). In all cases, comparison was straightforward since both Jolly (1966) and Keith-Lucas et al. (1999) used just three categories (foraging and feeding (active); travelling (active); resting, grooming and still (inactive), which easily map to the current ethogram. Shire (2012) used a more complex ethogram (e.g. climbing and walking/running as separate categories) but specifically listed whether an activity was active or inactive; this was used to inform the current ethogram to ensure comparability.

The behaviour of each individual in the troop was recorded every 5 minutes for 6 hours per day (12 observations per h; 72 per d). In total, 21 days of data were collected, spanning October/November 2013 and October/November 2014 to provide 1,512 timed observations of the troop over 126 hours. Although the behaviour of each individual in the troop was recorded at each and every recording point, individuals were not uniquely identified so no individual behavioural profiles could be created. This was because the additional time needed to uniquely identify each lemur would have either decreased the number of lemurs that could be studied or increased the amount of time taken, thus risking de-coupling the recording of the lemur behaviour from the collection of the visitor data. The researcher moved around the enclosure as there was no one location that gave a good view of all areas but they always kept at least 10 m from the lemurs and were restricted to the same path through the enclosure used by the visitors and moved slowly and quietly to avoid confounding the results. The study was entirely observational and no aspect of the enclosure or husbandry was altered. No animals were handled or approached by the researchers. There were thus no ethical implications of this work.

Data on the visitors present in the lemur enclosure were collected immediately after the scan sampling of the lemur group within the same 5 minute period. This data collection captured not only visitor numbers (crowd size) but also visitor behaviour (as per Choo et al. 2011). In Year 1 (2013), visitor data were collected categorically: (1) no visitors; (2) small groups of passive visitors; (3) large groups of passive visitors; (4) small groups of active visitors; and (5) large groups of active visitors. Groups of ≤5 people were classified as small, while groups >5 people were classified as large. Passive groups comprised visitors that were totally observatory and simply watched the lemurs in a relatively quiet and sedate manner, while active groups had at least one member that was active (shouting, running etc.) or that attempted to interact with the lemurs. This framework replicated the approach used previously for ring-tailed lemur behaviour in traditional enclosures (Hosey and Druck 1987; Mitchell et al. 1992); the thresholds used to distinguish small vs. large and passive vs. active groups were also based on these studies. In Year 2 (2014), the exact number of passive and active visitors present in the enclosure were counted as a continuous variable rather than simply classifying visitors as forming a small or large group. This was done to allow a much more detailed analysis of lemur behaviour in relation to visitor numbers and activity. The definitions of active and passive remained unchanged.

In Year 2, entire days were also classified as “busy” or “quiet”. This was done a priori based on likely visitor numbers taking into account the day of the week, school holidays, and planned school or other group visits. The rationale for doing this was three-fold. Firstly, it increased the chances of getting a good spread of visitor group sizes without being confounded by seasonality (Kuhar 2008). Secondly, previous research by Hutchings et al. (2003) has suggested that lemurs can be affected by visitor-related noise even when visitors are not specifically at the exhibit. Thirdly, any effect of visitors on lemurs might not only be based on the number of visitors in the enclosure at any one point but also the overall

Table 2. Active and inactive activity budget in current study (walk-through enclosure) compared to previous studies of traditional (non-walk-through) enclosures, semi wild (completely free-roaming on an island) and wild. Note that some entries do not sum to 100% because unspecified behaviours grouped as "other" have been omitted.

Type	Active	Inactive	Sampling method	Reference
Walk-through enclosure	56%	44%	Scan sampling at troop level	This study; all data combined
Traditional enclosure (inside)	32%	67%	Focal sampling to give troop-level mean	Shire (2012)
Traditional enclosure (outside)	31%	53%	Focal sampling to give troop-level mean	Shire (2012)
Semi wild	45%	55%	Scan sampling at troop level	Keith-Lucas et al. (1999)
Wild	44%	50%	Focal sampling to give troop-level mean	Jolly (1966)

number of visitors passing through the enclosure throughout the entire day if visitors had a cumulative effect (i.e. an effect of visitor frequency (daily effect) as well the crowd size at any one time (instantaneous effect) (Kuhar 2008; Collins et al. 2017)).

It was important to record time of day as this has been shown to affect behaviour in related lemur species (Hutchings et al. 2003) and could co-vary with visitor numbers. In Year 1, the pilot year, days were divided into three time periods: morning = 10:00 to 11:59 (immediately after lemurs were released from their overnight enclosure; generally fairly quiet in terms of visitors); lunchtime = 12:00 to 13:59 (generally busiest); and afternoon = 14:00 to 16:00 (getting progressively quieter towards the closure of the exhibit and the lemurs being taken to the indoor overnight enclosure). These categories were the same as used in previous work by Shire (2012). In Year 2, the start of each 5 minute window was recorded to provide a continuous variable.

Because weather can affect ring-tailed lemur behaviour (Farhall and Litten-Brown 2010), and could potentially co-vary with visitor numbers, weather data were collected. In the pilot Year 1, weather was classified into three types: sunny; overcast with complete cloud cover; and rain. In Year 2, two additional weather types were added: patchy cloud (sun obscured but blue sky evident) and intermittent rain. In Year 1, the weather was recorded for each separate 5 minute interval. Thus, although the series of weather types recorded on a given day were not independent of one another, the weather could and did change throughout the day, sometimes multiple times. In Year 2, survey data were only collected on days with similar weather conditions throughout the day. The rationale for this was similar to classifying whole days as busy or quiet: that the behaviour observed at a given point in time might be influenced not only by the weather at that time but also throughout the day, especially if conditions were changeable. This approach also avoided any relationships between behaviour and time, or behaviour and visitors being confounded by underlying correlations with weather.

Data analysis

To analyse the nominal data from Year 1, three separate G-tests were run on contingency tables of behaviours (n=7) against time category (n=3), weather category (n=3) and visitor categories (n=5). These results, together with graphical examination, allowed baseline conclusions to be drawn and acted as a springboard into Year 2.

In Year 2, the number of active visitors and the number of passive visitors were collected as continuous variables (rather than categorically with count data), while the time of day was collected as a continuous variable (rather than as a discrete variable). To analyse these data, a principal components analysis was performed on the behavioural data to obtain a single measure of behaviour of the troop at each sampling point (PC1). This was regressed against: (1) time; (2) weather (categorical variable: sunny, patchy cloud, overcast, intermittent rain, rain); (3) whether the day overall was busy or quiet (binary variable); (4) number of visitors in the enclosure during sampling period; (5) number of passive visitors in the enclosure during sampling period; and (6) number of active visitors in the enclosure during sampling period. A hierarchical model was used whereby time and weather—both variables that could be important but that were entirely natural—were put into the model first using an initial forced entry step, while the last four variables describing visitor numbers or activity were available for entry in a second stepwise step (criterion for entry α=005; subsequent removal criterion α=0.10). This model was then re-run for each of the specific behaviour variables using raw data. This combined approach, using PCA to summarise the overall behavioural profile and then examining individual behaviours, had the advantage of firstly allowing to draw overall conclusions regarding of the effect of time/weather/visitors on lemur behaviour and secondly establishing what was driving this in terms of effects on individual behaviours. This also allowed for the fact that the mutually-exclusive nature of the ethogram categories meant that analysing all behaviours separately, without first assessing any overall effect, can be somewhat circular since if the incidence of one behaviour increases, the incidence of another behaviour must, de facto, decrease (Aitchison 1986). This means that effects of independent variables on behaviour can easily be overestimated (Lehner 1996).

The rationale for using a regression approach rather than a General Linear Model approach (e.g. the Generalised Estimating Equation model used by Collins et al. (2017)) was to be able to specify the order of entry of variables into the model. This allowed the baseline variables of time and weather to be added into the model in step one and visitor variables to be added into the model in step two so that any additive effect of visitor parameters was obvious, both in terms of statistical contribution and change in effect size reflecting biological importance. This reflects the approach used in previous multivariate research on primate behaviour, including that of Herman (2010) on social buffering of stress behaviours in rhesus macaques (*Macaca mulatta*), Ha et al. (2011) on aggression behaviours in pigtailed macaques (*Macaca nemestrina*), and Birnie et al (2012) on play behaviours in white-faced marmosets (*Callithrix geoffroyi*).

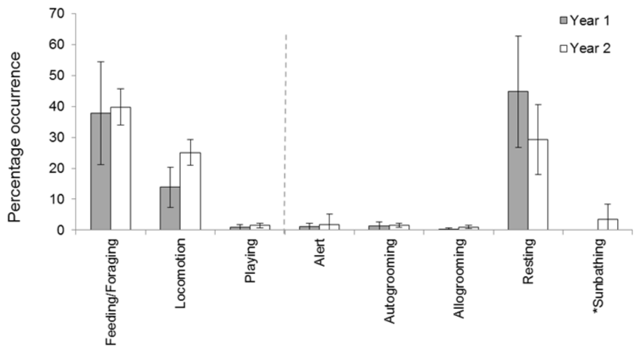

Figure 1. Troop-level activity budget for 19 lemurs housed in a walk-through enclosure in the UK in the autumn/winter for two successive years (Year 1 = 2013; Year 2 = 2014). Behaviours to the left of the dashed line are active; those to the right are inactive. Sunbathing was only recorded as a separate category in Year 2; in Year 1 it was subsumed within resting. Data show mean (±95% confidence intervals) occurrence of each behaviour at troop-level. There was no significant difference in the incidence of any of the measured behaviours between the two years (see Results).

Results

Activity budgets

At troop level, feeding/foraging, locomotion and resting (encompassing sunbathing) were the predominant behaviours in both years, totalling ~90% of activity budget (Figure 1). Still alert was the next most common behaviour, while autogrooming, allogrooming and playing occurred only rarely (Figure 1). There were very few out-of-sight records (0.039%), and these were thus excluded from the dataset. There was no significant difference in the incidence of any of the measured behaviours between the two years of the study (chi square goodness of fit test P>0.509 in all cases except locomotion where χ^2=3.103, df=1, P=0.078). Overall, 56% of time was spent undertaking active behaviours, which is substantially above the levels seen for lemurs housed in traditional (non-walk-through) enclosures (31–32%) or in the wild/semi-wild (44–45%) using comparable ethograms and either troop-level scan sampling or focal samplings to create troop-level means (Table 2). As data from other studies comprised only mean percentage, it was not possible to compare differences statistically.

Baseline analyses: lemur behaviour in relation to time, weather and visitor categories

G-tests performed on data from Year 1—when time, weather and visitor independent variables were all recorded as frequencies within simple categories—indicated that there were effects of all three independent variables on behavioural of lemurs at troop level (time: G=567.719, df=12, P<0.001; weather G=2780.602, df=12, P<0.001; visitors G=686.767, df=28, P<0.001; Figure 2). Specifically, feeding/foraging was highest in the morning (<11:59 hr) while resting was highest at lunchtime (12:00–13:59 hr). The incidence of alert behaviours increased in the afternoon (14:00–16:00 hr); autogrooming and allogrooming occurred both at lunchtime and in the afternoon but were largely absent in the morning. Regarding weather, there was little difference in troop-level behaviour between sunny and overcast conditions other than a little more resting during sunshine (probably because of sunbathing activity, which was grouped within resting in year one). However, behaviour during rain was completely different with almost 92% of time being spent resting (versus ~33% during sunny and overcast conditions). Visitors also seemed to influence behaviour profile. The differences seen in lemur behaviour between the visitor categories were largely driven by differences in the amount of time spent resting (lower when large groups were present) and locomotion, which ranged from 8% when there were no visitors to 25% when there were large active groups. Alert behaviours were highest when there were passive visitors in the enclosure.

Full behavioural models: lemur behaviour in relation to time, weather and visitor variables

The analyses described above suggested that visitors, time and weather had a complex, multifaceted, effect on lemur behaviour. However, it was not possible to disentangle exactly how these variables interacted and which, if any, were the more important. Analysis of the second year of data was designed to answer these

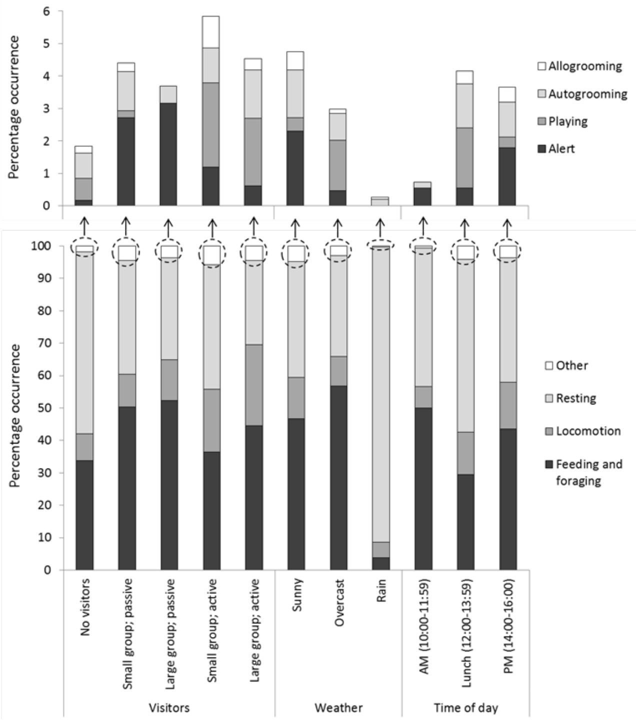

Figure 2. Percentage frequency of behaviours observed through scan sampling at troop level in relation to visitor category, weather and time of day in study Year 1 (2013). For clarity of display, the bottom chart element shows the incidence of the main three behaviours (feeding/foraging, locomotion, resting) together with “other” and all bars sum to 100%. The top chart element shows the behaviours previously grouped under “other” (alert, playing, autogrooming and allogrooming) and bars sum to the same percentage occurrence as summarised by “other” on the bottom chart element.

Table 3. Hierarchical regression models of lemur behaviour (overall behaviour based on PC1 of a Principal Components Analysis and individuals behaviours) against, in order, time of day and weather (forced entry) and the visitor variables (candidate variables: total number of visitors, number of active visitors, number of passive visitors, whether the day overall was busy or not – stepwise entry). Significant results shown in bold. See Methods for details of assumption testing and controlling for autocorrelation.

Dependent variable (and PC loading)	Independent variable(s)	F	df	P	Direction of relationship	R^2	"Visitor effect" (R^2 change from base model)
PC1	Time	0.854	1, 526	0.356	N/A	0.400	
	+Weather	22.117	2, 525	<0.001	N/A	0.301	
	+Active visitors	20.832	3, 524	<0.001	N/A	0.326	
	+Busy day (y/n)	18.273	4, 5,23	<0.001	N/A	0.350	
Resting (0.897)	Time	0.053	1, 526	0.818	N/A	0.100	
	+Weather	48.543	2, 525	<0.001	Increases as weather worsens	0.395	
	+Active visitors	36.280	3, 524	<0.001	Decreases with more visitors	0.415	0.020
	+Busy day (y/n)	28.472	4, 5,23	<0.001	Decreases on busy days	0.423	0.028
Feeding/foraging (0.618)	Time	2.324	1, 526	0.128	N/A	0.066	
	+Weather	6.647	2, 525	0.001	Decreases as weather worsens	0.157	
	+Busy day (y/n)	7.497	3, 524	<0.001	Decreases on busy days	0.203	0.046
	+Total visitors	7.048	4, 5,23	<0.001	Decreases with more visitors	0.226	0.069
Locomotion (-0.413)	Time	5.643	1, 526	0.018	Increases as day progresses	0.103	
	+Weather	2.916	2, 525	0.011	Decreases as weather worsens	0.145	0.042
	+Active visitors	3.752	3, 524	0.002	Increases with more visitors	0.179	0.076
Sunbathing (-0.410)	Time	9.721	1, 526	0.002	Decreases as day progresses	0.135	
	+Weather	41.321	2, 525	<0.001	Decreases as weather worsens	0.369	
	+Busy day (y/n)	29.444	3, 524	<0.001	Decreases on busy days	0.380	0.011
	+Total visitors	24.576	4, 5,23	<0.001	Decreases with more visitors	0.400	0.031
Alert (-0.361)	Time	0.068	1, 526	0.795	N/A	0.011	
	+Weather	2.711	2, 525	0.047	Decreases as weather worsens	0.101	
	+Active visitors	15.269	3, 524	<0.001	Increases with more visitors	0.284	0.083

questions. A principal components analysis was undertaken to produce a single measure of overall lemur behaviour (PC1), which explained 70% of the overall variation in the dataset. The PC loadings suggested that this factor was strongly influenced by resting and feeding/foraging behaviours (loadings of 0.897 and 0.618, respectively), while location, sunbathing and alert behaviours were fairly important (loadings of −0.413, −0.410 and −0.361, respectively). All other loadings were <0.200.

Regressing PC1 as a general index of lemur behaviour against the total number of visitors in the enclosure showed a significant relationship ($F_{1, 528}$=3.74; P=0.048; R^2=0.108), indicating that there was a visitor effect present. To further investigate this, separate hierarchical models were created for PC1 and also for individual behaviours, whereby time was forced into the model first, weather was forced in second, and then four visitor variables were available for stepwise entry: total visitors; active visitors; passive visitors; and whether the day was busy overall (1) or not (0), see Methods. For resting, feeding/foraging, location, sunbathing and alertness (all the behaviours with high loadings in PC1), either time or weather (or both) was significantly related to lemur behaviour (Table 3). Specifically, time was related to locomotion (increased as day progressed) and sunbathing (decreased as day progressed) whereas weather was related to feeding/foraging, locomotion, sunbathing and alertness (all decreased as weather worsened) and resting (increased as weather worsened). These results were broadly similar to the conclusions drawn from the pilot analyses of the year one data. In all cases, at least one visitor variable was added into the explanatory model after the effects of time and weather had been accounted for (Table 3). Specifically, the total number of visitors was related to feeding/foraging (−) and sunbathing (−), while the number of active visitors was related to resting (−), locomotion (+) and alertness (+). The overall busyness of the entire day (as opposed to the number of people in the enclosure at a given time) was related to resting, feeding/foraging and sunbathing (all −). The number of passive visitors was not entered into any model. No time, weather or visitor variables were significantly related to playing, autogrooming or allogrooming (tests not shown).

The more complex models show the importance of including time and weather in models of visitor effect on behaviour. For resting, feeding/foraging, locomotion and sunbathing, visitor effects were only detectable after these baseline variables had been accounted for. It should be noted, however, that the visitor effect (additive to the general effects of time and/or weather) were relatively weak, explaining another ~3–8% of variation in the incidence of each behaviour (Table 3). In the case of alertness, the univariate model suggested that visitor effects accounted for ~20% of the variability in the incidence of that behaviour, however when the effect of visitors was examined after weather had been included, this dropped to ~8%.

Discussion

In this study, time of day, weather and visitor numbers were analysed in descending order to determine, for the first time, the factors driving captive ring-tailed lemur behaviour in a walk-through enclosure. The overall activity budget was dominated by feeding/foraging, resting and locomotion, which is typical for ring-tailed lemurs in the wild (Jolly 1966; Keith-Lucas 1999). The time spent on locomotion (18%) is very similar to that found in semi-wild lemurs and substantially above that found in lemurs in an indoor enclosure (19% and 4%, respectively) (Keith-Lucas 1999; Shire 2012). The time spent feeding/foraging by the lemurs in this study (38%) was also broadly similar to that seen in the wild (31%: (Jolly 1966), but the amount of time spent resting was considerably lower. Even when resting was combined with both sunbathing and grooming to allow comparison with previous studies, the total of 37% was still well below what seen in the wild (50%: Jolly 1966) or semi-wild (55%: Keith-Lucas 1999). The time spent sunbathing (4%) is very close to the 5% found for wild ring-tailed lemurs (5%: Rasamimanana et al. 2006). No non-desirable or stereotypical behaviours, such as pacing or over-grooming, were observed.

The largest effects on lemur behaviour were time and weather conditions. Locomotion and sunbathing were both affected by time, while feeding/foraging, locomotion, sunbathing and resting were affected by weather. Sunbathing was more likely to occur in the mornings, while locomotion increased in the afternoons. The effect of rainfall on resting behaviour was particularly pronounced, averaging ~80% in rainy conditions versus 31% in other weather conditions. This has knock-on effects on the amount of time spent undertaking other behaviours, especially feeding/foraging and locomotion. The effect of weather on lemur behaviour is natural and cannot, of course, be prevented. However, effects can be mitigated through the use of specific enclosure designs such as heated shelters, additional covered shelters, and cleared areas for sunbathing, which should be positioned behind barriers so that visitors cannot encroach on the lemurs' space to prevent lemur–lemur aggression (Pereira and Weiss 1991).

Despite the underlying influence of time and weather on behaviour, visitors still had a significant effect on the behaviours exhibited. Generally, visitors were associated with a decrease in feeding/foraging, resting and sunbathing, and an increase in locomotion and alertness. For two of these behaviours (feeding/foraging, sunbathing), the pattern was driven by the total number of visitors, suggesting that the number of visitors was more important than their activity, while for the others it was the number of active visitors that was important, suggesting the reverse. The positive relationship between the number of active visitors and locomotion agrees with work by Flemming (2008) on ring-tailed lemurs in a traditional enclosure (positive correlation between overall visitor numbers and locomotion), Hosey and Druck (1987) and Mitchell et al. (1992) (positive correlation between visitor active behaviour and locomotion). It also largely reflects work on lemurs free-ranging across an entire captive collection, when number of visitors was positively related to locomotion (Collins et al. 2011). Interestingly, there was a significant negative relationship between the overall busyness of the day and both resting and sunbathing activity. This might be because the behaviour of lemurs at any one point in time, and how they respond to visitors at that specific time, is partly driven by the conditions experienced so far that day. Alternatively, it might suggest that the overall noise level within the captive collection area (which is likely to correlate with overall busyness) might have an effect, as seen previously by Hutching et al. (2003).

Although visitor numbers and activity did influence lemur behaviour, effects were very small both in real terms and in relation to the underlying effects of time and weather. Together, time and weather accounted for 10–37% of variation in each behaviour, with visitor variables adding an extra 3–8 percentage points to the overall explanatory power of the model. This broadly concurs with recent work by Collins et al. (2017), which demonstrates that all the aspects of lemur behaviour that they studied were correlated with time and/or weather, whereas only locomotion correlated with visitor numbers (with the P value being less significant than weather variables in the same model).

As with all studies, there are some important limitations and caveats to this work. Firstly, although data were collected over two years and the results demonstrate that the overall behavioural profiles do not differ between years, the main modelling work is based on data from just one year. This means that any effect of differing troop size or group make-up, including the number and age of juveniles, cannot be ascertained. Moreover, effects of season (shown to be important in Collins et al. 2017) could not be analysed. More importantly, it should be noted that lemurs were studied at troop-level. Thus, although the behaviour of each animal was recorded at each sample point, individual activity budgets could not be constructed and it was not possible to establish whether time, weather and visitor variables affected individuals differently.

Walk-through enclosures have proven to be popular and attractive to visitors viewing lemurs (Webster 2000; Jens et al. 2012; Mun et al. 2013). The results here suggest that, for this group of lemurs in this enclosure, visitor effects do occur, but they are generally fairly minimal after the effects of time of day and weather (which co-vary with visitor numbers) have been accounted for. It might thus be concluded that the benefits of walk-through enclosures on visitor experience and education outweigh the minimal effects of visitors on behaviour, especially as no non-desirable or stereotypical behaviours were recorded. However, as the majority of observed effects of visitors on lemur behaviour involved active visitors, any measures keepers can take to reduce the level of visitor noise and interaction would be useful to reduce any negative effect of visitors. Further work is needed to disentangle whether the links between overall busyness and some aspects of lemur behaviour are due to residual carry-over effects of visitors on lemurs throughout the day or whether this relates to noise disturbance external to the exhibit. We also suggest that follow-up work is needed at an individual level, possibly using focal animal sampling, to establish inter-individual variations not only in behavioural profile but also in the effects of weather, time and visitor variables upon behaviour.

Acknowledgements

We thank the lemur keepers and head of section at West Midlands Safari Park, particularly Shelley Tudor and Michelle Howes, for their support and assistance in conducting this research.

References

Aitchison J. (1986) The statistical analysis of compositional data. *Journal of the Royal Statistical Society B* 44: 1313–1325.

Anderson U.S., Benne M., Bloomsmith M.A., Maple T.L. (2002) Retreat space and human visitor density moderate undesirable behavior in petting zoo animals. *Journal of Applied Animal Welfare Science* 5: 125–137.

Birke L. (2002) Effects of browse, human visitors and noise on the behaviour of captive orang-utans. *Animal Welfare* 1: 189-202.

Birnie A.K., Hendricks S.E., Smith A.S., Milam R., French J.A. (2012) Maternal gestational androgens are associated with decreased juvenile play in white-faced marmosets (*Callithrix geoffroyi*). *Hormones and Behavior* 62: 136–145.

Blaney E.C., Wells D.L. (2004) The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal Welfare* 13: 111–118.

Carder G., Semple S. (2008) Visitor effects on anxiety in two captive groups of western lowland gorillas. *Applied Animal Behaviour Science* 115: 211–220.

Chamove A.S., Hosey G.R., Schaetzel P. (1988) Visitors excite primates in zoos. *Zoo Biology* 7: 359–369.

Claxton A.M. (2011) The potential of the human–animal relationship as an environmental enrichment for the welfare of zoo-housed animals. *Applied Animal Behaviour Science* 133: 1–10.

Collins C., Corkery I., Haigh A., McKeown S., Quirke T., O'Riordan R (2017). The effects of environmental and visitor variables on the behavior of free-ranging ring-tailed lemurs (*Lemur catta*) in captivity. *Zoo Biology* 36: 250–260.

Davey G. (2007) Visitors' effects on the welfare of animals in the zoo: a review. *Journal of Applied Animal Welfare Science* 10: 169–183

Farhall E.J., Litten-Brown J.C. (2010) Ring-tailed Lemur (*Lemur catta)* behaviour and nutrition at Cotswold Wildlife Park. *Advances in Animal Biosciences* 1: 110–110.

Fernandez E.J., Tamborski M.A., Pickens S.R. Timberlake W. (2009) Animal-visitor interactions in the modern zoo: Conflicts and interventions. *Applied Animal Behaviour Science* 120: 1–8.

Fleming C. (2008) *Personality in Captive Ring-tailed Lemurs (Lemur catta): Trait Structure and the Interaction with Dominance Hierarchy and Zoo Visitor Effects*. Thesis: University of Edinburgh.

Ha J.C., Alloway H., Sussman A. (2011) Aggression in pigtailed macaque (*Macaca nemestrina*) breeding groups affects pregnancy outcome. *American Journal of Primatology* 73: 1169–1175.

Hediger H. (1969) *Man and Animal in the Zoo*. UK: Routledge Kegan Paul.

Herman K.N. (2010) *Factors affecting rates of social buffering in juvenile rhesus macaques (Macaca mulatta)*. Thesis. University of Maryland, College Park.

Hosey G. (2000) Zoo animals and their human audiences: What is the visitor effect? *Animal Welfare* 9: 343–357

Hosey G. (2008) A preliminary model of human-animal relationships in the zoo. *Applied Animal Behaviour Science* 109: 105–127.

Hosey G.R., Druck P.L. (1987) The influence of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science* 18: 19–29.

Hosey G.R., Skyner L.J. (2007) Self-injurious behavior in zoo primates. *International Journal of Primatology* 28: 1431–1437.

Hosey G., Melfi V., Formella I., Ward S.J., Tokarski M., Brunger D., Brice S. Hill S.P. (2016) Is wounding aggression in zoo-housed chimpanzees and ring-tailed lemurs related to visitor numbers? *Zoo Biology* 35: 205–209.

Hutchings K, Mitchell H, Gilbert T.C. (2003) A comparison of the behaviour of captive lemurs subjected to different causes of disturbance at Marwell Zoological Park. In *Proceedings of the 5th Annual Symposium on Zoo Research*, Marwell Zoological Park, Winchester, UK, pp. 139–143, Federation of Zoological Gardens of Great Britain and Ireland

Jens W., Mager-Melicharek C.A.X., Rietkerk F.E. (2012) Free-ranging New World primates in zoos: cebids at Apenheul. *International Zoo Yearbook* 46: 137–149.

Jolly A. (1966) *Lemur Behavior: A Madagascar Field Study*. Chicago: University of Chicago Press.

Jones H., McGregor P., Farmer H., Baker K. (2016) The influence of visitor interaction on the behavior of captive crowned lemurs (*Eulemur coronatus*) and implications for welfare. *Zoo Biology* 35: 222–227.

Keith-Lucas T., White F.J., Keith-Lucas L., Vick L.G. (1999) Changes in behavior in free-ranging *Lemur catta* following release in a natural habitat. *American Journal of Primatology* 47: 15–28.

Kirchgessner M.L., Sewall B.J. (2015) The impact of environmental, social, and animal factors on visitor stay times at big cat exhibits. *Visitor Studies* 18: 150–167.

Kuhar C.W. (2008) Group differences in captive gorillas' reaction to large crowds. *Applied Animal Behaviour Science* 110: 377–385.

Larsen M.J., Sherwen S.L. Rault J.-L. (2014) Number of nearby visitors and noise level affect vigilance in captive koalas. *Applied Animal Behaviour Science* 154: 76–82.

Lee H.S. (2012) Perception and satisfaction among zoological park visitors. *Journal of the Korean Institute of Landscape Architecture* 40: 51–59.

Lehner P.N. (1996) *Handbook of Ethological Methods.* Cambridge: Cambridge University Press.

Luebke J.F., Matiasek J. (2013) An exploratory study of zoo visitors' exhibit experiences and reactions. *Zoo Biology* 32: 407–416.

Maia C.M., Volpato G.L., Santos E.F. (2012) A case study: the effect of visitors on two captive pumas with respect to the time of the day. *Journal of Applied Animal Welfare Science* 15: 222–235.

Mallapur A., Chellam R. (2002) Environmental influences on stereotypy and the activity budget of Indian leopards (*Panthera pardus*) in four zoos in southern India. *Zoo Biology* 21: 585–595.

Margulis S.W., Hoyos C., Anderson M. (2003) Effect of felid activity on zoo visitor interest. *Zoo Biology* 22: 587–599.

Mitchell G., Tromborg C.T., Kaufman J., Bargabus S., Simoni R., Geissler V. (1992) More on the 'influence' of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science* 35: 189–198.

Morgan J.M., Hodgkinson M. (1999) The motivation and social orientation of visitors attending a contemporary zoological park. *Environment and Behavior* 31: 227–239.

Morris D. (1964) The response of animals to a restricted environment. *Symposium of the Zoological Society of London* 13: 99–118.

Moss A., Esson M. (2013) The educational claims of zoos: Where do we go from here? *Zoo Biology* 32: 13–18.

Moss A., Francis D., Esson M. (2008) The relationship between viewing area size and visitor behavior in an immersive Asian elephant exhibit. *Visitor Studies* 11: 26–40.

Mun J.S.C., Kabilan B., Alagappasamy S., Guha B. (2013) Benefits of naturalistic free-ranging primate displays and implications for increased human–primate interactions. *Anthrozoös* 26: 13–26.

Nimon A.J., Dalziel F.R. (1992) Cross-species interaction and communication: a study method applied to captive siamang (*Hylobates syndactylus*) and long-billed corella (*Cacatua tenuirostris*) contacts with humans. *Applied Animal Behaviour Science* 33: 261–272.

Owen C. (2004) Do visitors affect the Asian short-clawed otter in a captive environment. In *Proceedings of the 6th Annual Symposium on Zoo Research-BIAZA*, 202–211.

Pereira M.E., Weiss M.L. (1991) Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology* 28: 141–152.

Ramsay N.F. (1995) *The influence of environmental constraints on aspects of the eco-ethology of the lemurs (Lemur catta) Linnaeus 1785 and (Eulemur fulvus mayottensis) Schlegel 1866 in wild and captive environments.* PhD Thesis. University College Cork, Cork, Ireland.

Rasamimanana H., Andrianome V.N., Rambeloarivony H., Pasquet P. (2006) Male and female ringtailed lemurs' energetic strategy does not explain female dominance. In: Jolly, A, Sussman, R.W., Koyama, N. & Rasamimanana, H. (Eds) *Ringtailed Lemur Biology*, Springer US. 271–295.

Sellinger R.L., Ha J.C. (2005) The effects of visitor density and intensity on the behavior of two captive jaguars (*Panthera onca*). *Journal of Applied Animal Welfare Science* 8: 233–244.

Sherwen S.L., Hemsworth P.H., Butler K.L., Fanson K.V., Magrath M.J. (2015) Impacts of visitor number on Kangaroos housed in free-range exhibits. *Zoo Biology* 34: 287–295.

Shire T. (2012) *Differences in behavior between captive and wild ring-tailed lemur (Lemur catta) populations: Implications for reintroduction and captive management. MSc Thesis number 12459. Iowa State University.*

Sickler J., Fraser J. (2009) Enjoyment in zoos. *Leisure Studies* 28: 313–331.

Skibins J.C., Powell R.B. (2013) Conservation caring: Measuring the influence of zoo visitors' connection to wildlife on pro-conservation behaviors. *Zoo Biology* 32: 528–540.

Webster D. (2000) The setting up of a public walk-through mixed lemur exhibit. *Ratel* 27: 156–164.

Wood W. (1998) Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes)*. *Zoo Biology* 17: 211–230.

Woods B. (2002) Good zoo/bad zoo: Visitor experiences in captive settings. *Anthrozoös* 15: 343–360.

Woolway E.E., Goodenough A.E. (2017) Effects of visitor numbers on captive European red squirrels (*Sciurus vulgaris*) and impacts on visitor experience. *Zoo Biology* 36: 112–119.