Received: 1 September 2016 | Revised: 24 April 2017 | Accepted: 8 May 2017
DOI: 10.1002/zoo.21370

RESEARCH ARTICLE

WILEY ZOOBIOLOGY

The effects of environmental and visitor variables on the behavior of free-ranging ring-tailed lemurs (*Lemur catta*) in captivity

Courtney Collins[1] | Ilse Corkery[2] | Amy Haigh[1] | Sean McKeown[3] | Thomas Quirke[1] | Ruth O'Riordan[1]

[1] School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

[2] IRD Duhallow, Newmarket, Cork, Ireland

[3] Fota Wildlife Park, Carrigtwohill, Cork, Ireland

Correspondence
Courtney Collins, School of Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Ireland.
Email: courtney.collins1@umail.ucc.ie

Funding information
The Irish Federation of University Teachers; School of Biological, Earth and Environmental Sciences at UCC

The effect of the zoo environment on captive animals is an increasingly studied area of zoo research, with visitor effects and exhibit design recognized as two of the factors that can contribute to animal welfare in captivity. It is known that in some situations, visitors may be stressful to zoo-housed primates, and this may be compounded by environmental factors such as the weather, the time of day, and zoo husbandry routines. Exhibit design and proximity of the public are also known to influence behavioral response of primates to visitors; however, there is minimal research on free-ranging zoo animals, even though they are potentially subjected to intense interactions with visitors. The current study explores the effect of the zoo environment, several visitor variables and specific animal–visitor interactions on the behavior of free-ranging ring-tailed lemurs (*Lemur catta*) at Fota Wildlife Park, Ireland. Data were obtained through scan samples collected over 18 months (n = 12,263) and analyzed using a range of statistical tests, including general estimating equations (GEE). Results demonstrate that the free-ranging lemurs' behavior at Fota Wildlife Park is affected by season, weather and time of day. Similarities in feeding behavior exist between the free-ranging group and lemurs in the wild when resources are plentiful. Visitor variables had a limited effect on lemur behavior and behavioral diversity level. Lemurs rarely reacted to visitors when specific interactions were considered. Generally, the results indicate that the ring-tailed lemurs in this study have adapted well to the zoo environment and habituated to visitors.

KEYWORDS
animal behavior, free-ranging, ring-tailed lemur, visitor effects, zoo environment

1 | INTRODUCTION

As fragmentation and destruction of natural habitats continues, the potential for zoos to contribute to conservation and education has increased (Rabb, 2004). Most zoos list conservation and education as two of their main goals (Patrick, Matthews, Ayers, & Tunnicliffe, 2007), although many visitors report that entertainment is their primary reason for visiting a zoo (Reade & Waran, 1996). However, visitors may be more likely to engage in pro-conservation behavior, if they develop a positive connection to wildlife during a zoo visit (Skibins & Powell, 2013). Yet, there is limited quantifiable data surrounding animal–visitor interactions, even though they are a daily part of life in the zoo.

Thus the stated goals of zoos might be incompatible, if the visitors to be educated and entertained are causing stress and diminished welfare to captive animals as a result of their presence and/or behavior (Fernandez, Tamborski, Pickens, & Timberlake, 2009; Hosey, 2000).

Human–animal relationships (HARs) can develop in the zoo over time from successive general interactions between animals and humans (Hosey, 2008). Yet, it is unlikely that individual relationships form with visitors, rather an animal probably perceives all unfamiliar humans in a general way and one HAR forms with all visitors (Hosey, 2008). Of course zoo visitors may perceive this differently; some visitors report a positive emotional connection to a specific animal or species while viewing them (Clayton, Fraser, & Saunders, 2009; Myers, Saunders, & Birjulin, 2004). The animal's perception of the interaction will vary depending on variables such as personality and previous experience with humans. Cumulative positive experiences with familiar humans could lead to more positive perceptions of unfamiliar humans like visitors (Hosey, 2008). This has led to the development of a model which can help to predict an animal's response to visitors (which varies from visitors inducing high stress to visitors being enriching) based largely on that animal's previous experience with both familiar and unfamiliar humans (Claxton, 2011; Hosey, 2008). However, empirical evaluations of direct human–animal interactions (HAI) in the zoo are rare compared to other areas like agricultural settings (Hosey & Melfi, 2014), even though visitor experiences involving close contact with animals are becoming more prevalent in zoos. In fact in the United Kingdom, 16 out of 36 BIAZA (British and Irish Association of Zoos and Aquariums) zoos currently offer visitor feeding experiences with lemurs (Jones, McGregor, Farmer, & Baker, 2016). One study which observed the behavioral response of crowned lemurs' (*Eulemur coronatus*) during a visitor feeding experience found that the experience had very little effect on the primates (Jones et al., 2016). The authors conclude that there were even indications of improved welfare through reduced lemur aggression (compared to keeper only feeds), perhaps due to reduced competition, and no indication of compromised welfare.

Visitor effects, a more established area of zoo research, considers the effect of visitors on the behavior (and more recently physiological effects, Clark, Fitzpatrick, & Hartley, 2012) of exhibited animals. As with HAR and HAI, the presence of visitors has been described as potentially having no effect, an enriching effect, or a stressful effect on captive animals (Hosey, 2000). Research in this area has primarily focused on primates, and broadly, it has shown that as visitor numbers increase, visitor directed aggression, con-specific aggression, threats, and activity levels increase, while feeding, resting, and affiliative behaviors decrease (Birke, 2002; Carder & Semple, 2008; Glatston, Geilvoet-Soeteman, & Van Hooff, 1984; Kuhar, 2008; Mitchell et al., 1991; Wells, 2005; Wood, 1998). Large, active, noisy crowds may be the most stressful to captive primates (Hosey, 2000, 2005; Mitchell et al., 1992). Specifically, in ring-tailed lemurs (*Lemur catta*) housed in traditional zoo enclosures, visitor presence has been associated with increased activity and aggression, but decreased grooming; this display of behavior expressed by lemurs and monkeys when zoo visitors are present, and has been described as stressful excitement (Chamove, Hosey, & Schaetzel, 1988; Hosey, 2008). However, this is a broad summary, and it is not only species type and individual animal characteristics, but several environmental variables of the zoo setting such as season, weather, time of day, husbandry routines, and exhibit design that may influence behavioral response to visitors (Clark et al., 2012; Hosey, 2000; Stoinski, Jaicks, & Drayton, 2012).

A recurring finding from visitor effect studies, which extends to various taxonomic groups, is that the ability to retreat from visitors lessens visitor induced stress (Carlstead & Shepherdson, 2000; Collins & Marples, 2015; Hosey, 2000). Thus, exhibit design is of significant importance when considering visitor effects (Sherwen, Hemsworth, Butler, Fanson, & Magrath, 2015). One area that visitor effect studies have almost entirely overlooked is that of free-ranging zoo animals. Free-ranging zoo animals have the opportunity to retreat from visitors, but can potentially be exposed to more intense interactions with the public,who might attempt to chase, touch or even feed free-ranging animals (Jens, Mager-Melicharek, & Rietkerk, 2012; Mun, Kabilan, Alagappasamy, & Guha, 2013), depending on the zoo management strategy. There is evidence that visitors prefer to see animals in more naturalistic settings and specifically free-ranging animals, and that visitors may develop more positive attitudes to free-ranging animals (Coe, 1989; Finlay, James, & Maple, 1988; Hosey, 2005; Mun et al., 2013; Price, Ashmore, & McGivern, 1994), but there is only minimal research on how free-ranging animals are affected by their environment and zoo visitors.

A recent study on two kangaroo species (*Macropus fuliginosus fuliginosus*, and *Macropus rufus*), who were kept in a free-range exhibit, found the animals' behavior changed little between quiet and busy days (Sherwen et al., 2015). The absence of avoidance behavior, aggression or change in FGM (fecal glucocorticoid metabolites) concentration between quiet and busy days suggested that visitors had a minimal effect on the kangaroos, however, the kangaroos did spend most of their time in retreat zones when visitors were present (Sherwen et al., 2015). Additionally, Choo et al. (2011) investigated several aspects of visitors on free-ranging captive orang-utan (*Pongo pygmaeus*) behavior and found that visitors had little influence on the primates' behavior and that the orang-utans in their study have primarily habituated to visitors. However, in both studies, visitor access was in some way restricted so that they were not able to touch, feed or approach too closely during the study period which inherently limits the potential for HAIs.

Mun et al. (2013) considered both primate and visitor reaction at three different free-range exhibits at Singapore Zoo. The exhibits included cotton-top tamarins (*Saguinus oedipus*), where some barriers and ranging restrictions were in place, White-faced saki (*Pithecia pithecia*), where no barriers or ranging restrictions were in place, and Orangutan (*P. pygmaeus* and *P. abelii*), where hotwire barriers and ranging restrictions were in place. Visitors most enjoyed seeing the cotton-top tamarins, which is the exhibit where animals were the most visible (92.1%) and in closest proximity to visitors. However, this is also the exhibit that attracted the highest number of visitors and where the most intense negative animal–visitor interactions occurred, including touching or feeding by humans and biting or scratching by the tamarins

(Mun et al., 2013). However, visitors thought that all three exhibits contributed to enhanced animal welfare, and that they had high educational value.

Additionally, Price et al. (1994) discovered that visitors spent more time looking at free-ranging cotton-top tamarins (*S. oedipus*), made more comments about them, perceived them to have improved welfare and a higher educational value than their caged counterparts. Apenheul Primate Park, the Netherlands and Durrell Wildlife Park, UK, use several different ways of communicating to the public about free-ranging animals, including "guard keepers" and volunteers; however, undesirable animal–visitor interactions still occur (Jens et al., 2012; Price et al., 2012). Yet, more than 90% of visitors reported that they appreciate the close encounters with the animals (Jens et al., 2012). Price et al. (2012) found the monkeys' reaction to visitors varied between the two zoos and among the species studied, which suggests differences in species temperament and adaptation to their surroundings were important in the free-ranging animals observed in the study.

An early study considered how environmental variables affect ring-tailed lemur behavior in a range of captive environments (Ramsay, 1995). It was found that lemur behavior varied based on time of day and season in particular. This pattern was most evident in the free-ranging group at Fota Wildlife Park, which may be attributable to the lemurs' ability to feed naturally (Ramsay, 1995). Although Ramsay (1995) speculated that disturbance from visitors may influence the lemurs' use of the park during the summer months, the behavior of the free range group was found to be most similar to wild lemurs.

When considering the effect of the zoo environment on a captive species, it is practical to first consider the natural history of the species and the behavior of conspecifics in the wild (Hosey et al., 2013; Sherwen et al., 2015). Ring-tailed lemurs are characterized by their behavioral flexibility and adaptability (Gould, Sussman, & Sauther, 1999; Sauther, Sussman, & Gould, 1999). Yet, the wild population continues to decline due to habitat destruction and hunting and they are now classified as endangered (IUCN, 2017). Lemurs are a commonly held species in captivity with an estimated 3,318 ring-tailed lemurs in zoos around the world as of 2014 (Species 360, 2017). While the future may comprise life in zoos and wildlife parks for this species, their adaptability, social intelligence, opportunistic behavior, and ability to adjust to new environments make them one of the most suitable primate species for free-range displays (Dishman, Thomson, & Karnovsky, 2009; Jolly, 1966a; Keith-Lucas, White, Keith-Lucas, & Vick, 1999). However, more research is needed to clarify the animals' behavioral response to the zoo setting, in order for zoos to meet their goals of visitor enjoyment, conservation and animal welfare. The purpose of the present research is (1) to investigate the effects of environmental and visitor variables of the zoo on the behavior of free-ranging ring-tailed lemurs; (2) to explore the relationship between crowd size and visitor frequency on the behavioral diversity level of the lemur group; and (3) to examine interactions between zoo visitors and free-ranging ring-tailed lemurs.

2 | METHODOLOGY

2.1 | Study site

The study took place at Fota Wildlife Park (Fota), Carrigtwohill, Ireland (51.889585°N, 8.311276°W). Fota Wildlife Park has kept free-ranging ring-tailed lemurs since 1983. The animals are able to roam the entire park; their movements are completely unrestricted even at night. The staff have observed the lemurs leaving the park, though they are most often located in the lower half of the park, where all of the data for this study were recorded. Visitors are able to directly approach the lemurs, and they are not expected to follow a particular path to view the lemurs. In 2006, with the aim of promoting both lemur welfare and visitor enjoyment, Fota Wildlife Park began its "lemur patrol" project. "Lemur patrol" are staff employed by the park to manage and protect the free-ranging lemur group. The data used in the current study examine two 8-month periods of that project between March 2009 and October 2010. At the time that the research occurred, the wildlife park was approximately 75 acres and received about 300,000 visitors annually.

2.2 | Animals

The study involved a group of free-ranging ring-tailed lemurs. All of the animals in the study were captive born and mother reared. The number of animals varied between 13 lemurs (five males; eight females) in 2009 and 11 lemurs (four males; seven females) in 2010, after one male lemur died and one female lemur was transferred. Ideally, lemur patrol staff attempt to keep the visitors approximately 1 m away from the lemurs; however, this is not always possible and close contact interactions, such as touching, do occur. The study site consisted of a woodland environment with 26 different species of predominantly native trees, a lake, a stream and grassland areas. The lemurs had a "base," which included a sheltered hut where they were fed a scatter feed of monkey pellets, vegetables and a small amount of fruit by staff twice per day; natural foraging also contributed to their diet. The free-ranging ring-tailed lemurs at Fota Wildlife Park are known to feed on 20 species of plant, with considerable seasonal variation (Ramsay, 1995). Common Yew (*Taxus baccata*) is the most frequently foraged item (Foley, 2016).

2.3 | Procedure

Data were recorded using instantaneous scan sampling with an inter-scan interval of 10 minutes between approximately 09:30 and 17:30 hr each day (Altmann, 1974). The following were recorded during each scan, which began when the first lemur's behavior was recorded and ended when the last lemur's behavior was recorded: the number of visitors present, the behavior, position and location of the lemur group, any outside stimulus, the presence of a baby stroller, since primate interest in strollers is a concern with free-ranging monkeys (Jens et al., 2012), the weather conditions and the time (see Table 1–3 for details of variables and recording methods). During the scan, lemur–visitor interactions were also recorded. This included any overt visitor

TABLE 1 Ethogram of common lemur behaviors and positions at Fota Wildlife Park

Behaviors	Definition
Not visible	Out of sight (excluding hut)
Inactive	Lying down, sitting, no movement, sleeping, no contact or interaction with conspecifics
Groom	Autogroom; biting, licking, scratching
Feed/ forage	Ingesting food; eating, drinking, looking for food; head in contact with the ground, uncovering or searching for a food item.
Locomotion	Any movement from one location to another; walking, running, climbing
Affiliative	Allo-grooming; huddled or basking together; play
Hut	Not visible, but known to be in the hut
Positions	
"Up"	Elevated on any structure such as a roof, table, tree
"Down"	Touching the ground

behavior toward any lemur and any attempt of lemurs to interact with visitors. Any subsequent reaction of either the lemurs or visitors to the interaction was also recorded if it occurred during the duration of the scan. Lemur–visitor interactions that occurred outside the scan were excluded from the study. This led to a total of 12,263 instantaneous scans samples on 300 days during the study period.

Several different researchers, who were trained by the principal investigator and followed a standardized protocol, recorded data each year. It was not possible to test inter-observer reliability, therefore, "observer" was initially treated as a dependent variable; however, preliminary results showed virtually no observer effect so "observer" was discounted from any further analysis. Lemurs had habituated to the presence of the researchers, and did not impact the primates' behavior. Researchers were not counted as visitors, and they followed the lemur group throughout the park during the day; they did not interfere with the lemurs or visitors, but they came close enough to observe the interactions and behaviors of the lemurs and the visitors. The lemurs were difficult to distinguish individually; and, because of the large number of variables that were recorded during each scan, behavior of the group was observed, by recording the number of individuals engaged in a specific behavior at each scan sample point. Since lemurs are known to synchronize their activities this was considered an effective method of data collection (Sauther et al., 1999).

2.4 | Data analysis

Before applying any statistical models, data exploration, following the protocol described in Zuur, Ieno, and Elphick (2010) was carried out. Only observations including the entire lemur group were included in the analysis (n = 11,997). The total number of times specific lemur behaviors and positions were observed during varying environmental and visitor variables were modeled using generalized estimation equations (GEE) with a Poisson distribution and a normal error structure. Covariates considered in the model include: time, season, weather, stimulus, location, visitor number, visitor behavior, and presence of a baby stroller (Tables 2 and 4); all dependent variables were modeled separately. All interactions investigated in the model are shown in Table 4. The package geeM (McDaniel & Henderson, 2013) in the software R version 3.2.3 was used to estimate the parameters of the GEEs. Generalized estimating equations are an extension of generalized linear models and allow for correlated responses (Diggle, Liang, & Zeger, 1995). Originally, these methods were developed for longitudinal data and repeated measures models. We specified an auto-regressive correlation; the correlation between observations separated by one time unit (each consecutive sampling day) is likely to be more similar than those separated by larger time units.

Additionally, as there is substantial evidence that increased behavioral diversity is a positive result of a treatment or condition (Carlstead & Shepherdson, 2000; Clark & Melfi, 2012), we considered overall behavioral diversity (BD) level as an indicator of welfare. Behavioral diversity was calculated for each observation, using the Shannon-Weaver diversity index H (Shannon & Weaver, 1949). For a full description of the methodology, see Collins, Quirke, Overy, Flannery, and O'Riordan, (2016).

Spearman's rank correlation tests (SPSS 22, Inc.) were used to examine the relationship between behavioral diversity and visitor number. Both the instantaneous and daily effect of visitors were analyzed (Kuhar, 2008; Stevens, Thyssen, Laevens, & Vervaecke, 2013). To test the instantaneous effect of visitors (e.g., "crowd size," Fernandez et al., 2009, p. 5), we used the full dataset (n = 11,997) and for each scan noted how many visitors were present (visitor number as a continuous independent variable; corresponding behavioral diversity level as the continuous dependent variable). To test the daily or cumulative effect of visitors (e.g., "visitor frequency," Fernandez et al., 2009, p. 5) on behavioral diversity, we calculated the total number of visitors per day by summing the total number of visitors recorded per scan sample for 1 day, while this does not include visitors that viewed lemurs between scans it was as accurate as was feasible for this study, and then the mean behavioral diversity was calculated per day (n = 300).

Finally, to investigate the number of scans during which an interaction occurred between zoo visitors and free-ranging ring-tailed lemurs some brief descriptive statistics are offered. Then, to explore if specific visitor behaviors were associated with specific lemur actions, a Fisher's Exact Test was performed. Hosey et al. (2013; p. 475) defines interaction as "some kind of behavior performed by one individual that influences the behavior of another [individual]", based on the definition by Estep and Hetts (1992). Additionally, we consider that visitor behavior may not lead to an obvious lemur response; however, only observations that included an overt visitor behavior toward the lemurs (n = 76) were included (Table 3).

Post hoc testing using adjusted residuals to calculate p-values was performed to determine where differences among cells of the contingency table occurred (see Beasley & Schumacker, 1995). Where multiple comparisons occurred, all p-values were adjusted using the Bonferroni correction. Throughout the analysis all tests were two-tailed and the accepted alpha level was $p < 0.05$ unless stated otherwise.

TABLE 2 Summary of environmental and visitor variables included in the study

A. Environmental variables	Definition of categories	Recording method
Time	1 = Morning (9:30–12:59)	Each scan was categorized as either morning or afternoon
	2 = Afternoon (13:00–17:30)	
Season	1 = March/April	Data were collected between March–October and categorized accordingly
	2 = May/June	
	3 = July/August	
	4 = September/October	
Weather	1 = Very bad; constant rain, wind, cold	Data were recorded at every scan by the observer on a scale of 1–4.
	2 = Poor; some rain and wind, cool	
	3 = Okay; some cloud, light wind	
	4 = Very good; sunny, mild, no wind	
Stimulus	1 = No	The presence of a stimulus (zoo vehicle, zoo staff, other species present) was recorded at each scan
	2 = Yes	
Location	Locations 1–5 (see Figure 1)	The location of the group was recorded at each scan.
B. Visitor related variables	**Definition of categories**	**Recording method**
Visitor number	Total number of visitors present when a scan occurred	Visitors had to be within 3 m of any lemur with at least one member of the visitor group actively watching/looking at/ engaged with the lemurs, rather than walking by; visitors were counted and recorded by the observer.
Visitor behavior	1 = Visitors compliant with park rules or not present	If any member of the visitor group engaged or attempted to engage in any behavior not compliant with park rules, the incident was recorded for that scan; unsuccessful actions that may have been stopped by staff were included here.
	2 = Visitors not compliant with park rules (See Table 3 for details of specific behaviours)	
Baby Stroller	1 = No baby stroller is present	The presence or absence of at least one child's stroller was recorded at each scan.
	2 = Baby stroller is present	

3 | RESULTS

3.1 | Effect of environmental variables on lemur behavior and position

In summary, the effect of the environmental variables within the zoo setting had varying effects on ring-tailed lemur behavior and positions. Season and weather influenced all lemur behaviors (except feeding); they had similar effects on grooming and hut behavior with an increase in grooming later in the season and as the weather improved, and a converse decrease in hut use across both variables. Increased affiliative behavior and inactivity were observed more often later in the season. Additionally, lemurs spent less time "not visible," and in the hut and more time in locomotion and on the ground as weather conditions improved. From morning to afternoon (time), there was a decrease in feeding/foraging and an increase in inactivity and hut use. The presence of a zoo stimulus was associated with an increase in feeding/foraging, locomotion, and time on the ground, and a decrease in affiliative behavior. Time and stimulus interact in their effects on several behaviors; for example, time of day has no effect on the number of lemurs on the ground when there is a stimulus present, but in the absence of a stimulus, more lemurs are recorded on the ground in the afternoon (Figure 1 and Table 4).

3.2 | Effect of visitor variables on lemur behavior and position

Visitor related variables had varying effects on lemur behavior. As the number of visitors present at any one time increased, the numbers of lemurs in locomotion and on the ground also increased. Visitor behavior did not affect any lemur behavior or position. The presence of a baby stroller was associated with a decrease in locomotion and grooming; however, if the stroller was present in the afternoon grooming increased (Table 4).

TABLE 3 Lemur–visitor interactions observed during the study

A. Lemur behavior	Description of behavior	Recording method
1 = No response	1 = no action directed at visitor group by lemurs	If any lemurs engaged in any of these behaviors (2, 3, or 4) during the scan the behavior was recorded for that scan. Not all actions were successful (e.g., obtaining food), but an overt attempt (within 1 m) that may have been interrupted or stopped by staff was included here.
2 = Approach	2 = lemur(s) approach visitors	
3 = Food related	3 = lemur(s) beg, receive or attempt to get food	
4 = Retreat	4 = lemur(s) run away	
B. Visitor behavior	**Description of behavior**	**Recording method**
1 = Approach	1 = visitor(s) pet or touch lemurs	If any member of the visitor group engaged in any of these behaviors during the scan the behavior was recorded for that scan; not all actions were successful, but an overt attempt (within 1 m) that may have been stopped by staff was included here.
2 = Food related	2 = visitor(s) give food to lemurs	
3 = Negative action (Frighten)	3 = visitors chase, kick throw something at lemurs	

3.3 | Behavioral diversity

3.3.1 | Instantaneous "crowd size"

The Spearman rank correlation test revealed a very weak association between the number of visitors present at each scan "crowd size" and the behavioral diversity level at each scan for all observations ($r_s = 0.056$, $p = <0.001$).

3.3.2 | Daily total "visitor frequency"

The Spearman rank correlation test indicated a weak negative association between total number of visitors per day "visitor frequency" and mean daily behavioral diversity level ($r_s = -0.158$; $p = 0.006$). As daily number of visitors or "visitor frequency" increased, behavioral diversity of the lemur group decreased.

3.3.3 | Visitor–Lemur interactions

Visitors were present during 45.9% ($n = 5512$) of the observations. The number of visitors present ranged from 1 to 65. In only 76 cases (1.38%), visitors attempted to interact with the lemurs, and in only 96 (1.03%) cases, the lemurs directed behaviors at the public. In 20 of the 96 cases (21%), when lemurs directed behavior at the public there was no reciprocal action from the visitors. Out of the 76 times that visitors attempted to interact with the lemurs; 0.04% ($n = 3$) of the interactions were approaches to the lemurs, 59.21% ($n = 45$) of the interactions were attempts to feed the lemurs, and 36.84% ($n = 28$) of the interactions were attempts to frighten the lemurs.

Because no overall effect of visitor behavior (as a binary variable) on lemurs' behavior was found (Table 4), Fisher's exact test was used to isolate effects of specific visitor behaviors on lemur actions. A significant difference between visitor behavior and lemur action ($p < 0.001$) was detected. However, after the Bonferroni correction was applied (at $0.05/12\ \alpha = 0.004$), none of the comparisons between visitor behavior and lemur action remained significant (Figure 2 and Table 5).

4 | DISCUSSION

Common environmental and visitor variables within the zoo affect the behavior, position, and behavioral diversity level of a free-ranging ring-tailed lemur group to varying degrees. Previous research has shown that time of day, season and weather affect free-ranging ring-tailed lemur behavior (Ramsay, 1995) and these results support that. In both studies, lemurs were more active during drier, warmer, lighter conditions, and conversely lemurs spent more time in their hut and not visible during colder, wetter, darker conditions (later in the day). Ramsay (1995) also reported an increase in feeding/foraging due to seasonality. Here, feeding was the only behavior not influenced by weather or season, though this is probably because the current data were collected from March to October when food was plentiful. However, the current results concur with Ramsay (1995) and studies from the wild (Jolly, 1966b) that intense feeding/foraging is likely to occur in the morning.

The increase in inactivity, grooming, and affiliative behavior and the absence of intra-group aggression observed in this study from March to October indicates that the lemurs have a diverse repertoire of behavior when resources are not limited. Additionally, the increase in affiliative behavior observed in this study coincides with the early stage of lemurs' natural breeding period at Fota Wildlife Park, which has also been observed in wild populations (Jolly, 1966b). The breeding period at Fota occurs approximately 6 months after the natural breeding period of wild lemurs in the Southern hemisphere, as is

TABLE 4 Results from GEE test, showing estimated parameters and *p*-values for each statistically significant covariate ($p < 0.05$)

Behaviors	Feeding	Grooming	Hut	Affiliative	NV	Locomotion	Inactive	Up/down
Model intercept	0.338 (0.493)	−2.288 (<0.001)	1.807 (<0.001)	2.129 (<0.001)	0.370 (0.383)	−1.386 (<0.001)	0.713 (0.004)	−0.435 (0.2)
Environmental variables								
Time	↓−0.458 (0.006)	–	↑ 0.534 (0.009)	–	–	–	↑ 0.149 (0.048)	↑ 0.458 (<0.001)
Season	–	↑ 0.104 (0.025)	↓ −0.828 (<0.001)	↑ 0.1418 (0.003)	–	–	↑ 0.192 (<0.001)	↓ 0.250 (<0.001)
Weather	–	↑ 0.245 (< 0.001)	↓ −0.502 (<0.001)	–	↓ −0.086 (0.005)	↑ 0.072 (0.005)	–	↑ 0.032 (<0.001)
Stimulus	↑ 0.572 (<0.001)	–	–	↓ −1.087 (<0.001)	–	↑ 0.940 (<0.001)	–	↑ 0.041
Location	–	–	NA	↓ −0.317 (<0.001)		–	–	–
Visitor variables								
Visitor number	–	–	–	–	–	↑ 0.031 (0.009)	–	↑ 0.021 (0.037)
Visitor behavior	–	–	–	–	–		–	–
Baby stroller	–	↓ −0.660 (0.011)	–	–	–	↓ −0.381 (0.024)	–	–
Interactions								
Time:pram	–	↑ 0.420 (0.005)	–	–	–	–	–	–
Time:stimulus	↑ 0.231 (0.004)	–	–	–	–	↓ −0.241 (0.006)	↓ −0.164 (<0.001)	↓ 0.282 (<0.001)
Time:visitor no.	–	–	–	–	–	–	–	–
Location:visitor behavior	–	–	NA	–	–	–	–	–

Statistical analysis began with the baseline or the lowest category of a variable and was then compared against the higher categories (see Table 2 for reference categories). Arrows refer to a statistically significant increase (↑) or decrease (↓) in behavior. Hut behavior could only occur in one location.

expected in Northern hemisphere populations (Parga & Lessnau, 2005). Wild lemurs are known to exhibit sexual consortships during the breeding season, though they also become more aggressive during mating, which was not observed here (Jolly, 1966b; Sauther et al., 1999).

It was discovered that in general, behavior does not vary with location at Fota Wildlife Park. Therefore, it is unlikely that the group is traveling to certain locations to exploit a specific food source, as lemurs in the wild are known to do (Sauther et al., 1999). This is probably due to the abundance of food available to the lemurs at Fota Wildlife Park. The nature of the zoo means that even for free-ranging animals, resources will never truly be scarce, which inherently limits certain behaviors and potential environmental stressors (Parga & Lessnau, 2005). Though it is difficult to directly compare Fota's free-ranging lemur group behavior to wild lemur behavior because of differences in methodology, similarities in behavior between free-ranging groups in captivity and wild lemurs in Madagascar are known to exist (Keith-Lucas et al., 1999). Here, we suggest that the behavior patterns of the free-ranging lemurs at Fota Wildlife Park are similar to lemurs in the wild when food is not scarce. We did not observe intra-group aggression, which can occur when resources are limited in wild populations (Budnitz & Dainis, 1975; Sauther et al., 1999), nor did we observe stereotypies sometimes displayed by traditionally caged captive lemurs (Dishman et al., 2009; Tarou, Bloomsmith, & Maple, 2005). Additionally, the number of species foraged and the daily foraging pattern observed at Fota Wildlife Park is similar to wild populations. The free-ranging lemur group at Fota has been observed to forage 20 different plant species (Ramsay, 1995), 17 species were foraged at another free-range environment (Keith-Lucas et al., 1999), and 24 in the wild (Jolly, 1966b). The current study observed the lemurs between 09:30 and 17:30 hr; however, during the summer months the lemurs might continue to be active later in the evening and future work should include longer daily observation periods and, if possible, observations when resources are limited to capture the full repertoire of lemur behavior.

One of the complexities of zoo research can be the sudden and unexpected appearance of staff or a zoo vehicle. Many researchers have ceased observations because of the obvious change in an animal's behavior at the appearance of an unexpected stimulus. However, here,

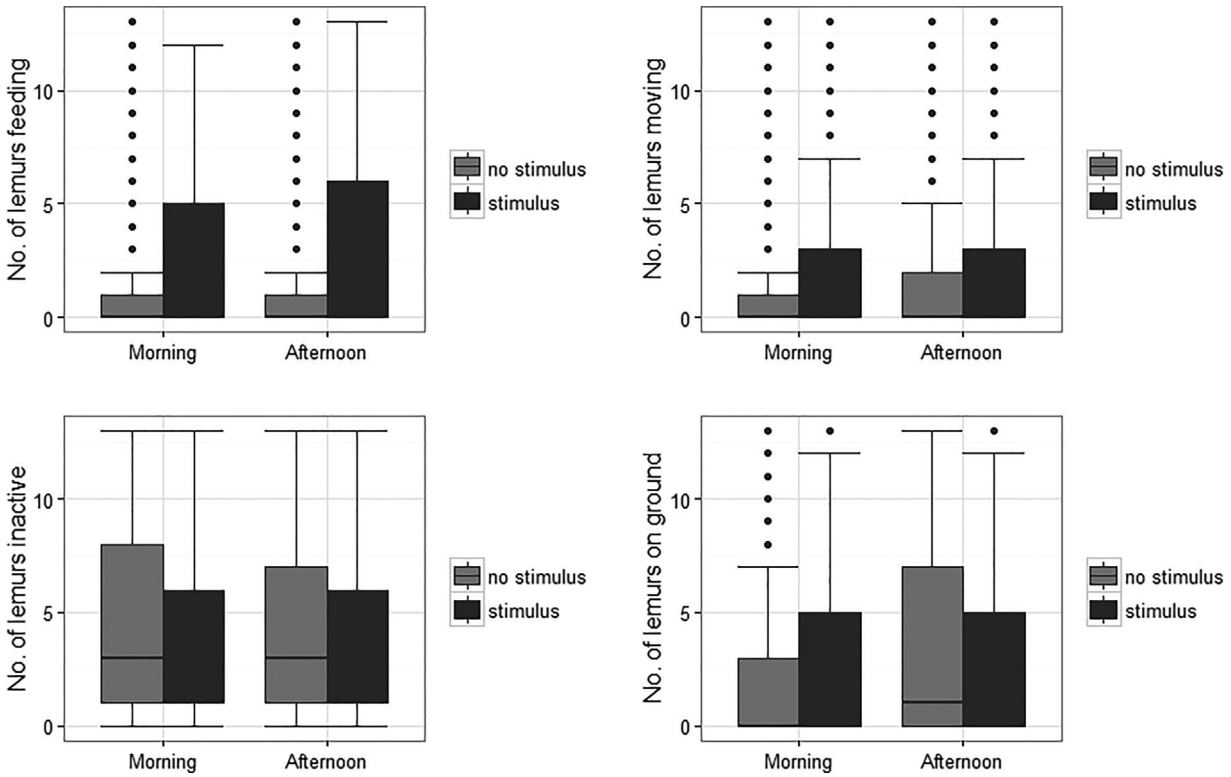

FIGURE 1 The effect of the interactions between time of day and stimulus on the following recorded behaviors; feeding, locomotion, inactivity and "on ground." The horizontal lines are the limits of the nominal range of the data inferred from the upper and lower quartiles, the points that fall outside this range are denoted as open circles

it was decided to use this information in order to quantify one of the most frequently occurring variables of the zoo setting on animals' behavior. The presence of a zoo stimulus was associated with an increase in feeding, locomotion and being on the ground and a decrease in affiliative behavior. The animals may associate zoo staff and vehicles with food, since when a stimulus occurs, locomotion and feeding increase, as lemurs presumably run to investigate and are then fed. The decrease in affiliative behavior when a stimulus occurs is probably because of the increase in feeding and locomotion. An interaction effect of time and stimulus may indicate lemurs' awareness of the husbandry routine and zoo schedule (Figure 1). More research is needed to clarify this and tease out lemur reaction to different types of zoo stimuli at different times of day.

In conjunction with considering environmental zoo variables, we also considered visitor related variables. Like Choo et al. (2011), we investigated several different aspects of visitors including number, behavior, and the presence of a baby stroller. Visitor number had a limited influence on lemur behavior, which is similar to what other studies on free-ranging species report (Choo, Todd, & Li, 2011; Sherwen et al., 2015). As visitor number increased locomotion and "on the ground" increased, this is supportive of the visitor attraction hypothesis (Hosey, 2000). The moving, visible animals probably attracted a larger crowd. The fact that the lemurs were visible on the ground suggests that they were not frightened of visitors, though it is possible that they were retreating. However, results from this study on lemur–visitor interactions indicate that the lemurs rarely retreat. Manna, Rodeano, and Ferrero (2007) found little effect on lemur behavior or welfare in a visitor walk through exhibit, but like the present study, they observed an increase in terrestrial locomotion when visitors were present. Hosey, Melfi, and Formella (2016) reported no correlation between increased agonistic wounding rate in ring-tailed lemurs and increased visitor numbers in a walk through exhibit. Conversely, a study within a traditional enclosure with and without visitors present found that agonistic behavior increased, and inactivity and grooming decreased when visitors were present, which again indicates that the animals' housing system and ability to retreat is of significant importance (Chamove et al., 1988).

We found that high daily total visitor numbers were associated with a slight decrease in behavioral diversity level, whereas there was almost no association between instantaneous behavioral diversity level and crowd size. This offers tentative evidence that lemurs are perhaps stimulated or not bothered by intermittent large groups, but when there are continual large groups of visitors (high daily totals), behavioral diversity is reduced, which could indicate an upper limit of tolerance for visitors, which has been found in some captive bird species (Collins & Marples, 2015; Nimon & Dalziel, 1992).

Previous studies have reported that free-ranging monkeys are adept at jumping on and obtaining food from baby strollers (Jens et al., 2012; Price et al., 2012). At Fota, the presence of a baby stroller was associated with a decrease in grooming, as well as a decrease in locomotion. This suggests that lemurs do not run toward or away from strollers, but may stop their usual behaviors when they are present. It

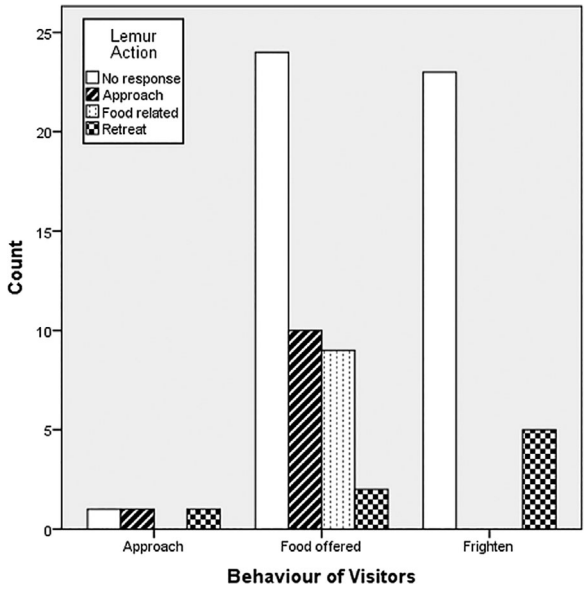

FIGURE 2 Total count of lemurs' actions (no response, approach, food related, and retreat) during three different visitor behaviors (approach, food offered, and frighten)

may be that the lemurs are anticipating food, though this is unclear, as feeding was not observed to increase when a baby stroller was present. In fact, the presence of a stroller is the only variable that was associated with a statistically significant reduction in locomotion, whereas a zoo "stimulus" caused an increase in locomotion, which is evidence that the lemurs may discriminate between visitors and staff

TABLE 5 Results of Fisher's exact test comparing visitor behavior and lemur action

	Lemur action			
	No response, *n* = 48	**Approach, *n* = 11**	**Food, *n* = 9**	**Retreat, *n* = 8**
Visitor behavior				
Approach, *n* = 3	$Z = -1.09$	$Z = 0.95$	$Z = -0.65$	$Z = 1.31$
	$\chi^2 = 1.19$	$\chi^2 = 0.90$	$\chi^2 = 0.42$	$\chi^2 = 1.72$
	$p = 0.276$	$p = 0.342$	$p = 0.516$	$p = 0.190$
	$n = 1$	$n = 1$	$n = 0$	$n = 1$
Food, *n* = 45	$Z = -2.14$	$Z = 2.31$	$Z = 2.65$	$Z = -2.08$
	$\chi^2 = 4.58$	$\chi^2 = 5.34$	$\chi^2 = 7.02$	$\chi^2 = 4.33$
	$p = 0.324$	$p = 0.021$	$p = 0.008$	$p = 0.038$
	$n = 24$	$n = 10$	$n = 9$	$n = 2$
Frighten, *n* = 28	$Z = 2.62$	$Z = -2.74$	$Z = -2.44$	$Z = 1.59$
	$\chi^2 = 6.86$	$\chi^2 = 7.51$	$\chi^2 = 5.95$	$\chi^2 = 2.53$
	$p = 0.009$	$p = 0.006$	$p = 0.015$	$p = 0.112$
	$n = 23$	$n = 0$	$n = 0$	$n = 5$

$\alpha = 0.004$ after Bonferroni correction.

(Hosey 2008; Hosey et al., 2013). More research is needed to understand the impact of strollers on free-ranging primates. Results indicate a change in lemur behavior occurred when a stroller was present, but the implications of that are ambiguous.

When visitors engaged in behaviors that were not compliant with the park's rules, there was no effect on lemur behavior, but in order to further disentangle visitor–lemur interactions in the zoo setting, we analyzed specific visitor behaviors and lemur actions. After post hoc testing, none of the comparisons between visitor behavior and lemur action were statistically significant. However, some interactions between lemurs and visitors were close to significance so, in order to avoid a type II error, they are briefly considered here. If visitors exhibited a negative action toward the lemurs (frighten), the lemurs' most common action was not to respond; however, there is also evidence that sometimes they retreated, but they did not approach or receive food when disturbed. When visitors offered food to the lemurs, again the lemurs did not often respond; however, they were sometimes observed to receive food and approach visitors, but rarely retreat. It has been suggested that food solicitation by animals is indicative of a lack of fear toward visitors (Choo et al., 2011), which these results support.

Overall results indicate that the ring-tailed lemurs at Fota Wildlife Park have probably habituated to the presence of visitors and are not suffering from diminished welfare. Even though the free-range environment offers the opportunity for intense visitor–animal interactions these rarely occur and when they do there is no indication that the lemurs are distressed. Furthermore, the present results, based on these behavior data, show that if lemurs are disturbed or frightened by visitors they can respond by running away, which allows them the opportunity to give a species-typical response to a stressful situation, which may diminish the stress of captivity (Carlstead & Shepherdson, 2000). Morgan and Tromborg (2007) give several reasons for stress in captive animals, including limited retreat space and forced proximity to humans, but at Fota Wildlife Park the lemurs can retreat at will and their movement is in no way restricted.

Visitors are especially drawn to the active, charismatic, free-ranging lemurs at Fota Wildlife Park (T. Power, personal communication, July 27, 2016) and, similar to Jones et al. (2016), we found no evidence of compromised lemur welfare during animal–visitor interactions, which may indicate that lemurs could be a useful species for enhancing educational opportunities and developing personal connections with animals. In fact, Kreger and Mench (1995, p. 155) state that "[the] human-animal bond may be the most effective way for the zoo to communicate its educational messages to the visitor." Previous research from early animal–visitor interaction studies indicates that not only do visitors desire a response from zoo animals, but that they would also like a personal connection with wild animals; zoos may facilitate this need through animal–visitor feeding experiences, which may lead to better attitudes toward individual animals and species (Kreger & Mench, 1995). However, Jones et al. (2016) issue the caveat that these types of animal–visitor interactions should focus on conservation and education, not entertainment, yet there is little evidence from current interaction experiences to show how visitors' attitudes and behavior toward conservation are influenced by

interactive experiences. Since these types of interactions are becoming more popular in zoos, more research is needed to elucidate the effect that the interactions have on both the visitors and the animals. Combining visitor–animal interactions with an educational experience, such as interpretative material and staff talks, may enhance visitor learning and improve animal welfare (Fernandez et al., 2009; Kratochvil & Schwammer 1997; Moss & Esson, 2010; Mun et al., 2013), but again more research is needed to clarify which animals are most suitable for interactions and if visitor learning is indeed affected by close interactions.

The current study has only considered one species in one environment and results are not applicable to all captive lemurs; further work on more species in more institutions with varying exhibit types is needed. However, certain species that have repeatedly not shown an adverse reaction to visitors or interactions with them under several different circumstances and that are known to have developed positive HARs could be beneficial in promoting conservation education within the zoo (Fernandez et al., 2009; Hosey & Melfi, 2015; Jones et al., 2016). The free-range environment at Fota Wildlife Park, in which the lemurs can control interactions with visitors, in combination with the ability to exhibit species-typical behavior patterns and their natural adaptability, has probably contributed to the lemurs' habituation to humans, lack of visitor induced stress and positive welfare.

5 | CONCLUSIONS

1. This study found that free-ranging ring-tailed lemur behavior is affected by time of day, season, and weather. Generally, the lemurs are more active in drier, warmer conditions.
2. The Fota lemurs exhibit similar feeding behavior patterns to wild lemurs, when resources are not limited.
3. Relatively minor effects of visitors on the free-ranging animals were detected. It was found that the animals have largely habituated to the presence of visitors, and that they benefit from being able to retreat from visitors.
4. There were relatively few animal–visitor interactions; however, continuous large crowds may lead to a reduction in behavioral diversity.
5. Ring-tailed lemurs are likely to do well in a free-range display, but it is essential that their reaction to environmental and visitor variables is investigated and understood.

ACKNOWLEDGMENTS

The authors would like to thank the staff at Fota Wildlife Park for their ongoing support of this project. Additionally, the authors would like to thank The Irish Federation of University Teachers and the School of Biological, Earth and Environmental Sciences at UCC for providing funding for this research. We are also very grateful to the anonymous reviewers for their comments and suggestions which have led to a much improved manuscript.

REFERENCES

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3), 227–266.

Beasley, T. M., & Schumacker, R. E. (1995). Multiple regression approach to analyzing contingency tables: Post hoc and planned comparison procedures. *The Journal of Experimental Education*, *64*(1), 79–93.

Birke, L. (2002). Effects of browse, human visitors, and noise on the behaviour of captive orang-utans. *Animal Welfare*, *11*, 189–202.

Budnitz, N., & Dainis, K. (1975). Lemur catta: Ecology and behavior. In I. Tattersall & R. W. Sussman (Eds.), *Lemur biology* (pp. 219–235). Plenum, New York: Springer US.

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

Carlstead, K., & Shepherdson, D., (2000). Alleviating stress in zoo animals with environmental enrichment. In G. P. Moberg & J. A. Mench (Eds.), *The biology of animal stress: Basic principles and implications for animal welfare* (pp. 337–354). Wallingford, UK: CABI.

Chamove, A. S., Hosey, G. R., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo Biology*, *7*(4), 359–369.

Choo, Y., Todd, P. A., & Li, D. (2011). Visitor effects on zoo orangutans in two novel, naturalistic enclosures. *Applied Animal Behavior Science*, *133*(1), 78–86.

Clark, F. E., Fitzpatrick, M., Hartley, A., et al. (2012). Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology*, *31*(3), 306–321.

Clark, F. E., & Melfi, V. A. (2012). Environmental enrichment for a mixed-species nocturnal mammal exhibit. *Zoo Biology*, *31*(4), 397–413.

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), 1–10.

Clayton, S., Fraser, J., & Saunders, C. D. (2009). Zoo experiences: Conversations, connections, and concern for animals. *Zoo Biology*, *28*(5), 377–397.

Coe, J. C. (1989). Naturalizing habitats for captive primates. *Zoo Biology*, *8*(S1), 117–125.

Collins, C. K., & Marples, N. M. (2015). Zoo playgrounds: A source of enrichment or stress for a group of nearby cockatoos? A case study. *Journal of Applied Animal Welfare Science*, *18*(4), 375–387.

Collins, C. K., Quirke, T., Overy, L., Flannery, K., & O'Riordan, R. (2016). The effect of the zoo setting on the behavioral diversity of captive Gentoo penguins and the implications for their educational potential. *Journal of Zoo and Aquarium Research*, *4*(2), 85–90.

Diggle, P. J., Liang, K. Y., & Zeger, S. L. (1995). *Analysis of longitudinal data*. Oxford: Clarendon.

Dishman, D. L., Thomson, D. M., & Karnovsky, N. J. (2009). Does simple feeding enrichment raise activity levels of captive ring-tailed lemurs (*Lemur catta*)? *Applied Animal Behaviour Science*, *116*(1), 88–95.

Estep, D. Q., & Hetts, S. (1992). Interactions, relationships and bonds: the conceptual basis for scientist–animal relations. *The inevitable bond: Examining scientist*–animal interactions (pp. 6–26). New York, NY: Cambridge University Press.

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

Finlay, T., James, L. R., & Maple, T. L. (1988). People's perceptions of animals the influence of zoo environment. *Environment and Behavior*, *20*(4), 508–528.

Foley, S. (2016). *A Comparative Study on the Behavior of Free Ranging Ring-Tailed Lemurs (Lemur catta) at Fota Wildlife Park, Cork* (Final Year Research Thesis). University College Cork, Cork, Ireland.

Glatston, A. R., Geilvoet-Soeteman, E., Hora-Pecek, & Van Hooff, J. A. R. A. M. (1984). The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, (*Saguinus oedipus oedipus*). *Zoo Biology*, *3*, 241–253.

Gould, L., Sussman, R. W., & Sauther, M. L. (1999). Natural disasters and primate populations: The effects of a 2-year drought on a naturally

occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. *International Journal of Primatology*, *20*(1), 69–84.
Hosey, G. R. (2000). Zoo animals and their human audiences: What is the visitor effect? *Animal Welfare*, *9*, 343–357.
Hosey, G. R. (2005). How does the zoo environment affect the behavior of captive primates? *Applied Animal Behavior Science*, *90*(2), 107–129.
Hosey, G. R. (2008). A preliminary model of human-animal relationships in the zoo. *Applied Animal Behaviour Science*, *109*(2), 105–127.
Hosey, G. R., & Melfi, V. A. (2014). Human-animal interactions, relationships and bonds: A review and analysis of the literature. *International Journal of Comparative Psychology*, *27*(1), 117–142.
Hosey, G. R., & Melfi, V. A. (2015). Are we ignoring neutral and negative human-animal relationships in zoos? *Zoo Biology*, *34*(1), 1–8.
Hosey, G. R., Melfi, V. A., & Pankhurst, S. (2013). *Zoo animals: Behavior, management, and welfare*. New York: Oxford University Press.
Hosey, G. R., Melfi, V. A., Formella, I., Ward, S. J., Tokarski, M., Brunger, D., . . .Hill, S. P. (2016). Is wounding aggression in zoo-housed chimpanzees and ring-tailed lemurs related to zoo visitor numbers? *Zoo Biology*, *35*(3), 205–209.
The IUCN Red List of Threatened Species. Version 2017-1. <http://www.iucnredlist.org>. Downloaded on 22 February 2017.
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*(1), 137–149.
Jolly, A. (1966a). Lemur social behavior and primate intelligence. *Science*, *153*(3735), 501–506.
Jolly, A. (1966b). *Lemur behavior: A Madagascar field study*. Chicago, IL: The University of Chicago Press (p. 187).
Jones, H., McGregor, P. K., Farmer, H. L. A., & Baker, K. R. (2016). The influence of visitor interaction on the behavior of captive crowned lemurs (*Eulemur coronatus*) and implications for welfare. *Zoo Biology*, *35*(3), 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*(1), 15–28.
Kratochvil, H., & Schwammer, H. (1997). Reducing acoustic disturbances by aquarium visitors. *Zoo Biology*, *16*(4), 349–353.
Kreger, M. D., & Mench, J. A. (1995). Visitor-animal interactions at the zoo. *Anthrozoos*, *8*, 143–158.
Kuhar, C. W. (2008). Group differences in captive gorillas' reaction to large crowds. *Applied Animal Behavior Science*, *110*(3), 377–385.
Manna, D., Rodeano, M., & Ferrero, E. A. (2007). A lemur mixed exhibit at Parco Zoo Punta Verde. *Italy. International Zoo News*, *361*, 452–457.
McDaniel, L., & Henderson, N. (2013). geeM: Fit Generalized Estimating Equations. Available online at: http://CRAN.R-project.org/package=geeM R package version 0.06. p. 181.
Mitchell, G., Herring, F., Obradovich, S., Tromborg, C., Dowd, B., Neville, L. E. & Field, L. (1991). Effects of visitors and cage changes on behaviors of mangabeys. *Zoo Biology*, *10*, 417–423.
Mitchell, G., Tromborg, C. T., Kaufman, J., Bargabus, S., Simoni, R. & Geissler, V. (1992). More on the 'influence' of zoo visitors on the behavior of captive primates. *Applied Animal Behavior Science*, *35*, 189–198.
Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behavior Science*, *102*(3), 262–302.
Moss, A., & Esson, M. (2010). Visitor interest in zoo animals and the implications for collection planning and zoo education programmes. *Zoo Biology*, *29*(6), 715–731.
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. *Anthrozoos*, *26*, 13–26.
Myers, O. E., Saunders, C. D., & Birjulin, A. A. (2004). Emotional dimensions of watching zoo animals: An experience sampling study building on insights from psychology. *Curator: The Museum Journal*, *47*(3), 299–321.
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 Behavior Science*, *33*(2), 261–272.
Parga, J. A., & Lessnau, R. G. (2005). Female age-specific reproductive rates, birth seasonality, and infant mortality of ring-tailed lemurs on St. Catherine's island: 17-year reproductive history of a free-ranging colony. *Zoo Biology*, *24*(4), 295–309.
Patrick, P. G., Matthews, C. E., Ayers, D. F., & Tunnicliffe, S. D. (2007). Conservation and education: Prominent themes in zoo mission statements. *The Journal of Environmental Education*, *38*(3), 53–59.
Price, E. C., Ashmore, L. A., & McGivern, A. M. (1994). Reactions of zoo visitors to free-ranging monkeys. *Zoo Biology*, *13*(4), 355–373.
Price, E. C., Wormell, D., Brayshaw, M., Furrer, S., Heer, T., & Steinmetz, H. W. (2012). Managing free-ranging callitrichids in zoos. *International Zoo Yearbook*, *46*(1), 123–136.
Rabb, G. B. (2004). The evolution of zoos from menageries to centers of conservation and caring. *Curator: The Museum Journal*, *47*(3), 237–246.
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 Dissertation). University College Cork, Cork, Ireland.
Reade, L. S., & Waran, N. K. (1996). The modern zoo: How do people perceive zoo animals? *Applied Animal Behaviour Science*, *47*(1–2), 109–118.
Sauther, M. L., Sussman, R. W., & Gould, L. (1999). The socioecology of the ring-tailed lemur: Thirty-five years of research. *Evolutionary Anthropology Issues News and Reviews*, *8*(4), 120–132.
Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of information*. Urbana, IL: University of Illinois Press.
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*(4), 287–295.
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*(5), 528–540.
Species 360. Available online at: https://www.species360.org/ Date accessed December 17, 2017.
Stevens, J., Thyssen, A., Laevens, H., & Vervaecke, H. (2013). The influence of zoo visitor numbers on the behavior of harbour seals (*Phoca vitulina*). *Journal of Zoo and Aquarium Research*, *1*(1), 31–34.
Stoinski, T. S., Jaicks, H. F., & Drayton, L. A. (2012). Visitor effects on the behavior of captive western lowland gorillas: The importance of individual differences in examining welfare. *Zoo Biology*, *31*(5), 586–599.
Tarou, L. R., Bloomsmith, M. A., & Maple, T. L. (2005). Survey of stereotypic behavior in prosimians. *American Journal of Primatology*, *65*(2), 181–196.
Wells, D. L. (2005). A note of the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, *93*, 13–17.
Wood, W. (1998). Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes*). *Zoo Biology*, *17*, 211–230.
Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14.

How to cite this article: Collins C, Corkery I, Haigh A, McKeown S, Quirke T, O'Riordan R. The effects of environmental and visitor variables on the behavior of free-ranging ring-tailed lemurs (*Lemur catta*) in captivity. *Zoo Biology*. 2017;36:250–260.
https://doi.org/10.1002/zoo.21370