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# Behaviour and welfare: the visitor effect in captive felids

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## Abstract

*The influence of visitors on the welfare of captive animals, known as the visitor effect, may in some instances be stressful, adversely affecting animal health. Although the survival of many felid species depends on captive breeding programmes, little is known about this effect. A better understanding of the visitor effect is required to ensure the well-being of felids and the success of breeding programmes. We sought to determine whether the presence of visitors affects behaviour patterns and space use in five feline species in two Spanish zoos: Eurasian lynx (*Lynx lynx*), jaguar (*Panthera onca*), bobcat (*Lynx rufus*), ocelot (*Leopardus pardalis*) and Asiatic lion (*Panthera leo persica*) and, if so, whether the effect on animal welfare is positive or negative. To our knowledge, no previous research has addressed the visitor effect in these species, with the exception of the jaguar. Data on animal behaviour, enclosure use, and visitor density were collected during the spring and summer of 2011 and 2012. Changes were observed for all studied species when the zoo was open to the public: four species devoted less time to complex behaviour (ie play, walk) and spent more time resting; ocelots and bobcats made more use of hidden spaces and less use of areas closer to visitors, while the jaguar tended to do the opposite. No correlation was found between visitor density and animal activity, indicating that animals are affected by the mere presence of visitors, regardless of their number. Our findings are in line with those reported by other authors, who have suggested that these behavioural changes are linked to chronic stress. Visitor effect was classed as negative for the welfare of all studied species apart from the jaguar. We advocate the need for future research into potential solutions to mitigate the adverse effect of visitors on felids.*

**Keywords**: *animal welfare, felids, space use, stress, visitor effect, zoo*

## Introduction

Modern zoos have three main objectives: conservation, research and education. It is essential to attract paying visitors in order to finance the pursuit of these objectives (Reade & Waran 1996; Fernández *et al* 2009), but their very presence may undermine conservation and research efforts.

The visitor effect is the change in behaviour and/or physiological responses of animals in the presence of zoo visitors (Davey 2006a). This influence has been classed as positive (a form of environmental enrichment) or negative, when it harms animal welfare leading to chronic stress (Hosey 2000; Davey 2005).

Changes in animal behaviour have been widely used as a tool to evaluate zoo animal welfare. Numerous studies of the visitor effect, mostly among primates, have reported changes in behaviour and related these variations to chronic stress and poor welfare. The most commonly observed adverse effects range from an increase in agonistic behaviours (Maki *et al* 1987; Chamove *et al* 1988; Mitchell *et al* 1992; Cook & Hosey 1995; Wormell *et al* 1996; Lambeth *et al* 1997; Anderson *et al* 2002; Simpson 2004; Wells 2005), hiding behaviour (Birke 2002; Condon *et al* 2003), vigilance time (Clark *et al* 2012; Larsen *et al* 2014; Quadros *et al* 2014), and abnormal stereotypies and/or self-directed behaviours (Mallapur *et al* 2005; Wells 2005), a decrease in affiliative behaviours (Glatson *et al* 1984; Chamove *et al* 1988; Simpson 2004), or an increase in glucocorticoids (Carlstead & Brown 2005; Davis *et al* 2005; Todd *et al* 2007; Pifarré *et al* 2012). However, there have also been some studies in which the visitor effect is neutral for the studied species (Fa 1989; Nimon & Dalziel 1992; Mather 1999; Choo *et al* 2011; Sherwen *et al* 2014).

Although recent years have seen more research in non-primates, such studies remain scarce. A number of authors (Hosey 2000; Davey 2007; Fernández *et al* 2009) have highlighted the need for research focused on other animal groups.

There are few feline studies in the literature on visitor effect and results are variable, providing a rather confused picture varying from no response to an apparent stressed response. Mallapur and Chellam (2002) observed a decrease in activity in leopards (*Panthera pardus*) when the zoo was open to the public; Wielebnowski *et al* (2002) found in clouded leopard (*Neofelis nebulosa*) that the concentration of faecal glucocorticoid metabolites was higher for individuals housed in exhibit compared with those individuals off exhibit; and, finally, Sellinger and Ha (2005) observed an increase in abnormal stereotypies and in agonistic and hiding behaviour in two jaguars (*Panthera onca*). Moreover, O'Donovan *et al* (1993) did not detect that visitors affected the behaviour of cheetah (*Acinonyx jubatus*), and the same result was obtained by Margulis *et al* (2003) in six feline species.

Measuring how animals choose to use their space can provide information about animals' preferences and internal states, hence, space-use measures can be utilised as a method to determine positive or negative aspects of captive environments. Ross *et al* (2009) suggest space-use analysis as another tool to evaluate animal welfare. The way animals utilised enclosure space is influenced not only by social and biological factors, but also by environmental circumstances, such as visitors. However, few studies have linked space use and visitors, with variable results. In a study among captive primates, Hosey and Druck (1987) found differences in space use in relation to the type of audience, with more use of the areas closer to visitors in response to active audiences. Similar results were found by Mitchell *et al* (1992) also in captive primates. Fa (1989) observed that in the presence of visitors, green monkeys (*Cercopithecus aethiops sabaeus*) spent more time around the edges of the exhibit. Vrancken *et al* (1990) observed a group of five gorillas (*Gorilla gorilla graueri*) that did not modify the use of space in the enclosure in the presence of visitors, except for one that spent more time near to visitors. In contrast to the findings on primates, Sellinger and Ha (2005) found that jaguars spent more time out of view in the presence of visitors. Eltorai and Sussman (2010) observed that adult prairie dogs (*Cynomys ludovicianus*) move closer to visitors when audiences were larger; whereas meerkats (*Suricata suricatta*) did not change the distance that they positioned themselves from visitors in response to variation in the intensity of visitor behaviour (Sherwen *et al* 2014).

Given that the presence of visitors is known to affect the lives of zoo-housed animals, research clearly needs to focus on how the visitor effect is developed, and how it affects different species. Hosey (1997, 2000) argues that the visitor effect needs to be studied since it may be a source of stress, undermining the welfare of captive animals, as well as potentially influencing behavioural studies carried out in zoos.

According to Hill and Broom (2009), animal welfare can be defined as the state of an animal as regards its attempts to cope with its environment. When an animal fails in its attempt to cope with a changing environment, chronic stress and so poor welfare can occur. Dantzer (1991) defines stress as a situation in which intrinsic or extrinsic demands exceed an individual's resources for responding to those demands. The tendency of the body to maintain a steady state is referred to as homeostasis; a stressor, for some authors, is anything that challenges that homeostasis (Selye 1976), and this may include the presence of zoo visitors (Carlstead & Brown 2005; Davis *et al* 2005; Pifarré *et al* 2012). Visitors are a source of variability over which the animals have no control and, as such, constitute a potential source of long-term stress that could compromise animal welfare (Morgan & Tromborg 2007). Chronic stress is associated with a number of physiological effects, including diabetes, hypertension, infertility, loss of libido, inhibition of growth and of the inflammatory response, and an increase in peripheral autoimmune reactions (Casey 2002). Therefore, visitors may be contributing to the appearance of pathologies and failure of captive breeding programmes. Hence, it is essential to determine whether visitors affect the welfare of each species and, if so, how they achieve this. Armed with this information, zoos will be better equipped to reduce or eliminate negative visitor effects.

The survival of many feline species is threatened due to habitat destruction; captive felids in zoos will therefore play a crucial role in maintaining viable populations, for example of Iberian lynx (*Lynx pardinus*) or Asiatic lions (*Panthera leo persica*). Yet, surprisingly little research has addressed the visitor effect in this animal group. The Asiatic lions studied here are part of an international captive breeding programme, as they are classed as 'endangered' (Breitenmoser *et al* 2008).

The present study aims to provide an overview of the visitor effect among felids, therefore it dealt with five feline species, only one of which, the jaguar, has previously been the subject of visitor-effect studies. We sought to determine whether the presence of visitors affects behaviour patterns and space use in several feline species and, if so, whether the effect on animal welfare is positive or negative. Possible solutions or methods for mitigating negative effects are suggested. Three hypotheses were tested:

- The frequency of certain behaviours differs depending upon whether the zoo is open or closed to the public;
- Animal activity levels depend on visitor density; and
- Animals use the enclosure space differently depending on whether the zoo is open or closed to the public.

## Materials and methods

The study was carried out in two zoos in southern Spain: Parque Zoobotánico in Jerez de la Frontera, and Zoológico Municipal in Córdoba. Eleven animals belonging to five feline species were studied, as described in Table 1. None of the animals were hand-reared. Animals were fed six days per week with a diet composed mainly of horse, chicken and beef. All the exhibits had an indoor retreat space to which animals retired when the zoo closed at 1800h, and where they ate and spent the night. Every morning, the outdoor area was cleaned prior to the animals being put out. The indoor area was cleaned daily with pressurised water and disinfected regularly. In Córdoba, both the jaguar and the Eurasian lynxes (*Lynx lynx*) were separated from the public by two glass-fronted viewing windows, allowing close interaction from two sides of each exhibit. In Jerez, the public could only view animals from one side of the enclosure. Visitors were kept back by an iron fence which was further protected by a roughly 1 $m^2$ planted area and then an outer wooden rail. None of the enclosures in either zoo had large retreat areas where animals could hide, merely small hiding places where a single animal could lie down partly obscured from view.

Data were collected between 1000 and 1400h in the spring and summer of 2011 and 2012. Davey (2006b) has previ-



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**Table 1 General data on study animals and enclosures.**

| Species | Subjects | Sex | Age (years) | Location | Time in the enclosure | Outdoor area (m²) | Separation and distance to visitors | Hiding places | Animals per enclosure |
|---|---|---|---|---|---|---|---|---|---|
| Jaguar (*Panthera onca*) | JM | M | 12 | Córdoba | 4 years | 383 | Glass-fronted viewing window | No | 1 |
| Eurasian lynx (*Lynx lynx*) | ELF | F | 2 | Córdoba | 2 years | 143 | Glass-fronted viewing window | No | 4–6 |
| | ELYF | F | 1 | Córdoba | 1 year | | | | |
| | ELYM | M | 1 | Córdoba | 1 year | | | | |
| Asiatic lion (*Panthera leo persica*) | ALM | M | 5 | Jerez | 2 months | 124 | Iron fence and 1-m wide wooden rail | No | 2 |
| | ALF | F | 9 | Jerez | 8 years | | | | |
| Bobcat (*Lynx rufus*) | BM | M | 12 | Jerez | 8 years | 36 | Iron fence and 1-m wide wooden rail | Partly (see text) | 3 |
| | BF | F | 5 | Jerez | 5 years | | | | |
| | BYM | M | 1 | Jerez | 1 year | | | | |
| Ocelot (*Leopardus pardalis*) | OM | M | 6 | Jerez | 6 years | 36 | Iron fence and 1-m wide wooden rail | Partly (see text) | 2 |
| | OF | F | 5 | Jerez | 5 years | | | | |

**Table 2 Ethogram used, and description of behavioural categories, ordered from low to high activity.**

| Activity scale | | Description |
|---|---|---|
| Inactivity | Sleeping | Animal lying, head down, eyes closed. No reaction to what happens in surroundings |
| | Dozing | Animal lying, eyes half-closed, head down or up. Opens eyes in response to sounds or movements in surroundings |
| | Attentive | Animal looking around. Lying or sitting. Head up |
| | Grooming | Animal uses tongue to clean his/herself or another animal |
| Medium activity | Alert | Animal focuses eyes and ears on a specific stimulus. Lying, sitting or standing |
| | Marking | Animal rubs, sprays urine on, or scratches objects or plants in the enclosure |
| | Locomotion: walking | Animal walks around the enclosure |
| High activity | Locomotion: running | Animal runs or leaps around the enclosure |
| | Playing | Animal interacts with object, plant or trunk in enclosure without marking it. Animal interacts with other animal in enclosure, simulating fighting or chasing. Animal interacts with visitors, simulating fighting or hunting |
| | Sexual behaviour | Copulation or courtship |
| | Abnormal stereotypies | Stereotyped walking: animal repeats a fixed, almost unvarying gait pattern. Inappropriate sexual activity (jaguar): animal rubs pelvis against floor then rolls on back |
| | Agonistic behaviour | Animal vocalises, bites, scratches, strikes or snorts at other animal or at the barrier separating it from a particular visitor |

ously described mornings as the period of maximum visitor interest in animals and, therefore, there was an expectation of finding this to have the strongest effect on animal behaviour. To compare behaviour and space use as a function of visitor presence, data were collected on open (Tuesday to Saturday) and closed days (Monday). Animals were fasted on Sundays, so these days were excluded from the study. Keeper routines were the same in zoo open and closed days. Closed days with different keeper routines, yard works or any other disturbance were excluded from the study. Data collection started in a different enclosure every day, to ensure that observations for each species were distributed uniformly over the entire morning. To facilitate data collection in multiple animal enclosures, video-recording was used. Once in front of an enclosure, a 1-min recording was made every 5 min. At the 30-s mark of each 1-min recording, scan sampling (Crockett & Ha 2010) was carried out to register the activity and situation of all animals. Also, each scan on zoo open days was labelled with the number of visitors standing in front of the enclosure, looking or not toward the exhibit. A minimum of 150 scans and 15 h of activity per animal were recorded, distributed over a minimum of eight days when the zoo was open to the public and six when closed. Preliminary data for each species were used to develop an ethogram comprising twelve ordered activity levels (Table 2), based on activity


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**Table 3 Significant results for the statistical analysis (Fisher's exact test) of space use by species and area of enclosure (Total, 1, 2, 3 and 4), on days when the zoo was open or closed to the public.**

| Species | Area | df | *P*-value | *E* |
|---|---|---|---|---|
| Jaguar | Total area | 3 | 0.002 | – |
| | 2 | 1 | 0.031 | 0.119 |
| | 4 | 1 | < 0.001 | –0.484 |
| Asiatic lions | Total area | 3 | < 0.001 | – |
| | 2 | 1 | 0.002 | 0.234 |
| | 4 | 1 | < 0.001 | –0.361 |
| Bobcats | Total area | 2 | < 0.001 | – |
| | 1 | 1 | 0.013 | –0.516 |
| | 4 | 1 | < 0.001 | 0.393 |
| Ocelots | Total area | 2 | < 0.001 | – |
| | 1 | 1 | < 0.01 | –0.876 |
| | 4 | 1 | 0.003 | 0.352 |

*E* is the value of the electivity index, positive values indicating over-utilised areas and negative values under-utilised areas on zoo open days.

scales suggested by various authors for carnivores in general or felids in particular (Bekoff & Corcoran 1975; Margulis *et al* 2003; Macri & Paterson-Kane 2011). For the purposes of statistical analyses, these twelve activities were later grouped into the three levels indicated in Table 2.

Finally, the study sought to establish whether animals spent similar times on the same activities and in the same area of the enclosure on days when the zoo was open to the public or not.

## Statistical analysis

Statistical analyses were carried out using R statistical software, version 3.2.2 (The R Foundation for Statistical Software). Significance level was set at $P < 0.05$. Data were presented by species. We have tried to present an overview of visitor effect on behaviour and space use by the different felid species. However, a factorial correspondence analysis including all studied species was included in order to expose possible similarities between species.

### *Behaviour*

In order to obtain preliminary findings covering all of the studied species, a factorial correspondence analysis (FCA) was performed. FCA is a multi-dimensional statistical method well suited to representing contingency or frequency tables, and provides a reliable overview of the inter-relationships among data (Cuadras 1991; Maniatis 2010). Here, it was used to detect associations common to different feline species, by analysing the relationships between individual animals and three levels of activity (inactivity, medium activity, high activity), on zoo open and closed days.

For each species, a Fisher's exact test was then performed for the three activity levels and then another one for each of the twelve activities involved. Frequencies of each activity were used for the statistical analysis, comparing data from zoo closed days with observed values from open days.

### *Effect of visitor density*

Data from zoo open days were used to analyse the correlation between the variables 'level of activity' and 'number of visitors' for each observation; level of activity corresponded to one of the 12 levels shown in Table 2. Spearman rank correlation was used for this purpose (Siegel 1956; Corder & Foreman 2009).

### *Space use*

Data on animal location were recorded on ground-plans for each enclosure. These plans were then divided into four areas (1–4) according to their increasing distance from visitors. In the jaguar and Asiatic lion enclosures, area 4 was the furthest from the public, while in the bobcat (*Lynx rufus*) and ocelot (*Leopardus pardalis*) enclosures, area 4 was not visible to the public, so animals could hide there. Since they were smaller, these latter enclosures were divided into only three areas (1, 2 and 4; see Table 1). Eurasian lynxes were excluded from this part of the study as their enclosure underwent various internal rearrangement during the data-collection period.

A Fisher's exact test was performed for each area in Table 3, comparing frequencies of use on zoo closed days versus frequencies of use on open days. Also, to measure preferences for different areas of the enclosure, the electivity index designed by Vanderploeg and Scavia (1979) was employed to identify under- and over-utilised areas with respect to expected values.

$$E = \frac{W_i - (1/n)}{W_i + (1/n)}$$

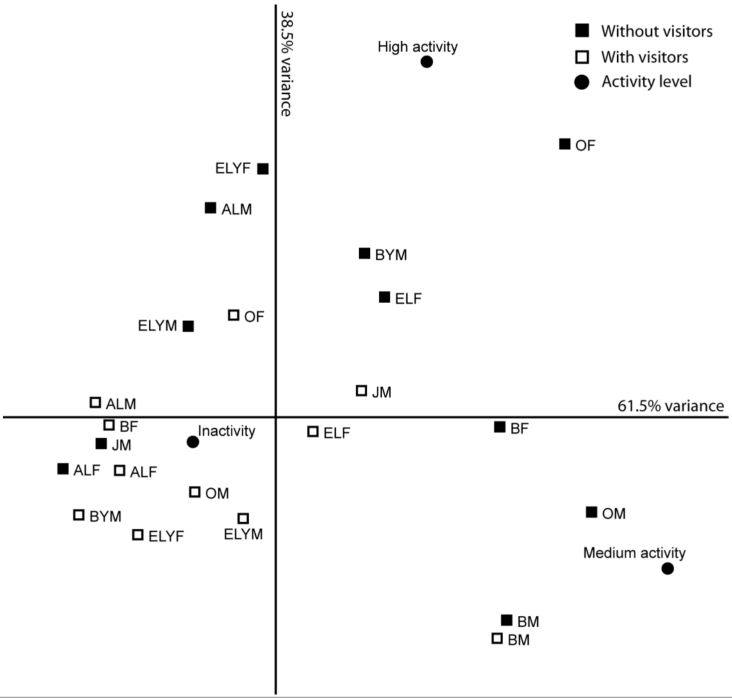
Where; $W_i = (r_i/p_i)/\Sigma r_i/p_i$; $r_i$ is observed use (fraction of time spent in area $i$ on zoo open days), and $p_i$ is expected use (fraction of time spent in area $i$ on zoo closed days); $n$ is the number of areas. An area used more on zoo open than on zoo closed days is defined as over-utilised ($1 > E > 0$), while an area used less is defined as under-utilised ($-1 < E < 0$).

# Results

## Behaviour

The results of FCA indicated a highly significant relationship ($\chi^2 = 343.844$, n = 42; $P < 0.001$) between animals on zoo open and closed days, for all three activity levels. As Figure 1 shows, the 'inactivity' category is located close to the centroid, suggesting that animals spent much of their time on the activities comprising that category, whilst 'medium activity' and 'high activity' lie further from the centroid, indicating that the behaviours assigned to these categories were engaged in less frequently. The most striking finding, however, was a clear grouping of animals around the 'inactivity' category on zoo open days, although the reverse was true for the jaguar (JM), while the male bobcat (BM) displayed no apparent variation in activity as a function of visitor presence. This grouping contrasts strongly with the scattered distribution of animals across the plot on closed days.

**Figure 1**




Results for factorial correspondence analysis, by individual animal and three activity levels. Identification of animals as in Table 1. See inactivity category located close to the centroid, and a clear grouping of animals around this category on days when the zoo was open to the public, contrasting strongly with the scattered distribution of animals across the plot on days when the zoo was closed to the public, suggesting that in the absence of visitors animals displayed varying degrees of activity, while in the presence of visitors, they tended to be inactive.

These findings support the results of the rest of the behavioural statistical analysis which revealed significant differences for all species in the distribution of activities and in total activity (except for Asiatic lions) on zoo open versus zoo closed days (Table 4). Open days were characterised by an increase in the time spent on behaviours included in the 'inactivity' category, and a decrease in that devoted to behaviours in the 'high activity' category (see Figure 2). Asiatic lions displayed significant differences for 'abnormal stereotypies'; lynxes for 'sleeping' and 'playing', bobcats for 'sleeping', 'attentive', 'grooming', 'walking' and 'playing', and finally ocelots for 'sleeping', 'walking' and 'abnormal stereotypies'. By contrast, the jaguar devoted more time to 'high activity' behaviours and less time to 'inactivity' behaviours in the presence of visitors, with significant differences for 'dozing', 'grooming' and 'walking'.

Interestingly, the jaguar were observed performing 'playing' activities twice as often in zoo open days, and these were sometimes directed at visitors.

To summarise, during zoo open mornings, lynxes, bobcats and ocelots were less active, spending more time sleeping; they played and walked less, and ocelots and Asiatic lions devoted less time to abnormal stereotypic behaviours. By contrast, the jaguar displayed greater activity, spent less time dozing and more time grooming and walking in the presence of visitors.

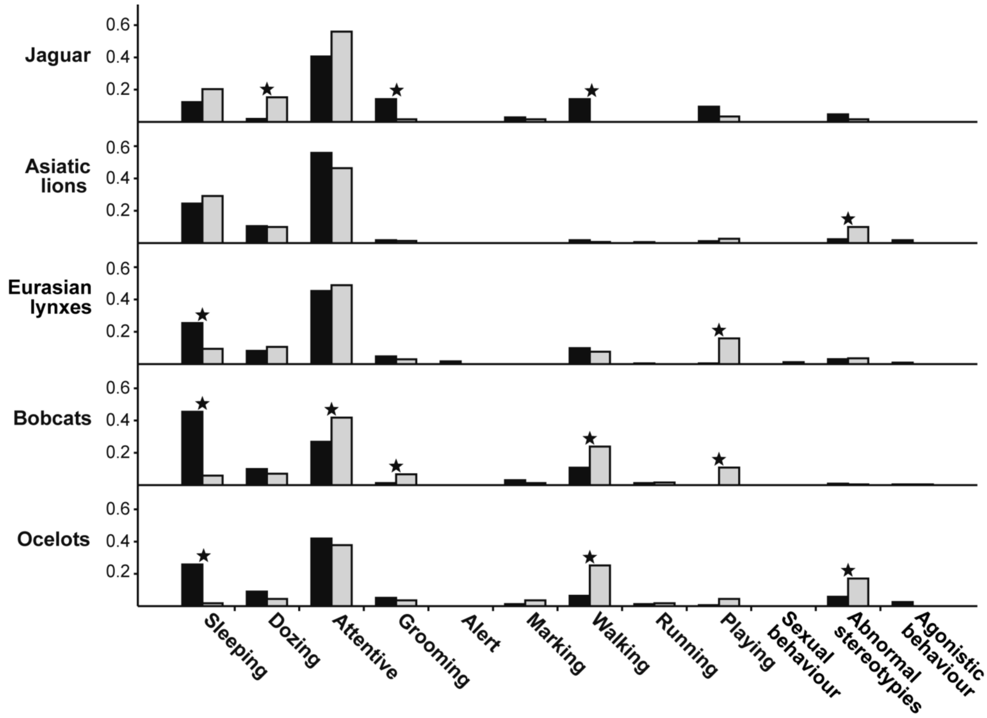
## Effect of visitor density

In Asiatic lions ($r_s = 0.187$, n = 172; $P = 0.014$) and ocelots ($r_s = 0.204$, n = 156; $P = 0.011$), a significant positive correlation was observed, however, the correlation can be ruled out since, in both cases, the value lay below 0.3 (Cohen 1988). In short, no actual correlation was observed between visitor density and activity levels in the feline species studied.

**Table 4 Significant results for the statistical analysis (Fisher's exact test) of behaviour, by species and activity, on days when the zoo was open or closed to the public.**

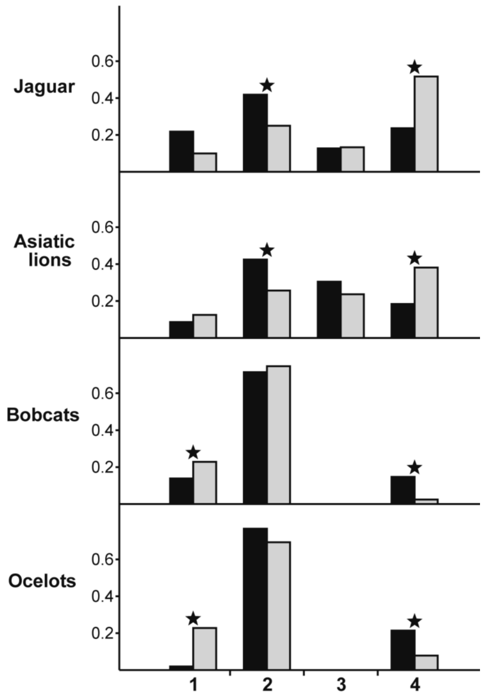
| Species | Activity | df | *P*-value |
|---|---|---|---|
| Jaguar | Total | 2 | < 0.001 |
| | Dozing | 1 | 0.002 |
| | Grooming | 1 | 0.011 |
| | Walking | 1 | 0.001 |
| Asiatic lions | Stereotypies | 1 | 0.004 |
| Eurasian lynxes | Total | 2 | < 0.001 |
| | Sleeping | 1 | < 0.001 |
| | Playing | 1 | < 0.001 |
| Bobcats | Total | 2 | < 0.001 |
| | Sleeping | 1 | < 0.001 |
| | Attentive | 1 | < 0.001 |
| | Grooming | 1 | 0.004 |
| | Walking | 1 | < 0.001 |
| | Playing | 1 | < 0.001 |
| Ocelots | Total | 2 | < 0.001 |
| | Sleeping | 1 | < 0.001 |
| | Walking | 1 | < 0.001 |
| | Stereotypies | 1 | 0.004 |

**Figure 2**




Relative frequency for each activity by species, with visitors (black bars) versus without visitors (grey bars). Stars indicate significant differences (Fisher's exact test). (See Table 1 for information about enclosure type).

**Figure 3**




Relative frequency of enclosure use, by species and area of enclosure (1, 2, 3 and 4 where area 1 = closest to visitors and 4 furthest - see text), with visitors (black bars) versus without visitors (grey bars). Stars indicate significant differences (Fisher's exact test). For ocelots and bobcats, enclosure area 3 does not exist because enclosures are smaller (see Table 1 for information about enclosure type).

## Space use

A significant variation was observed in enclosure use by all species on zoo open days (Figure 3). Table 3 shows preferences of use and significant differences in the use of enclosure areas. Areas 1 and 4 were used less on zoo open days by Asiatic lions, while areas 2 and 3 were over-utilised, with significant differences for areas 2 and 4. For bobcats and ocelots, there were significant differences in the use of areas 1 and 4; in both enclosures, area 4 was over-utilised and area 1 was under-utilised on zoo open days. Both ocelots and bobcats tended to hide from view in the presence of visitors, and made less use of the area closest to the public, while lions made greater use of central areas on open days.

Differences were recorded for space use by the jaguar, with over-use of area 1 and 2 (ie closer to visitors) and under-use of area 4, the furthest from visitors, on zoo open days, with significant differences for areas 2 and 4.

## Discussion

It has been hypothesised that the visitor effect could induce stress in zoo animals (Maki *et al* 1987; Chamove *et al* 1988; Mitchell *et al* 1992; Cook & Hosey 1995; Wormell *et al* 1996; Lambeth *et al* 1997; Anderson *et al* 2002; Simpson 2004; Carlstead & Brown 2005; Wells 2005; Pifarré *et al* 2012). Dantzer (1991) defines stress as a situation in which intrinsic or extrinsic demands exceed an individual's resources for responding to those demands. Visitors are a source of variability over which the animals have no control and, as such, constitute a potential source of long-term



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stress (Morgan & Tromborg 2007). Chronic stress is associated with numerous physiological deleterious effects, including infertility (Casey 2002). Therefore, visitors may be contributing to the appearance of pathologies and failure of captive breeding programmes.

Our findings point to a significant variation in the distribution of activities, for all species, on days when the zoo was open to the public and, accordingly, visitors were present at the zoo. These findings suggest that the presence of visitors is associated with changes in animal behaviour. However, no correlation was found between activity levels and visitor density, suggesting that diurnal behaviour is modified by the presence of visitors, regardless of their number.

On zoo open days, lynxes, bobcats and ocelots spent more time sleeping and devoted less time to complex behaviours, such as playing (lynxes and bobcats), walking (bobcats and ocelots) and abnormal stereotypies (ocelots and lions). Lynxes, lions and ocelots displayed agonistic behaviour only when visitors were present, whereas the jaguar was more active on zoo open days, and even directed some playful behaviour towards visitors.

Similar findings were recorded for space use. On zoo open days, the jaguar made more use of areas closer to visitors, while bobcats and ocelots spent more time in retreat spaces and hiding places, and less time in areas closer to the public. These data run counter to the findings reported by O'Donovan *et al* (1993) for cheetahs and by Margulis *et al* (2003) for six feline species: African lion (*Panthera leo*), Amur leopard (*Panthera pardus orientalis*), Siberian tiger (*Panthera tigris altaica*), snow leopard (*Panthera uncia*), clouded leopard and fishing cat (*Felis viverrinus*). However, the results of the present study are very similar to those obtained by Mallapur and Chellam (2002) for sixteen leopards in four Indian zoos; leopards spent more time sleeping, and in central and remote areas of the enclosure, on zoo open days, and displayed increased activity on closed days.

These disparities may reflect differences in experimental design, in the size of animal groups, and in enclosure design. In the present study, observations were made when the zoo was closed to the public, and compared with those made on open days, whereas O'Donovan *et al* (1993) and Margulis *et al* (2003) considered 'no-visitor' times simply to be those periods of zoo open days when no visitors happened to be present. Here, such periods were considered as zoo open periods with zero visitors.

Sellinger and Ha (2005) also detected changes in the behaviour of two jaguars in the presence of visitors, although these took the form of an increase in abnormal stereotypies, aggression and hiding. These jaguars were housed together, thus allowing for the possibility of social interaction, which the jaguar in the present study might have been seeking through its interest in visitors.

Exposure to the public is a stimulus over which captive animals have no control, other than retreating or hiding. None of the species here had a large, comfortable retreat space, but only small hiding places where they could lie down out of view, and which they had to share with others except for the solitary jaguar. This lack of control over the immediate environment has been identified as one of the major sources of stress in captive animals; forced proximity to visitors is therefore likely to intensify the deleterious impact (Morgan & Tromborg 2007). According to Rochlitz (1999), hiding behaviour in the domestic cat (*Felis catus*) occurs in response to changes in the environment and to avoid interactions with other cats or people, so enough rest areas in which cats can retire and stay hidden are essential for the cats' well-being. Moreover, in a study of domestic cats subjected to unpredictable handling routines, Carlstead *et al* (1993) found a negative correlation between urine cortisol levels and hiding time, suggesting that hiding plays an important role in coping with uncontrollable captive environments. This may also help to account for the difference between the results obtained here and the findings reported by O'Donovan *et al* (1993) and Margulis *et al* (2003) in felids; in both these studies, animals were able to hide. In the leopard study by Mallapur and Chellam (2002), there is no mention of hidden retreat spaces, whilst in the jaguar study by Sellinger and Ha (2005) only small hiding places are reported.

Having confirmed that the presence of visitors is linked with changes in animal behaviour, an analysis was made of the positive or negative nature of those changes. Chronic stress has been associated, among other things, with a reduction in exploratory behaviour (Carlstead & Brown 2005), a decline in complex behaviours (Rutherford *et al* 2004), and increased aggression (Bartolomucci *et al* 2004). Changes similar to those observed here have been reported in cats subjected to a 21-day period of altered caretaking involving a number of stressful situations (Carlstead *et al* 1993). The study noted that active exploratory and play behaviours were reduced, and more time was spent attempting to hide. Urinary cortisol levels also increased. Chosy *et al* (2014) also found an increase in hiding behaviour and faecal cortisol metabolites, and a reduction in overall activity in four feline species in response to exhibit construction. Here, all study species apart from the jaguar displayed a marked decrease in overall activity, due mainly to a reduction in complex and exploratory behaviours (playing and locomotion), while lynxes, ocelots and Asiatic lions exhibited a non-significant increase in aggressive behaviour, and bobcats and ocelots made greater use of enclosure areas hidden from public view. According to Chosy *et al* (2014), one explanation for these behavioural changes may be that visitor presence is prompting chronic stress in four of the five species studied. Further research is required to confirm this. By contrast, the findings for the jaguar pointed to a preference for interaction with visitors. Visitor presence may therefore be exerting a beneficial, enriching effect on the well-being of the jaguar, although the precise nature of this interaction requires detailed clarification through, for example, measurement of glucocorticoid levels. Our male bobcat was apparently the least affected by visitors (Figure 1). As the male bobcat and the jaguar were also the oldest animals, it would be interesting for future research to consider age and time in the enclosure as mitigating factors of visitor effect.

## Animal welfare implications

The effects of chronic stress include immunosuppression, infertility and retarded growth (Casey 2002). It is, therefore, essential to reduce or eliminate, as far as possible, the negative impact of visitors. This is particularly significant for endangered species in captive breeding programmes, such as the Asiatic lion, and in growing animals like the young lynxes and bobcats. This must take visitor preferences into account. The distribution of enclosures in a zoo must reflect not only the varying sensitivity of each species to the presence of visitors, but also their relative ability to attract visitors. More sensitive species, for example, could be located at the end of paths, in less busy areas and at a greater distance from the most popular species. This may involve no more than a rearrangement of paths, incurring only a small cost for the zoo.

Our results illustrate that in zoo open days, animals under-utilise the nearest areas to the public. This means than the effective space of the enclosure was reduced on these days. When designing enclosures, we must take this fact into account and care should be taken to provide sufficiently large retreat spaces, hidden from public view. Moreover, knowing that visitors can affect animal welfare, the design of visitors' areas and paths should become as important as other internal features of animals enclosures. The aim should be to create a scenario whereby animals do not notice the presence of visitors and this could be achieved via concealment of visitors' areas and deployment of the public in covered walkways with one-side viewing windows. This could lead to a marked reduction of stress levels, by enabling animals to cope better with the stress induced by constant visitor presence and reduced effective space in the exhibit on zoo open days.

Zoos need to attract visitors, and visitors find active animals more attractive (Margulis *et al* 2003; Fernández *et al* 2009), yet their very presence prompted a reduction in the activity of the feline species studied here (except the jaguar). Mitigation of the negative effect of visitors on captive felids would not only enhance the welfare of the animals but also make them more interesting to visitors. This strategy was successfully attempted in a study of gorillas (*Gorilla gorilla*) by Blaney and Wells (2004), who installed a camouflage net barrier at the viewing area of the enclosure, which reduced the deleterious visitor effect and increased visitor interest in the gorillas. Although the most effective way of reducing the visitor effect is to address it during the design phase of new exhibits, there are a number of economic options available for modifying existing exhibits. Setting visual barriers, such as one-side viewing windows, adding vegetation, hideaways and vertical space are cost-effective options that could improve felid well-being.

Further research into the visitor effect is required, in order to fully clarify its influence and identify and solve the specific issues to which it gives rise. As Figure 1 shows, individual differences appear to exist regarding the response of felids to the presence of visitors. Personality assessment could be interesting in order to analyse the nature of these differences. Measurement of physiological parameters, for example, would provide more detailed information. Once a visitor effect has been confirmed, the precise factors involved in the negative effect on animals, such as the smell, noise, or sight of visitors, need to be identified.

## Conclusion

The presence of visitors was associated with changes in behaviour and space use by felids. Observations in four out of the five species studied revealed a decrease in activity levels and in the amount of time spent in enclosure areas closest to the public, an increase in time spent resting, and a decline in activities such as playing and walking. In the case of the jaguar, however, the reverse was true.

Since a reduction in complex behaviours and an increase in time spent hiding are associated with chronic stress, the visitor effect may be classed as negative in four of the five species, so visitors should be considered as a potential source of stress to be taken into account in order to assure felid welfare. For the jaguar, behavioural changes appear to indicate an attempt at inter-species socialisation. In this case, the visitor effect could be considered as enriching.

To ensure the well-being of zoo-housed felids and the success of *ex situ* breeding programmes, the visitor effect should be mitigated as much as possible. This can be done by applying the results of this research to zoo design, for example by providing felids with appropriate retreat spaces and by limiting the flow of visitors.

Future research should include the measurement of glucocorticoid levels in order to identify specific visitor-related factors which adversely affect animals. Personality assessment could also be helpful for maximising felid well-being.

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