

EFFECTS OF ENVIRONMENTAL ENRICHMENTS ON THE BEHAVIORS OF FOUR CAPTIVE JAGUARS: INDIVIDUALITY MATTERS

Débora Boccacino¹, Caroline Marques Maia²*, Eliana Ferraz dos Santos³ & Ricardo Tadeu Santori⁴

- ¹ Museu Nacional, Universidade Federal do Rio de Janeiro, Programa de Pós-Graduação em Zoologia, Setor de Vertebrados, Quinta da Boa Vista, São Cristóvão, CEP 20940-040, Rio de Janeiro, RJ, Brazil.
- ² Universidade Estadual Paulista, Instituto de Biociências, Departamento de Fisiologia, Laboratório de Fisiologia Animal e Comportamento, Rua Prof. Dr. Antônio Celso Wagner Zanin, 250, Distrito de Rubião Junior, CEP 18618-689, Botucatu, SP, Brazil.
- ³ Prefeitura Municipal de Campinas, Secretaria do Verde e Desenvolvimento Sustentável, Departamento de Proteção e Vem-Estar Animal, Rua das Sapucaias, 115, Vila Boa Vista, Campinas, SP, Brazil.
- ⁴ Universidade do Estado do Rio de Janeiro, Faculdade de Formação de Professores, Departamento de Ciências, Programa de Pós-Graduação em Ensino de Ciências, Ambiente e Sociedade, Rua Dr. Francisco Portela, 1470, Patronato, CEP 24435-000, São Gonçalo, RJ, Brazil.

E-mails: deboccacino@gmail.com; carolmm_luzi@hotmail.com (*corresponding author); ferrazlili@uol.com.br; rsantori.uerj@gmail.com

Abstract: The effects of different environmental enrichments on the behaviors of four captive jaguars, *Panthera onca* (Carnivora, Felidae), were individually evaluated. The frequency of jaguar behaviors were recorded in three phases: before, during and after environmental enrichments application. These included hose ball, scent trail, meat tubes, cardboard boxes with meat or elephant feces, stuffed pumpkins, meat ice cream, meat with animal hair, bags with meat, and sounds. The enrichments reduced inactivity and the time duration when jaguars were out of sight, and increased general activity and maintenance behaviors of all tested jaguars. However, the behavioral responses expressed considering other behaviors and after the removal of environmental enrichments varied among individuals. When there were no more enrichments in their enclosures, two jaguars seemed to be in a worse condition than before the introduction of them, while the oldest jaguar maintained all the positive effects. The other jaguar expressed intermediate responses between these two patterns after the removal of the enrichments. Although the tested enrichments improved the welfare of the jaguars, we conclude that individual variability of response to the enrichments highlights the need to consider individual variation in future studies, since some individuals may take better advantages from the enrichments than others.

Keywords: animal welfare; individual responses; mammal behavior; Panthera onca; zoo animals.

INTRODUCTION

Captive conditions in zoological institutions restrict the interactions animals may have with their natural environment. In this context, environmental enrichment, which is any technique developed to improve the conditions of an animal in human care by making modifications to its environment (Newberry 1995), is an approach widely applied for animals in zoological institutions (Mellen & MacPhee 2001). Enrichment aims to increase the ability of the animal to overcome challenges, expand its behavioral repertoire and the positive use of the environment, and reduce or eliminate aberrant behaviors, such as stereotypies (Young 2003). These behaviors are composed of regularly repeated movements with no apparent purpose or goal (Dantzer & Mormède 1983), which may be induced by frustration, repeated attempts to cope with the environment, or also brain dysfunction (Mason 2006). Thus, preventing or, at least, reducing the appearance of abnormal behaviors, such as stereotypies, by successful environmental enrichment implementation is relevant for welfare purposes. In this context, many studies have evaluated environmental enrichment effects considering the behavioral changes expressed by animals facing the enrichments (see Swaisgood & Shepherdson 2005).

Taking into account that conditions of the environment and maintenance routine may vary considerably among different captivities, we may expect that individuals vary their response facing environmental enrichments. Considering wild cats, which are common animals in zoos expressing some kind of stereotype or much inactivity, deserving more attention to environmental enrichment programs, many studies have reported a significant individual variation of response when these animals are exposed to environmental enrichments (Bond & Lindburg 1990, Lyons et al. 1997, McPhee 2002, Van Metter et al. 2008, Vidal et al. 2016). This individual response is so significant that other studies have even focused on the effects of enrichments on the behaviors of just one animal (e.g., Markowitz 1995, Walters 2003). It is reasonable to expect that such individual variability may be a consequence of natural differences of internal state among individuals, such as differences of health state, age or also particular preferences. However, such individual variability of response when facing enrichments may also be influenced by differences of environmental conditions among different captivities. In fact, different sizes and structures of captive environments affect the behavior of individuals of several wild cat species (Lyons et al. 1997). Moreover, differences of wild cats being individually housed or grouped in captivities may

also affect individual responses to enrichments (*e.g.*, Bond & Lindburg 1990). Thus, the relevance to evaluate environmental enrichment effects on the behaviors of zoo felines in an individual level is evident.

Furthermore, no single type of environmental enrichment is indefinitely effective for wild cats (Mellen 1997). These animals frequently get used quickly with environmental enrichments such as toys, smells and changes in the structure of captive environments (Mellen 1997). Therefore, it is important to keep a constant search for different enrichments that improve the welfare conditions of captive wild cats. In addition, different enrichments may affect different behaviors of these animals (e.g., Powell 1995), complementing the effect of each other depending on the behaviors expressed in response for different enrichments. In this line, providing different enrichments for the same animals may also allow wild cats to perform a wider range of behaviors and being more active, besides reducing the probability of animals getting used to the enrichments (Powell 1995).

Considering wild cats frequently housed in zoos, the jaguar Panthera onca (Carnivora, Felidae) is a species that is intensely threatened by habitat degradation and fragmentation, illegal hunting and conflicts with cattlemen. Such conditions have led to a high risk of extinction in the wild in the medium run for this species (Ministério do Meio Ambiente 2003), which is considered Near Threatened by the International Union for Conservation of Nature (IUCN 2007). For this reason, preservation of healthy individuals in zoos is fundamental to ex situ conservation and the survival of jaguar populations in the wild. However, the reduced reproductive success in zoological institutions has been a barrier that must be overcome. Morato et al. (1999) demonstrated that male jaguars in zoos expressed a high level of morphologically abnormal sperm. In this way, considering that poor animal-welfare conditions may also threaten reproduction in zoos, there is a need to seek approaches that improve the conditions of these animals, such as by providing effects and monitoring the of different environmental enrichments. Despite of this, as far as we know, just few peer-reviewed papers effects considered the of environmental

enrichments on the behaviors of jaguars (Charlton 1998, Skibiel *et al.* 2007, Castillo-Guevara *et al.* 2012, Vidal *et al.* 2016). In this context, the effects of several environmental enrichments on the behavior of four captive jaguars were individually evaluated here. We hypothesized that the environmental enrichments would increase the active behaviors and decrease the inactivity of the jaguars, although each jaguar can also express significant individual responses.

MATERIAL AND METHODS

Specimens and enclosures

We studied two males ('Alexandre' and 'Cabeção') and two females (a melanic variant of *P. onca* 'Negona' and 'Gabi') jaguars (Table 1) in 2008 at Rio de Janeiro Zoo Foundation (RIOZOO), located in a wooded area of 138,000 m² at Quinta da Boa Vista Park, Rio de Janeiro state, Brazil. This work was authorized by the Ethics Committee at RIOZOO, and all procedures attempted to avoid animal suffering.

Three of the jaguars had access to two enclosures. The outdoor area had 85 m^2 with cement walls, a grid and a dirt floor, a cement stair, wooden platforms, a waterfall and overlapping

tree trunks. Overnight or for routine-management purposes there was also an indoor area of 5 x 3 m, where the animals could be separated. One of the jaguars (Cabeção) was maintained in an extra sector of 52 x 58 m that contained an iron platform with cement and grid walls, a dirt floor, a small cement ramp, a wooden trunk and a small water fountain, with a background chamber of 4 m² for management.

Daily management

Every morning, the zookeepers cleaned the outdoor enclosures before the jaguars were released from the indoor chambers. Only Cabeção was maintained in the extra sector during the entire study. The jaguars were released into the enclosure or the extra sector around 08:00 h and returned to their individual indoor chambers at 17:00 h. During the hours when the public visited the zoo, there were always only two jaguars in the outdoor enclosures. Gabi or Alexandre was released with Negona to the outdoor enclosures on alternate days. All jaguars were fed on alternate days and food, 2 kg of meat (chicken or bovine heart/muscle) was provided only inside the chambers, invariably during the three test phases (before, during and after enrichments). In the period leading up to the study, no enrichment was provided for these study jaguars.

Table 1. Demographic da	ta from the year	ear of 2008 fo	or the four	studied	jaguars	(Panthera	onca;	Carnivora,	Felidae)	at
Rio de Janeiro Zoo Founda	ation (RIOZOO)), Brazil.								

Name	Age (years)	Born	Rearing condition	Time at RIOZOO (years)	Parents
Cabeção	18	Zoo of Brasília city	Old and debilitated	9	-
Alexandre	11	Captured in the field	-	8	-
Negona	13	Captured in the field	Frequently limp with the right front leg	9	-
Gabi	6	RIOZOO	-	6	Negona and Alexandre

Behavioral observations

First, *ad libitum* observations were carried out in diurnal periods over 20 hours to familiarize the researchers with the jaguars and to organize an

ethogram (Table 2). The jaguars were then observed in three phases: before (first phase), during (second phase) and after (third phase) the application of environmental enrichments (Table 3). Observations were carried out each 30 s (focal scan sampling; 120 observations hour⁻¹) for two hours per day, which were distributed between 08:00 h and 17:00 h (one hour in the morning and one hour in the afternoon). The number of observation hours varied among the jaguars and phases, but each individual was observed for, at least, 20 h in each phase (Table 3). Moreover, as data were compared by a proportion test (see Statistical analyses), they were proportionally corrected in the analyses. In the second phase (during enrichment), the jaguars

were always observed during two consecutive hours following the introduction of each environmental enrichment, which was removed 24 hours later. This procedure was repeated for all tested enrichments.

To carry out the observations, researchers remained in an area above the enclosure, outside the animal's view. Binoculars were used to identify the behaviors. In the extra sector, there was no area outside the view of the jaguars. Thus, to minimize the influence of the human presence, researchers stood in front of the extra sector for

Table 2. Ethogram of the observed behaviors of the four jaguars (*Panthera onca*; Carnivora, Felidae) at Rio de Janeiro Zoo Foundation (RIOZOO), Brazil. Feeding behaviors were not registered, as the animals were always fed in the background chambers, where observations could not be carried out, and because many of the enrichments involved food items (which could influence the feeding responses for the regular diet).

Behavioral classes	Description of behaviors
Inactivity	Animal not moving around and did not express a directed gaze to the environment; could be sleeping or lying
Active Standing	Jaguar not moving around, but expressed a directed gaze to the environment; could be sitting or standing
Maintenance	Urinating, defecating, licking, scratching, sharpening the claws or ingesting vegetation of the enclosure, but these behaviors were never related to stereotyped actions
Drinking	Drinking water in the small fountains or in the waterfall
Vocalizing	Animal emitted any kind of sound through its mouth
Affiliative/sexual	Jaguar playing or involved in an attempted copulation with a conspecific
Agonism	Animal expressed any agonistic displays to another jaguar
Movement	Moving around the enclosure
Human interaction	Jaguar interacted or expressed directed gaze to visitors or zookeepers
Environmental interaction	Animal interacted with the enrichment provided by feeding, exploring, manipulating or rubbing against the enrichment items
Out of site	Jaguar was in any specific point of the enclosure that partially or completely prevented appropriate visualization

Table 3. Observation periods of the behaviors of the four jaguars (*Panthera onca*; Carnivora, Felidae) at Rio de Janeiro Zoo Foundation (RIOZOO), Brazil. In each observation phase, each jaguar was observed 1 hour in the morning and 1 hour in the afternoon per day, except on the second phase when jaguars were observed during two consecutive hours following the introduction of enrichments. Observation time varied among jaguars and there were days when it was only possible to make one period of observation.

	Year period (2008)	Jaguars					
Observation phases		Negona	Alexandre	Cabeção	Gabi		
Before enrichment (first)	Jan-Mar	43 h	20 h	21 h	28 h		
During enrichment (second)	Mar-Apr	20 h	21 h	21 h	20 h		
After enrichment (third)	Apr-Jun	25 h	26 h	20 h	20 h		

15 minutes before starting to record the behavioral activities. Because two observers recorded the behaviors, training sections were carried out, during which the behaviors of the same jaguar were registered by both observers during the same period. Later, the behavioral records across the observers were compared. This process was repeated until at least 90% of equal records across all the observers were achieved (based on Del-Claro 2002).

Environmental enrichments

The environmental enrichments were always delivered in the morning or in the afternoon, at different time varying between 09:00 h and 16:00 h. We prepared the items with the materials available at the zoo or with recycled items, which were delivered in the enclosures with the help of the zookeepers. Most enrichments included food items (feeding enrichments), but we also tested other kinds of enrichment aiming to maximize sensorial capabilities (sensorial enrichments) or to maximize physical and manipulative skills (occupational enrichments) of the jaguars. In total, we applied nine different enrichments in ten sessions, with no more than one session per test day and just one enrichment per session, except the scent trail that could or could not precede other enrichments (Table 4). Meat ice cream was applied twice, with and without smell trail. Thus, aiming to avoid possible habituation of the jaguars, no enrichment, but scent trail, was repeated.

Statistical analyses

Individual analyses were applied to characterize each jaguar, thus identifying possible differences of response among them, especially considering that they were housed in different enclosures, and that one was old and debilitated (Cabeção). The Goodman proportion test (Goodman 1964) was used to compare the frequencies of each behavioral class among the test phases (before, during and after the environmental enrichments) for each jaguar and to compare the individual interaction of the jaguars with the enrichments. As Goodman's proportion test compare frequencies, not means or medians, it was not necessary to test the normality or homogeneity distribution of the data for the analysis. Significant differences were considered at p < 0.05.

RESULTS

All jaguars significantly reduced 'inactivity' environmental enrichments behaviors with (second phase) (Figure 1). However, 'inactivity' was re-established (Gabi), significantly increased (Negona and Alexandre) or decreased (Cabeção) in the third phase, compared with the first phase (Figure 1). All individuals significantly increased 'active standing' and 'maintenance' behaviors with environmental enrichments (second phase; Figure 1). However, Cabeção maintained this significant increase in 'active standing' in the third phase, when there was no environmental enrichment, whereas the other jaguars significantly reduced these behaviors in this phase, such that only Gabi maintained significant higher levels of 'active standing' than in the first phase

Table 4. Details and classifications of the environmental enrichment items offered to the four jaguars (Panthera onca
Carnivora, Felidae) at Rio de Janeiro Zoo Foundation (RIOZOO), Brazil.

Environmental enrichment	Description
Hose ball (occupational)	An empty plastic gallon (4-5 litre) container wrapped with strips of firefighter's hose, forming a network that was secured with screws
Scent trail (sensorial)	Animal blood or cinnamon were used to create scattered trails inside the enclosures, which may or may not lead the subject animal to another hidden enrichment
Meat tubes (feeding)	Cardboard tubes filled with bovine/chicken meat or dead mice and closed on both sides with wood shavings; tubes were placed in the vegetation or in hollow parts of the tree trunks
Cardboard boxes with meat, wood shavings or elephant faeces (feeding and sensorial, respectively)	Cardboard boxes with wood shavings that contain pieces of bovine meat or elephant faeces closed by their overlapping flaps
Stuffed pumpkins (feeding)	Large pumpkins cut in half, seeds removed and filled with bovine meat; the two halves are held together with sheets of brown paper; this item was preceded by a scent trail or placed on platforms
Meat ice cream (feeding)	Pieces of meat wrapped in sheets of brown paper over which animal hair was wrapped; for example, hair from Llamas (<i>Lama glama</i>); these items were hidden around the enclosure
Bags with meat on the floor (feeding)	Pieces of meat were wrapped in bovine-blood soaked feed bags and placed on the floor of the enclosure
Hanging bags with meat (feeding)	Meat wrapped in feed bags and hung up with ropes; this item could be combined with scent trails. This enrichment was not offered to Cabeção because he could not jump because of his disability
Sound enrichment (sensorial)	A CD (one hour duration) with sounds of rain, ocean, waterfalls, thunder, birds, dogs and jaguar vocalizations was played at the side of the enclosure

(Figure 1). In the third phase, 'maintenance' behaviors were re-established to the same levels of the first phase, for Alexandre and Gabi, but not for Negona and Cabeção (Figure 1). Negona significantly reduced this behavior to lower levels and Cabeção maintained it in a significant higher frequency in relation to the first phase (Figure 1). Furthermore, considering the interaction with the environmental enrichments, Cabeção interacted significantly more when compared with the other jaguars (Figure 2).

All jaguars significantly increased 'movement' behaviors with the environmental enrichments in the second phase (Figure 1). In the third phase, although Gabi reduced these behaviors, 'movement' was still in a significant higher level than in the first phase (before environmental enrichments), whereas Cabeção maintained the high levels of 'movement' behaviors detected in second phase (during environmental the enrichment; Figure 1). Moreover, Negona and Alexandre re-established these behaviors to frequencies similar to those in the first phase (Figure 1). Considering 'human interaction' behaviors, both Alexandre and Cabecão maintained similar frequencies detected in the first phase, which were then significantly reduced when the environmental enrichments were removed in the third phase (Figure 1). However, Negona significantly reduced and Gabi significantly increased this behavioral frequency during the implementation of the environmental enrichments, while Negona maintained this response and Gabi re-established this behaviora



□ before enrichment (1rst phase) ■ during enrichment (2nd phase) ■ after enrichment (3rd phase)

Figure 1. Individual effects of environmental enrichments on the behaviors of jaguars (*Panthera onca*; Carnivora, Felidae) at Rio de Janeiro Zoo Foundation (RIOZOO), Brazil. Proportions of a same behavioral class with different lower-case letters are significantly different among the test phases (Goodman proportion test – among multinomials; p < 0.05).

frequency after the removal of environmental enrichments (Figure 1). The jaguars expressed significant different behavioral frequencies for 'out of sight', 'drinking', 'vocalizing', 'affiliative/sexual' and 'agonism' behaviors (Figure 1). Moreover, Alexandre developed a habit of pacing in the third test phase (just occurrence – qualitative data), a behavior not observed for any other jaguar in any other phase.

DISCUSSION

The individual variability expressed by the jaguars, especially after the removal of the environmental enrichments, related to how the individuals interacted with them, highlight the importance of analyzing environmental enrichment effects individually. Moreover, the results support the hypothesis that the environmental enrichments improved the conditions of the four jaguars, regardless the individual variation of response, as indicated by behavioral changes expressed by all tested jaguars, like a reduction in 'inactivity' and activity-related an increase in behaviors. Considering that there are, to our knowledge, only a few peer-reviewed publications in this area for jaguars in zoos (Charlton 1998, Skibiel et al. 2007, Castillo-Guevara et al. 2012, Vidal et al. 2016), and that a systematic assessment of the environmental enrichment effects is the exception (Mellen & MacPhee 2001), the study reported here also adds to this literature.



Figure 2. Interaction of the jaguars (*Panthera onca*; Carnivora, Felidae) with environmental enrichments at Rio de Janeiro Zoo Foundation (RIOZOO), Brazil. Proportions with different capital letters are significantly different (Goodman proportion test – among multinomials; p < 0.05). Cabeção (highlighted in the figure) interacted significantly more.

The jaguars expressed some responses that were common for the four tested individuals. However. they also expressed significant individual responses for 'drinking', 'vocalizing' 'human interaction' behaviors, besides and differences in 'affiliative/sexual' or 'agonism' interactions, excluding Cabecão that could not interact with other jaguars, considering the three test phases (Figure 1). After the enrichments removal, there was also individual variability considering active-related behaviors ('active standing' and 'movement') and inactivity. These indicated that Gabi and mostly Cabeção probably took better advantages of the environmental enrichment than Alexandre and Negona (Figure 1). This may indicate behavioral plasticity or differences related to the different physiological/environmental conditions of the jaguars. In fact, Sellinger & Ha (2005) demonstrated different responses between two captive jaguars exposed to public visitation and also Vidal et al. (2016) found individual differences of three jaguars exposed to spice environmental enrichment. Moreover, these findings agree with studies evaluating environmental enrichment effects in other wild cat species, which found significant individual variability of response (Bond & Lindburg 1990, McPhee 2002, Van Metter et al. 2008). Thus, we highlight the need to evaluate the enrichments environmental effects at an individual level, as each animal may respond in a particular way, being more or less affected by the environmental enrichments.

Moreover, such individual variation of response when exposed to enrichments could also be related to the differences of age, health state and sex. According to Van Metter et al. (2008), African lions and Sumatran tigers from different ages and sex responded in different ways when facing environmental enrichments. This same author suggested that future studies should evaluate the environmental enrichment effects considering such variables as possible sources of individual variation of response. Despite sex may not account to explain our findings here, since both males or females better or worse responded to the environmental enrichments provided considering the variation of response for 'inactivity' or active-related behaviors after the removal of the enrichments (Figure 1), age and associated health state differences may have influenced our results. Cabeção interacted more with enrichments than the other jaguars in our study (Figure 2), thus indicating that the oldest and most debilitated jaguar benefited the most from the provision of enrichments. This is reinforced by the fact that the effects more indicative of an improvement in the condition of the jaguars ('inactivity', 'active standing' and 'movement') were only maintained by Cabeção when the enrichments were no longer in the enclosure (Figure 2). Moreover, as most enrichments evaluated here (six out of nine) included food items, it is also possible that individual food preferences could also have influenced our findings. This highlight the need to evaluate environmental enrichment effects individually.

Despite such significant individual variability of response, the enrichment items reduced 'inactivity' and 'out of sight' behaviors, except for Cabeção that was in an enclosure out from visitors area and without a hiding place, and increased 'maintenance', 'active standing' and 'movement' behaviors in all tested jaguars (Figure 1). Thus, the environmental enrichment improved the welfare of these four jaguars, because excessive inactivity has been considered as stressful for the animals (Davey 2007, Maia et al. 2012) or as a negative behavior in jaguars (Godinez et al. 2013). Moreover, an increase in non-stereotypic activestanding' related behaviors ('active and 'movement') may indicate that the jaguars were in a better condition during the enrichment (Bashaw et al. 2003). The reduction of 'out of sight' frequencies by the animals (Figure 1) may reflect that the four jaguars interacted with the enrichments in the visible area and also may be an effect of the increase in 'movement' behaviors. Thus, environmental enrichments may also have improved the public experience with these animals, considering that Godinez et al. (2013) demonstrated that the public form larger crowd sizes when the jaguars are visible and active. The general increase in 'maintenance' behaviors in the second phase may be a consequence of most enrichments involved food items, thus the jaguars may have licked after interacting with such enrichments.

Providing more than one environmental enri-

chment to African lions allowed them to perform a greater behavioral range and better stimulated such animals to be more active, reducing the probability of their habituation to the provided enrichments (Powell 1995). In this line, here we used several different environmental enrichments to avoid habituation of the jaguars that, in fact, resulted in an increase of the active behaviors of all tested animals. Moreover, most of the enrichments (seven from ten different items) we used included food items. According to Shepherdson et al. (1993), simple changes involving feeding methods were sufficient to cause significant behavioral changes of small captive wild cats, as we also observed here for the tested jaguars. Furthermore, here we found that, regardless the individual variation, the simple different enrichments we tested improved the jaguars' conditions. Thus, considering that no type of enrichment is permanently effective and that captive wild cats frequently get used quickly with environmental enrichments (Mellen 1997), we highlight the possibility of using the environmental enrichments we proposed here as alternatives to improve the conditions of the environment of, at least, captive jaguars. We recommend that future studies evaluate if similar environmental enrichments with the ones provided here would also improve the welfare conditions of other felines, as some studies have demonstrated that a same environmental enrichment improved the conditions of different wild cats (McPhee 2002, Skibiel et al., 2007).

After the removal of the environmental enrichment items, almost all general positive effects of the enrichments were abolished, except for Cabeção, which maintained a lower frequency of 'inactivity' and higher frequencies of 'active standing' and 'movement' behaviors in the third phase compared with the first one (Figure 1). In some cases, the behavioral changes expressed after the removal of the enrichments reflected a possible worse condition of the animals in this phase. 'Inactivity' was higher and 'active standing' was lower when there was no more environmental enrichment in the enclosures than in the first phase for Negona and Alexandre (Figure 1). Moreover, Alexandre started pacing, a common stereotype in captive wild felines, after the removal of the environmental enrichments, behavior not

observed before for any tested jaguar. This fact highlights the need to maintain environmental enrichment implementation systematically, otherwise, the benefits may be lost and the welfare conditions may even be worsened, at least, for some individuals. These findings agree with Castillo-Guevara *et al.* (2012), who found similar results for four captive jaguars.

summary, the individual variability In expressed here by the jaguars highlights the need to consider individual variation in future studies focused on the effects of environmental enrichments. Some individuals should better interact and take more advantages from the enrichments while others could be in a worse condition when enrichments are removed than they were before the implementation of them. Moreover, regardless such individuality of behavioral response, the different enrichments tested here improved the welfare conditions of the studied jaguars.

ACKNOWLEDGEMENTS

We thank Amanda Borges and all RIOZOO staff, for their help with data collection; Museu Nacional - UFRJ, for support; and Dr. Carlos Eduardo de Viveiros Grelle (UFRJ), for his advice. We also thank the two anonymous reviewers for their comments and suggestions to the manuscript, and Dr Michael Toscano and Dr. Octávio Menezes de Lima Jr., for editing the English language. This research was funded by FAPERJ and CNPq through grants and fellowships to researches. The authors declare no conflict of interest.

REFERENCES

- Bashaw, M. J., Bloomsmith, M. A., Marr, M. J., & Maple, T. L. 2003. To hunt or not to hunt? A feeding enrichment experiment with captive large felids. Zoo Biology, 22(2), 189–198. DOI: 10.1002/zoo.10065
- Bond, J. L., & Lindburg, D. G. 1990. Carcass feeding of captive cheetahs (*Acinonyx jubatus*): the effects of a naturalistic feeding program on oral

health and psychological well-being. Applied Animal Behavior Science, 26(4), 373–382. DOI: 10.1016/0168-1591(90)90036-D

- Castillo-Guevara, C., Unda-Harp, K., Iara, C., & Serio-Silva, J. C. 2012. Enriquecimento ambiental y su efecto en la exhibición de comportamientos estereotipados en jaguars (*Panthera onca*) del parque zoológico "Yaguar Xoo", Oaxaca. Acta Zoologica Mexicana, 28(2), 365–377. DOI: 10.21829/azm.2012.282839
- Charlton, N. 1998. The effects of an environmental enrichment device on the behaviour of captive jaguars. Ratel, 25(5), 178–188.
- Dantzer, R., & Mormède, P. 1983. De-arousal properties of stereotypical behavior. Applied Animal Ethology, 10(3), 233–244. DOI: 10.1016/0304-3762(83)90144-X
- Davey, G. 2007. Visitor's effects on the welfare of animals in the zoo: a review. Journal of Applied Animal Welfare Science, 10(2), 169–183. DOI: 10.1080/10888700701313595
- Del-Claro, K. 2002. Uma orientação ao estudo do comportamento animal. Uberlândia: Editora KDC: p. 90.
- Godinez, A. M., Fernandez, E. J., & Morrissey, K. 2013. Visitor behaviors and perceptions of jaguar activities. Anthrozoos, 26(4), 613–619. DOI: 10.2752/175303713X13795775535850
- Goodman, L. A. 1964. Simultaneous confidence intervals for contrasts among multinomial populations. The Annals of Mathematics and Statistics, 35(2), 716–725.
- IUCN Switzerland. 2007. The IUCN Red List of Threatened Species. Retrieved February 05, 2008 from http://www.iucnredlist.org/search /details.php/15953/summ.
- Lyons, J., Young R. J., & Deag, J. M. 1997. The effects of physical characteristics of the environment and feeding regime on the behavior of captive felids. Zoo Biology, 16(1), 71–83. DOI: 10.1002/(SICI)1098-2361(1997)1 6:1<71::AID-ZOO8>3.0.CO;2-8
- Maia, C. M., Volpato, G. L., & Santos, E. F. 2012. A case study: the effect of visitors on two captive pumas with respect to the time of the day. Journal of Applied Animal Welfare Science, 15(3), 222–235. DOI: 10.1080/10888705.2012.6 83758
- Markowitz, H., Aday, C. & Gavazzi, A. 1995. Effectiveness of acoustic "prey": environmental

enrichment for captive African leopard (*Panthera pardus*). Zoo Biology, 14(4), 371–379. DOI: 10.1002/zoo.1430140408

- Mason, G. 2006. Stereotypic behaviour in captive animals: Fundamentals and implications for welfare and beyond. In: G. Mason & J. Rushen (Eds.), Stereotypic animal behaviour: Fundamentals and applications to welfare. pp. 325–356. Wallingford, Oxfordshire: Centre for Agriculture and Biosciences International.
- McPhee, M. S. 2002. Intact carcasses as enrichment for large felids: effects on on- and off-exhibit behaviors. Zoo Biology, 21(1), 37–47. DOI: 10.1002/zoo.10033
- Mellen, J., & McPhee, M. S. 2001. Philosophy of environmental enrichment: past, present, and future. Zoo Biology, 20(3), 211–226. DOI: 10.1002/zoo.1021
- Mellen, J. D., & Shepherdson, D. J. 1997. Environmental enrichment for felids: an integrated approach. International Zoo Yearbook, 35(1), 191–197. DOI: 10.1111/j.1748-1090.1997.tb01209.x
- Ministério do Meio Ambiente Brasil. 2003. National list of Brazilian endangered species. Retrieved February 05, 2008 from http://www.mma.gov.br/port/sbf/fauna/index .cfm.
- Morato, R. G., Guimarães, M. A. B. V., Ferreira, F., Verreschi, I. T. N., & Barnabe, R. C. 1999. Características reprodutivas de onças-pintadas (*Panthera onca*) machos, mantidos em cativeiro. Brazilian Journal of Veterinary Research and Animal Science, 36(5), 261–266. DOI: 10.1590/S1413-95961999000500008
- Newberry, R. C. 1995. Environmental enrichment: increasing the biological relevance of captive environments. Applied Animal Behavior Science, 44(2-4), 229–243. DOI: 10.1016/0168-1591(95)00616-Z
- Powell D. M. 1995. Preliminary evaluation of environmental enrichment techniques for African lions (*Panthera leo*). Animal Welfare, 4(4), 361–370.

- Sellinger, R. L., & Ha, J. C. 2005. The effects of visitor density and intensity on the behavior of two captive jaguars (*Panthera onca*). Journal of Applied Animal Welfare Science, 8(4), 233–244. DOI: 10.1207/s15327604jaws0804_1
- Shepherdson, D. J., Carlsted K., Mellen, J., & Seidensticker, J. 1993. The influence of food presentation on the behavior of small cats in confined environments. Zoo Biology, 12(2), 203–216. DOI: 10.1002/zoo.1430120206
- Skibiel, A. M., Trevino, H. S., & Naugher, K. 2007. Comparison of several types of enrichment in captive felids. Zoo Biology, 26(5), 371–381. DOI: 10.1002/zoo.20147
- Swaisgood, R. R., & Shepherdson, D. J. 2005. Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next? Zoo Biology, 24(6), 499–518. DOI: 10.1002/zoo.20066
- Van Metter, J. E., Harriger, M. D., & Bolen, R. H. 2008. Environmental enrichment utilizing stimulus objects for African lions (*Panthera leo leo*) and Sumatran tigers (*Panthera tigris* sumatrae). Bioscience, 79(1), 7–16.
- Vidal, L. S., Guilherme, F. R., Silva, V. F., Faccio, M. C. S. R., Martins, M. M., & Briani, D. C. 2016.
 The effect of visitor number and spice provisioning in pacing expression by jaguars evaluated through a case study. Brazilian Journal of Biology, 76(2), 506–510. DOI: 10.1590/1519-6984.22814
- Walters, T. 2003. Observations of the short-term behavioural response of a captive male tiger (*Panthera tigris*) to changes in feeding enrichment. Ratel, 30(2), 29–47
- Young, R. 2003. Environmental enrichment for captive animals. New Jersey: Wiley–Blackwell: p. 240.

Submitted: 19 July 2017 Accepted: 11 December 2017 Associate Editor: Camila Barros