

Possible limits and advances of environmental enrichment for wild animals

ANGÉLICA DA SILVA VASCONCELLOS* & CÉSAR ADES**

University of São Paulo

The field of research in environmental enrichment aims at enhancing the welfare of captive animals through the assessment and establishment of adequate environmental and social features. It has generated significant amount of data about procedures which may reduce stress and undesirable behaviors, and promote the performance of the species-specific behaviors in captivity contexts. We here present a brief introduction on the concepts and methods used in the area followed by indications of possible advances through the integration of behavioural and physiological data, the adoption of a comparative perspective and the use of an individual approach in research and in husbandry.

Keywords: environmental enrichment, welfare, stress.

Limites e avanços possíveis do enriquecimento ambiental para animais silvestres.

A área de pesquisa em enriquecimento ambiental visa promover melhora na qualidade de vida de animais cativos através do estudo e da implementação de características ambientais e de interação mais adequadas. A área tem gerado conhecimento relevante para a redução do estresse e de comportamentos indesejáveis e para a promoção da exibição do repertório típico das espécies em animais mantidos no cativeiro. No texto, apresentamos uma breve revisão sobre conceitos e métodos utilizados na área, seguida da indicação de avanços possíveis, através da integração de dados comportamentais e fisiológicos, da adoção de uma perspectiva comparativa e do uso de uma abordagem individual na pesquisa e no manejo.

Palavras-chave: enriquecimento ambiental, bem-estar, estresse.

Introduction

The maintenance of captive animals in laboratories, farms, zoos and residences, serving the functions of transport, education, entertainment, research, conservation, companionship, among others, is a feature of our society that deserves examination from the point of view of the efficiency and ethical implications. There are clear indications that the conditions of captivity – deprivation of the appropriate environmental conditions, in particular those the species has in the natural environment, and the influence of inadequate aspects of enclosures, husbandry and interaction – can lead to physiological and behavioral problems in the animals.

The concern about the welfare of captive animals dates back to Yerkes (1925) and Hediger (1950,

1969) and denunciations made by Morris (1964) about behavioral disorders in zoo animals. The increase in research on different management techniques and the implementation of these in zoos has led to a condition propitious to the creation of a new multidisciplinary area: *environmental enrichment* (Shepherdson, Mellen & Hutchins, 1998). This area, which develops close to the practice of caring for captive animals, constitutes its own domain in applied research, in which it tries to determine, as accurately as possible, the positive and negative effects of the environmental conditions of captivity on aspects of animal behavior and physiology, related to welfare; it is a relatively recent area of research in Brazil.

The definition of environmental enrichment is obviously closely related to the criteria by which we define animal welfare. Increasing available alternatives of choice for the animal, the wealth of its social life, the availability of new items in the enclosure, the opportunities that it has to perform species-specific behaviors are some of the strategies that are assumed to promote high levels of welfare (Hurnik, 1992; Young, 2003). Welfare definitions differ, but are generally related (a) to the quality of biological

* Department of Experimental Psychology, Institute of Psychology, University of São Paulo. Avenida Professor Mello de Moraes, 1721, São Paulo, SP, CEP: 05508-030, Brazil Telephone: +55 11 4368-5143

** In memoriam. Department of Experimental Psychology, Institute of Psychology, University of São Paulo

functioning; (b) to affective aspects (how the animal “feels”); (c) to the animal’s ability to cope with environmental challenges (Duncan & Fraser, 1997).

The affective dimension is often considered essential to the definition of welfare (Duncan, 1993). A notion most recently used is the *sentience*, which means “the ability of an animal to evaluate the actions of others in relation to itself and to others, to remember some of its own actions and their consequences, to assess risks, to have some feelings and to have some degree of awareness” (Broom, 2006, p. 26). The problem with this approach, however, is finding accurate and reliable criteria to assess these subjective aspects (Mendl, 2001; Schilhab, 2002).

From another perspective, not necessarily incompatible, and more open to scientific evaluation, welfare is viewed as being associated to the animals’ strategies of adaptation to the environment they face (Broom, 2006; Barnard, 2007). The idea is that “a primary right of the animal is to live in an environment that allows full expression of its potential – naturally existent in the species, with perceptions, preferences and pre-programmed behavioral strategies” (Ades, 2010, p. 114). Difficult, labor-intensive, incomplete adaptations constitute conditions that potentially lead to poor welfare, and the indicators of these conditions are likely to be carefully measured and consequently evaluated.

Today we have significant results of the use of these techniques in zoological environments, obtained from the measurement of physiological and behavioral evidence of welfare. We are now more prepared to reduce undesirable behavior, to create conditions in which the animals can express species-typical characteristics (Seidensticker & Doherty, 1996) and, ultimately, to preserve and recover the behavioral skills necessary for a possible reintroduction of the animal into its natural environment. However, there is still much research to be done and the general theoretical framework for the area is to be built. In this paper, we present the broad outline of the recent effort in the area of environmental enrichment for wildlife, pointing out aspects which seem deserving research attention.

Welfare assessment

Studies on welfare and stress in wild animals generally use as parameters for evaluation behavioral and/or physiological indicators. Behavioral assessment of the status of captive animals, their level of

stress and the effects of enrichment relies on behavioral sampling and ethological description techniques (Lehner, 1998), with emphasis on responses that point to adjustment disorders; among them the repetitive acts known as stereotypies. Stereotypies can be quantitative – overactivity, excess water intake etc., or qualitative – behavior that the individual would never exhibit in nature and seems to serve no function: false chewing, repetitive and aimless walking (pacing), among others.

In the physiological approach, among other things, the levels of certain steroids which are known to be associated with stress are assessed (they are secreted in situations involving physical injury or that require dealing with environmental challenges). Unpredictable and threatening environmental components promote an “emergency state” resulting in changes in endocrine and metabolic patterns in the body. The environmental stimuli that lead to such changes in the organism are known as “stressors” (Möstl & Palme, 2002).

In warm-blooded animals, the efficiency of responding to stressful circumstances depends on the operation of two axes: the sympathetic-adrenal-medullary axis (SAM) and the hypothalamic-pituitary-adrenal axis (HPA). SAM axis hormones facilitate quick, explosive responses at a high energy cost, activating the cardiovascular, pulmonary, muscular and central nervous systems in the face of imminent danger. There is a general sympathetic activation, which is not sustainable for a long time, being limited to the elasticity of systems under the influence of these hormones (Gerra et al., 2001).

The release of adrenocorticotrophic hormone (ACTH) is part of the cascade produced by the HPA axis. This hormone activates the adrenal cells for the synthesis and secretion, in a matter of minutes, of glucocorticoids, primarily cortisol and corticosterone. Glucocorticoids typically have the functions of glucose modulation, amino acids mobilization and immune response modulation (Eckert, 1998), leading to metabolic changes related to energy production and the diversion of their usual route. Rather than being principally invested in physiological processes that are not essential for immediate survival, such as digestion or growth, energy is directed to the processes that allow the animals to deal with an emergency situation (Munck, Guyre & Holbrook, 1984; Sapolsky, 1992).

Stress, as a physiological mechanism, is not necessarily harmful; it is part of a selected strategy for facing challenging situations (Moberg, 2000).

Glucocorticoids can be released in response to situations not normally considered as stressful such as courting, mating and hunting (Broom & Johnson, 1993). The positive or negative effects of stress depend on the context and duration of the stressors (for a review, see Koolhaas et al., 2011). In relatively short periods of stress glucocorticoids increase the body's capability, facilitating the reception of stimuli and mobilizing the motor system (Raynaert, De Paeppe & Peeters, 1976). However, prolonged periods, in which cortisol levels are maintained chronically high, can reduce individual fitness by leading to immunosuppression and tissue atrophy (Munck, Guyre & Holbrook, 1984).

The measurement of glucocorticoid hormones can be used to monitor adrenal activity and, therefore, assess the level of physiological disturbance to which animals are subjected (Möstl & Palme, 2002). In studies focusing on welfare, non-invasive sampling methods are the most recommended: determining the concentration of glucocorticoids, or metabolites of these, present in urine (Hay & Mormède, 1998), saliva (Cooper et al., 1989), milk (Verkerk et al., 1998) or in faeces (Möstl & Palme, 2002).

Many studies have achieved an accurate assessment of welfare conditions through the combined use of different indicators (hormonal and behavioral, for example, Doyle, Baker & Cox, 2008; Moreira et al., 2007; Shivik et al., 2009). However, one of the existing questions, in the assessment of captive animal conditions, is related to the relationship between these indicators. They do not necessarily coincide and can lead to disparate, sometimes even conflicting conclusions. The progress of the area depends on studies that aim at describing the complex two-way process, through which behavior and hormones (or other physiological indicators) are integrated and thus guide animal responses to changes in their captivity environment.

Improvement in the environment

Although they are often intended to approximate the captive environment to the species' natural life conditions, enrichment interventions have to be made within the limits of captivity and within the contingencies of the indispensable contact with humans. The situation of captivity creates new contexts to which research and husbandry have to deal with.

The assessment of possibly harmful aspects of the captivity environments is the first step of the

analysis. Predictability and lack of novelty are characteristics that typify many of these environments. Animals are often kept in small enclosures with little stimuli, to which they become accustomed, and are subjected to repetitive management practices. In contrast, the natural environment constitutes a variable and not always predictable scenario, which stimulates the calculation of courses of action from probabilistic parameters. It often challenges previously found solutions and thus stimulates the exercise of cognitive processes. Animals devote a significant part of their time to exploratory behaviour, and dealing with environmental variability and novelty is part of their natural repertoire. Studies have demonstrated the need to carefully promote environmental challenges for captive animals (Hediger, 1950; 1969; Markowitz, Aday & Gavazzi, 1995; Vasconcellos, Adania & Ades, 2012; Yerkes, 1925; for revisions, Lutz & Novak, 2005; Shepherdson, Mellen & Hutchins, 1998; Wells, 2009; Young, 2003).

Captive environments may cause harm to animals by not offering full opportunity to perform species-typical behavior. The assumption here is that it is necessary for animals, for their welfare, to implement repertoires and strategies that constitute their means of survival in natural conditions (Shepherdson et al., 1993; Murray, Waran & Young, 1998; Rabbin, 2003; Young, 2003; Kistler et al., 2009).

Also relevant, in the characterization of captive environments, is the detection of potential sources of stress and aspects of management that reduce animal control over their immediate environment. Zoo enclosures establish an environment in which certain events are inevitable and the margin of control that animals have on this environment is reduced. One such condition is the absence of a refuge in the exhibition enclosure: causes the animals to be literally exposed, and offers no alternatives of escape (Shepherdson, Mellen & Hutchins, 1998). Imposing constant contact with humans can also be a factor affecting welfare. To what extent this contact can or should be modulated by the animals themselves is a relevant issue for research and management.

There are many ways in which it is possible to improve a captivity environment. Their description and use depends on research investment in an ethological/clinical approach, combined with physiological techniques which take into consideration specific and individual characteristics of the animals studied. Aspects already reasonably addressed, in terms of intervention, are the need to promote, in animals, a more active and exploratory interaction

with their environment, an increased likelihood that adaptive strategies and “species-typical” behaviors can be expressed and the reduction of aversive, threatening and stressful conditions, aspects potentially inductive of behavioral maladjustment (Universities Federation for Animal Welfare [UFAW], 2000, p. 3).

Useful experimental design

Research on environmental enrichment with wildlife usually has a reduced number of individuals. Consequently, most of the studies use, rather than experimental designs with different samples (keeping a group as control), a longitudinal design, with repeated measures, along which the physiological and/or behavioral patterns are compared under different conditions (Baseline/Enrichment, Baseline/Enrichment/Baseline etc.).

Designs that allow animals to choose between two or more environmental alternatives are an important complement to studies with repeated measures (Bean, Mason & Bateson, 1999; Heizmann et al., 1998; Inglis & Ferguson, 1986; Mason, Cooper & Clarebrough, 2001; Pines, Kaplan & Rogers, 2007; Vasconcellos, Adania & Ades, 2012). Preference tests allow animals to express their own scale of needs (Dawkins, 1990); thus provide relevant criteria, explicit in the behavior of the animals themselves, for the development of the ideal environment.

Positive effects of enrichment

Recent results confirm the efficiency of enrichment interventions in reducing undesirable behavior or stereotypies (Caws, Wehnelt & Aureli, 2008; Prado, Vasconcellos & Ades, 2007; Swaisgood et al., 2001; Wells & Irwin, 2008) and in increasing behavioral diversity or the performance of species-typical behavior (Basile et al., 2007; Dishman, Thomson & Karnovsky, 2009; Kistler et al., 2009; Shivik et al., 2009; Turner & Grantham, 2002; Wells & Irwin, 2009). In some studies, both increased activity and exploration, as well as a reduction in atypical behavior were promoted (Csatádi, Leus & Pereboom, 2008; Gupta, Prakash & Sinha, 2007; Mallapur, Waran & Sinha, 2007; Skibiél, Trevino & Naugher, 2007; Therrien et al., 2007; Videan et al., 2007). Integrating behavioral data with hormonal evidence (cortisol levels, Doyle, Baker & Cox, 2008; Moreira et al., 2007; Shivik et al., 2009, immune system

responses; Capitanio & Lerche, 1998; Schapiro et al., 2000, changes in weight without increased nutritional consumption; Schapiro & Kessel, 1993) has expanded the field of analysis.

Possible limits and advances

Enrichment interventions may, sometimes, lead to innocuous (Burgener, Gusset & Schmid, 2008; Hanbury et al., 2009; Liu et al., 2006; Schapiro et al., 1993; Spring, Clifford & Tomko, 1997; Wells et al., 2007; Wiedenmayer, 1998), or even harmful results (Hahn, 2000). Certain enrichment techniques are only effective in certain contexts, or for certain species (Wells, 2009). Even when significant changes are achieved in certain parameters of welfare, it is worth considering the need to perform causal analysis to broadly understand the produced effects. It is common in enrichment studies, for example, to increase the difficulty to reach food, thus creating higher levels of foraging activity (Cummings et al., 2007; Shivik et al., 2009). This increase, however, does not necessarily mean that there has been an increase in welfare: it simply shows that the animals reacted to an environmental challenge by modulating their behavior.

Interpreting a behavioral or physiological change as positive depends on the context in which it was obtained. Even an increase in the concentration of glucocorticoids, an effect opposite to what many studies seek, can paradoxically represent an indicator of success. A variation of external conditions, the necessity of “solving problems” and the investment of effort, that take animals out of a poor and repetitive environment, can pose challenges and generate an increase in the glucocorticoid concentration. Some studies found indications that increases in the concentrations of these steroids may occur in association with signs of improvement in welfare (Beattie et al. 2000; Marashi et al. 2003).

Behavioral or hormonal differences observed between males and females, and even between individuals – the result of genetic differences, age, past experience etc. – complicate the picture and show the limitations of the search for general enrichment strategies. Opposite hormonal effects were found between individuals in maned wolves that were subjected to standard food enrichment procedures (Cummings et al., 2007; Vasconcellos et al., 2009). Vasconcellos (2009) showed that this difference was related to the animal’s temperament profile. Other

studies used analyses that considered the individual differences in temperament or personality as explanatory variables (Bremner-Harrison, Prodohl & Elwood, 2004; Cooper & Mason, 2000; Harri et al., 2000; Kirkden & Pajor, 2006; Koolhaas et al., 1999; Mason, Cooper & Clarebrough, 2001; Powell & Svoke, 2008; Raffa, Havill & Nordheim, 2002; Walsh & Cummins, 1976).

Although the general principles of maintenance and management in zoos can be issued at a species level, we must, in most cases, complement this knowledge with data regarding individual characteristics of the animals. Enrichment interventions are clinical interventions, that can be potentialized if the past experiences and behavioral profiles of the animals are taken into account. Behavioral tests that evaluate the temperament profile of individuals can be helpful in choosing the appropriate enrichment technique.

Often, the principles that work for a particular species, even general ones, will not necessarily work for another. Comparative studies of enrichment are essential, as in any other area of Ethology. In addition to the classic welfare measures (absence of stereotypies, occurrence of exploratory behaviors etc.), it is pivotal to consider the ecological rules that define the welfare of each studied species.

The conclusion that enrichment occurred is often made from studies that have limited duration. The positive effects can be momentary, linked to the changes in management, with no guarantee of permanence, which is the basic objective of enrichment. An ideal scheme would include an extended assessment, in order to check the permanence or the fragility of the changes achieved. In some of the studies that have bothered to include, after the assessment of enrichment, a second round of observations, no lasting effects of improvements were found (Boinski et al., 1999, Vasconcellos et al., 2009; Vasconcellos, 2009).

Environmental enrichment must be implemented, in most cases, as a permanent husbandry protocol, not as an occasional intervention. It can even be used as a preventive practice – a way to protect animals which have not yet exhibited injurious effects of the stress of captivity. A step forward would be to adopt a philosophy of enrichment that is not restricted to correction, but seeks to improve the animals' physical and psychological health, even in animals that appear to be in perfect condition. There is a whole field of preventive enrichment, in addition to the enrichment that seeks to remedy problems that have already been detected.

Conclusion

Environmental enrichment, which in many cases, has proven effective in improving the quality of life of captive animals, still requires a research effort to unlock the processes in play and at the same time expand the area's theoretical basis and its practical efficiency. Our basic suggestions, quickly outlined here are related to the need to examine the several indicators of welfare – behavioral, physiological – of captive animals, seeking to understand their (interactive) influence on animal behavior; adopting an ethological, comparative perspective, focusing on behavioral functions and considering individual characteristics and preferences, both in research and in the management of wild species kept in captivity.

References

- Ades, C. (2010). Por uma ética animal centrada no animal. Em: V. B. Magalhães & V. Rall (Orgs.), *Reflexões sobre a tolerância: direitos dos animais* (pp. 105-116). São Paulo, SP: Editoras Evolução e Humanitas.
- Barnard, C. (2007). Ethical regulation and animal science: why animal behaviour is special. *Animal Behaviour*, 74, 5-13.
- Basile, B. M., Hampton, R. R., Chaudhry, A. M. & Murray, E. A. (2007). Presence of a privacy divider increases proximity in pair-housed rhesus monkeys. *Animal Welfare*, 16, 37-39.
- Bean, D., Mason, G. J. & Bateson, M. (1999). Contrafreeloading in starlings: testing the information hypothesis. *Behaviour*, 136, 1267-1282.
- Beattie, V. E., O'Connell, N. E., Kilpatrick, D. J. & Moss, B. W. (2000). Influence of environmental enrichment on welfare-related behavioural and physiological parameters in growing pigs. *Animal Science*, 70, 443-450.
- Boinski, S., Swing, S. P., Gross, T. S. & Davis, J. K. (1999). Environmental enrichment of brown capuchins (*Cebus apella*): behavioral and plasma and fecal cortisol measures of effectiveness. *American Journal of Primatology*, 48, 49-68.
- Bremner-Harrison, S., Prodohl, P. A. & Elwood, R. W. (2004). Behavioural trait assessment as a

- release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation*, 7, 313-320.
- Broom, D. M. (2006). The evolution of morality. *Applied Animal Behaviour Science*, 100, 20-28.
- Broom, D. M. & Johnson, K.G. (1993). Stress and animal welfare. London: Chapman and Hall.
- Burgener, N., Gusset, M. & Schmid, H. (2008). Frustrated appetitive foraging behavior, stereotypic pacing, and fecal glucocorticoid levels in snow leopards (*Uncia uncia*) in the Zurich zoo. *Journal of Applied Animal Welfare Science*, 11, 74-83.
- Capitanio, J. P. & Lerche, N. W. (1998). Social separation, housing relocation, and survival in simian AIDS: a retrospective analysis. *Psychosomatic Medicine*, 60, 235-244.
- Caws, C. E., Wehnelt, S. & Aureli, F. (2008). The effect of a new vertical structure in mitigating aggressive behaviour in a large group of chimpanzees (*Pan troglodytes*). *Animal Welfare*, 17, 149-154.
- Cooper, T. R., Trunkfield, H. R., Zanella, A. J. & Booth, W. D. (1989). An enzyme-linked immunosorbent assay for cortisol in the saliva of man and domestic farm animals. *Journal of Endocrinology*, 123, 13-16.
- Cooper, J. J. & Mason, G. J. (2000). Increasing costs of access to resources cause re-scheduling of behaviour in American mink (*Mustela vison*): implications for the assessment of behavioural priorities. *Applied Animal Behaviour Science*, 66, 135-151.
- Csatádi, K., Lei, K. & Pereboom, J. J. M. (2008). A brief note on the effects of novel enrichment on an unwanted behaviour of captive bonobos. *Applied Animal Behaviour Science*, 112, 201-204.
- Cummings, D., Brown, J.L., Rodden, M. D. & Songsasen, N. (2007). Behavioral and physiologic responses to environmental enrichment in the maned wolf (*Chrysocyon brachyurus*). *Zoo Biology*, 26, 331-343.
- Dawkins, M. S. (1990). From an animal's point of view: motivation, fitness, and animal welfare. *Behavioral and Brain Sciences*, 13, 1-61.
- 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, 88-95.
- Doyle, L. A., Baker, K. C. & Cox, L. D. (2008). Physiological and behavioral effects of social introduction on adult male rhesus macaques. *American Journal of Primatology*, 70, 542-550.
- Duncan, I. J. H. (1993). Welfare is to do with what animals feel. *Journal of Agricultural & Environmental Ethics*, 6, 8-14.
- Duncan, I. J. H. & Fraser, D. (1997). Understanding animal welfare. In: M. C. Appleby & B. O. Hughes (Eds.), *Animal Welfare* (pp. 19-31). Cambridge: CAB International.
- Eckert, R. (1998). Hypothalamus and pituitary. In: D. Randall, W. Burggren, K. French & R. Eckert (Eds.), *Animal Physiology, Mechanisms and Adaptations*. New York: W. H. Freeman.
- Gerra, G., Zaimovic, A., Mascetti, G. G., Gardini, S., Zambelli, U., Timpano, M., Raggi, M. A. & Brambilla, F. (2001). Neuroendocrine responses to experimentally-induced psychological stress in healthy humans. *Psychoneuroendocrinology*, 26, 91-107.
- Gupta, B. K., Prakash, S. & Sinha, A. K. (2007). Strategy for enriching the environment of captive Ursids. *Current Science*, 93, 147-152.
- Hahn, N. E. (2000). Environmental Enrichment-related Injury in the Macaque (*macaca fascicularis*): Intestinal Linear Foreign Body. *Comparative Medicine*, 50, 556-558.
- Hanbury, D.B., Fontenot, M. B., Highfill, L. E., Bingham, W., Bunch, D. & Watson, S. L. (2009). Efficacy of auditory enrichment in a prosimian primate (*Otolemur garnettii*). *Lab Animal*, 38, 122-125.
- Harri, M., Kasanen, S., Mononen, J. & Sepponen, J. (2000). Preferences of farmed blue foxes for different floor types. *Behavioural Processes*, 49, 111-119.
- Hay, M. & Mormède, P. (1998). Urinary excretion of catecholamines, cortisol and their metabolites in Meishan and Large White sows: validation as a non-invasive and integrative assessment of adrenocortical

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- and symphoadrenal axis activity. *Veterinary Research*, 29, 119-128.
- Hediger, H. (1950). *Wild Animals in Captivity*. London: Butterworths.
- Hediger, H. (1969). *Man and Animal in the Zoo*. London: Routledge and Kegan Paul.
- Heizmann, V., Jonas, I., Hirschenauer, K. & Havelec, L. (1998). Choice tests with groups of mice: nestbox, nesting material and tubes as enrichment items for laboratory mice. *Journal of Experimental Animal Science*, 39, 43-60.
- Hurnik, J. (1992). *Behaviour, animal farm and the environment*. Cambridge: CAB International.
- Inglis, I. R. & Ferguson, N. J. K. (1986). Starlings search for food rather than eat freely available, identical food. *Animal Behaviour*, 34, 614-617.
- Kirkden, R. D. & Pajor, E. A. (2006). Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. *Applied Animal Behaviour Science*, 100, 29-47.
- Kistler, C., Hegglin, D., Würbel, H. & König, B. (2009). Feeding enrichment in an opportunistic carnivore: The red fox. *Applied Animal Behaviour Science*, 116, 260-265.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. & Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, 23, 925-935.
- Koolhaas, J. M., Bartolomucci, A., Buwalda, B., de Boer, S. F., Flügel, G., Korte, S. M., Meerlo, P., Murison, R., Olivier, B., Palanza, P., Richter-Levin, G., Sgoifo, A., Steimer, T., Stiedl, O., van Dijk, G., Wöhr, M. & Fuchs, E. (2011). Stress revisited: A critical evaluation of the stress concept. *Neuroscience and Biobehavioral Reviews*, 35, 1291-1305.
- Lehner, P.N. (1998). *Handbook of ethological methods*. Cambridge: Cambridge University Press.
- Liu, J., Chen, Y., Guo, L., Gu, B., Liu, H., Hou, A., Liu, X., Sun, L. & Liu, D. (2006). Stereotypic behavior and fecal cortisol level in captive giant pandas in relation to environmental enrichment. *Zoo Biology*, 25, 445-459.
- Lutz, C. K., Novak, M. A. (2005). Environmental enrichment for nonhuman primates: Theory and application. *ILAR Journal*, 46, 178-191.
- Mallapur, A. Waran, N. & Sinha, A. (2007). A note on enrichment for captive lion-tailed macaques (*Macaca silenus*). *Applied Animal Behaviour Science*, 108, 191-195.
- Marashi, V., Barnekow, A., Ossendorf, E. & Sachser, N. (2003). Effects of different forms of environmental enrichment on behavioral, endocrinological, and immunological parameters in male mice. *Hormones and Behavior*, 43, 281-292.
- Markowitz, H., Aday, C. & Gavazzi, A. (1995). Effectiveness of acoustic prey-environmental enrichment for captive African leopard (*Panthera pardus*). *Zoo Biology*, 14, 371-379.
- Mason, G. J., Cooper, J. & Clarebrough, C. (2001). Frustrations of fur-farmed mink. *Nature*, 410, 35-36.
- Mendl, M. (2001). Assessing the welfare state. *Nature*, 410, 31-32.
- Moberg, G. P. (2000). Biological response to stress: implications for animal welfare. In: G. P. Moberg & J. A. Mench (Eds.) *The biology of animal stress* (pp. 123-146). New York: CABI Publishing.
- Moreira, N., Brown, J. L., Moraes, W., Swanson, W. F. & Monteiro-Filho, E. L. A. (2007). Effect of housing and environmental enrichment on adrenocortical activity, behavior and reproductive cyclicity in the female tigrina (*Leopardus tigrinus*) and margay (*Leopardus wiedii*). *Zoo Biology*, 26, 441-460.
- Morris, D. (1964). The response of animals to a restricted environment. *Symposia of the Zoological Society of London*, 13, 99-118.
- Möstl, E. & Palme, R. (2002). Hormones as indicators of stress. *Domestic Animal Endocrinology*, 23, 67-74.
- Munck, A., Guyre, P. M. & Holbrook, N. I. (1984). Physiological functions of glucocorticoids in stress and their relationship to pharmacological actions. *Endocrinology Reviews*, 5, 25-44.

- Murray, A. J., Waran, N. K. & Young, R. J. (1998). Environmental enrichment for Australian mammals. *Animal Welfare*, 7, 415-425.
- Pines, M.K., Kaplan, G. & Rogers, L. J. (2007). A note on indoor and outdoor housing preferences of common marmosets (*Callithrix jacchus*). *Applied Animal Behaviour Science*, 108, 348-353.
- Powell, D. M. & Svoke, J. T. (2008). Novel environmental enrichment may provide a tool for rapid assessment of animal personality: a case study with giant pandas (*Ailuropoda melanoleuca*). *Journal of Applied Animal Welfare Science*, 11, 301-318.
- Prado, A. M., Vasconcellos, A. S. & Ades, C. (2007). Behavioral enrichment reduces stereotypic pacing in maned wolves (*Chrysocyon brachyurus*). In: V. J. Hare & J. E. Kroszko (eds.), *Proceedings of the Eighth International Conference on Environmental Enrichment* (pp. 311-312). San Diego, CA: The Shape of Enrichment, Inc.
- Rabin, L. A. (2003). Maintaining behavioural diversity in captivity for conservation: Natural behaviour management. *Animal Welfare*, 12, 85-94.
- Raffa, K. F., Havill, N. P. & Nordheim, E. V. (2002). How many choices can your test animal compare effectively? Evaluating the critical assumption of behavioural preference tests. *Oecologia*, 133, 422-429.
- Raynaert, R., De Paepe, M. & Peeters, G. (1976). Influence of stress, age and sex on serum growth hormone and free fatty acids in cattle. *Hormone and Metabolic Research*, 8, 109-114.
- Sapolsky, R. M. (1992) Neuroendocrinology of the stressresponse. In J. B. Becker, S. M. Breedlove & D. Crews (Orgs.). *Behavioral Endocrinology I* (pp. 287-324). Cambridge: MIT Press.
- Schapiro, S.J., Bloomsmith, M. A., Kessel, A. L. & Shively, C. A. (1993). Effects of enrichment and housing on cortisol response in juvenile rhesus-monkeys. *Applied Animal Behaviour Science*, 37, 251-263.
- Schapiro, S. J., Nehete, P. N., Perlman, J. E. & Sastry, K. J. (2000). A comparison of cell-mediated immune responses in rhesus macaques housed singly, in pairs, or in groups. *Applied Animal Behaviour Science*, 68, 67-84.
- Schapiro, S.J. & Kessel, A. L. (1993). Weight gain among juvenile rhesus macaques – a comparison of enriched and control-groups. *Laboratory Animal Science*, 43, 315-318.
- Schilhab, T. S. S. (2002). Anthropomorphism and mental state attribution. *Animal Behaviour*, 63, 1021-1102.
- Seidensticker, J. & Doherty, J. G. (1996). Integrating animal behavior and exhibit design. In: D. G. Kleiman, M. E. Allen, K. V. Thompson & S. Lumpkin (Eds.), *Wild Mammals in Captivity: Principles and Techniques* (pp. 180-190). Chicago: University of Chicago Press.
- Shepherdson, D. J., Carlstead, K., Mellen, J. D. & Seidensticker, J. (1993). The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology*, 12, 203-216.
- Shepherdson, D. J., Mellen, J. D. & Hutchins, M. (Eds.). (1998). *Second Nature: environmental enrichment for captive animals* (pp. 01-12). Washington: Smithsonian Institution Press.
- Shivik, J. A., Palmer, G. L., Gese, E. A. & Osthaus, B. (2009). Captive Coyotes Compared to Their Counterparts in the Wild: Does Environmental Enrichment Help? *Journal of Applied Animal Welfare Science*, 12, 223-235.
- Skibiell, A.L., Trevino, H. S. & Naugher, K. (2007). Comparison of several types of enrichment for captive felids. *Zoo Biology*, 26, 371-381.
- Spring, S.E., Clifford, J. O. & Tomko, D. L. (1997). Effect of environmental enrichment devices on behaviors of single- and group-housed squirrel monkeys (*Saimiri sciureus*). *Contemporary Topics*, 36, 72-75.
- Swaigood, R. R., White, A. M., Zhou, X. P., Zhang, H. M., Zhang, G. Q., Wei, R., Hare, V. J., Tepper, E. M. & Lindburg, D. G. (2001). The quantitative assessment of the efficacy of an environmental enrichment programme for giant pandas. *Animal Behaviour*, 61, 447-457.
- Therrien, C.L., Gaster, L., Cunningham-Smith, P. & Manire, C. A. (2007). Experimental evaluation of environmental enrichment of sea turtles. *Zoo Biology*, 26, 407-416.
- Turner, P. V. & Granthan, L. E. (2002). Short-term effects of an environmental enrichment program for

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- adult cynomolgus monkeys. *Contemporary Topics in Laboratory Animal Science*, 41, 13-17.
- Universities Federation for Animal Welfare (2000). *Guia para o enriquecimento das condições ambientais do cativeiro* (S. Celotti, trad.). São Paulo: Sociedade Zoófila Educativa.
- Vasconcellos, A. S., Guimarães, M. A. B. V., Oliveira, C. A., Pizzutto, C. S. & Ades, C. (2009). Environmental enrichment for maned wolves: group and individual effects. *Animal Welfare*, 18, 289-300.
- Vasconcellos, A. S. (2009). *O estímulo ao forrageamento como fator de enriquecimento ambiental para lobos guarás: efeitos comportamentais e hormonais*. Tese de doutorado, Instituto de Psicologia, Universidade de São Paulo, São Paulo, SP.
- Vasconcellos, A. S., Adania, C. H., Ades, C. (2012). Contrafreeloading in maned wolves: implications for their management and welfare. *Applied Animal Behaviour Science*, 140, 85-91.
- Verkerk, G. A., Phipps, A. M., Carragher, J. F., Matthews, L. R. & Stelwagen, K. (1998). Characterization of milk cortisol concentrations as a measure of short-term stress responses in lactating dairy cows. *Animal Welfare*, 7, 77-86.
- Videan, E. N., Fritz, J., Howell, S. & Murphy, J. (2007). Effects of two types and two genre of music on social behavior in captive chimpanzees (*Pan troglodytes*). *Journal of the American Association for Laboratory Animal Science*, 46, 66-70.
- Walsh, R. N. & Cummins, R. A. (1976). The Open-Field Test: The Critical Review. *Psychological Bulletin*, 83, 482-504.
- Wells, D. L. (2009) Sensory stimulation as environmental enrichment for captive animals: A review. *Applied Animal Behaviour Science*, 118, 1-11
- Wells, D. L., Hepper, P. G., Coleman, D. & Challis, M. G. (2007). A note on the effect of olfactory stimulation on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, 106, 155-160.
- Wells, D. L. & Irwin, R. M. (2008) Auditory estimation as enrichment for zoo-housed Asina Elephants (*Elephas maximus*). *Animal Welfare*, 17, 57-69.
- Wells, D. L. & Irwin, R. M. (2009). The Effect of Feeding Enrichment on the Moloch Gibbon (*Hylobates moloch*). *Journal of Applied Animal Welfare Science*, 12, 21-29.
- Wiedenmayer, C. (1998). Food hiding and enrichment in captive Asian elephants. *Applied Animal Behaviour Science*, 56, 77-82.
- Yerkes, R. M. (1925). *Almost Human*. New York: Century.
- Young, R. J. (2003). *Environmental enrichment for captive animals*. Oxford: Blackwell Science.

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