

Frustrated Appetitive Foraging Behavior, Stereotypic Pacing, and Fecal Glucocorticoid Levels in Snow Leopards (*Uncia uncia*) in the Zurich Zoo

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This study hypothesized that permanently frustrated, appetitive-foraging behavior caused the stereotypic pacing regularly observed in captive carnivores. Using 2 adult female snow leopards (*Uncia uncia*), solitarily housed in the Zurich Zoo, the study tested this hypothesis experimentally with a novel feeding method: electronically controlled, time-regulated feeding boxes. The expected result of employing this active foraging device as a successful coping strategy was reduced behavioral and physiological measures of stress, compared with a control-feeding regime without feeding boxes. The study assessed this through behavioral observations and by evaluating glucocorticoid levels noninvasively from feces. Results indicated that the 2 snow leopards did not perform successful coping behavior through exercising active foraging behavior or through displaying the stereotypic pacing. The data support a possible explanation: The box-feeding method did not provide the 2 snow leopards with the external stimuli to satisfy their appetitive behavioral needs. Moreover, numerous other factors not necessarily or exclusively related to appetitive behavior could have caused and influenced the stereotypic pacing.

Many types of stereotypy appear to be environmentally induced, presumably developing in aversive situations involving lack of control, conflict, or frustration (Mason, 1991). In such aversive situations, nonhuman animals use a set of be-

havioral strategies, presumably in an attempt to cope with the stressful environment. As animals who are able to show a coping response have lower stress levels, the success of the coping behavior can be measured by its effectiveness in reducing behavioral and physiological measures of stress (Wechsler, 1995). It has also been suggested that stereotypies are associated with a reduction in physiological measures of stress and can thus be regarded as successful coping behavior—by whatever means—that ameliorates a suboptimal environment, but the results of different studies are not consistent (Mason, 1991; Wechsler, 1995).

In predators, where searching for prey can consume a significant amount of the daily time or energy budget, permanently frustrated, appetitive foraging behavior was hypothesized as being the most likely proximate cause for the stereotypic pacing regularly observed in captive carnivores (Carlstead, 1998). For captive carnivores with fixed feeding times, such as the snow leopards (*Uncia uncia*) in the Zurich Zoo, all appetitive foraging behavior is prevented from being functionally completed, as food is delivered at regular intervals not contingent on the animal's behavior. There is no coping strategy by which the animal can remove this potentially aversive situation and actively influence the foraging success. The motivation to perform foraging behavior, however, presumably remains high; this is so even if food is eventually provided (Hughes & Duncan, 1988), potentially causing frustration in the affected animals and—over a period of time—possibly leading to the development of stereotypic pacing (Shepherdson, Carlstead, Mellen, & Seidensticker, 1993; Wechsler, 1991).

The aim of our study was to experimentally test this “frustrated appetitive foraging behavior hypothesis” in snow leopards and make successful foraging possible under captive conditions by providing a novel feeding method: electronically controlled, time-regulated feeding boxes. In contrast to conventional feeding, the spatial and temporal availability of food was varied, and its availability was unpredictable and directly related to the animal's locomotory and exploratory behavior (Lindburg, 1988, 1998). We hypothesized that its effectiveness as a successful coping strategy would result in reduced behavioral and physiological measures of stress, compared with a control-feeding regime without feeding boxes (Carlstead & Shepherdson, 2000). Furthermore, we tested the hypothesis that stereotypies serve a coping function (“coping hypothesis”) by assessing the proposed association of stereotypic pacing with a reduction in fecal glucocorticoid levels.

METHOD

Animals and Housing

The focal animals were two 14-year-old female snow leopards, named F1 and F2, born and housed solitarily in the Zurich Zoo, Switzerland. Both animals performed well-established stereotypic pacing. The trials were conducted in the

outdoor enclosures of the 2 animals, measuring 66 m² and 99 m², respectively, with an enclosure height of 3.5 m. The two enclosures were structured with rocks, tree trunks, water ponds, and elevated resting places.

Experimental Design

Three feeding boxes (65 × 35 × 35 or 80 × 40 × 40 cm) made of steel were installed at different places in each outdoor enclosure. Before 0930 hr, a sufficient amount of meat was distributed to all feeding boxes (in the absence of the snow leopard), and the boxes were closed by a horizontal sliding door with handle. A strong magnet, which was connected to, and controlled by, an electronic timer kept the door closed when switched on, and the meat was not accessible to the snow leopard then. Each magnet was independently switched off during two 30-min periods, semirandomly spread over the period of 0930 to 1815 hr. This happened without any associated noise, and the sliding doors did not move or open themselves. Because the animals did not know which feeding box would be available next or exactly when, they had to investigate all feeding boxes on a regular basis so as not to miss a feeding opportunity. Over a 4-week initial phase, both animals had learned to open the sliding door by catching hold of the handle with their paws and to obtain the meat.

Eight trials were conducted with each snow leopard, with each replication consisting of two temporally matched observations two days apart, one with a box-feeding regime as described earlier and one with a control-feeding regime. Under this control-feeding regime, the animals received a similar portion of meat at roughly the same place and time as on the corresponding box-feeding day but without having to investigate the feeding boxes. On the day in between two observations with different feeding regimes, the animals were not fed and the order of the two feeding regimes was reversed for each replication.

Data Collection and Analysis

The behavior of the 2 snow leopards was observed directly over a period of 2 months for 16 nonconsecutive days each (6.25 hr per day between 0930 and 1815 hr and therefore 200 hr in total). The animals were continuously visible and the duration of five behavioral categories (sleeping, resting, locomotion, stereotypic pacing, and others) was recorded by continuous focal sampling (Martin & Bateson, 1993). Stereotypic pacing was defined as repetitive locomotion in a fixed pattern. An activity index was calculated as the time an animal was active divided by the total observation time and a stereotypy index as the time an animal showed stereotypic pacing divided by the time spent active. The behavior of

the 2 snow leopards during the night following an observation day was filmed and recorded using a time-lapse video recorder.

The glucocorticoid level was assessed noninvasively from feces collected the morning after an observation day to account for the lag time associated with hormone excretion into the feces (Graham & Brown, 1996; Schatz & Palme, 2001; Young et al., 2004). This method was previously demonstrated to reflect individual adrenocortical responses to environmental changes in felids (Carlstead, Brown, Monfort, Killens, & Wildt, 1992; Carlstead, Brown, & Seidensticker, 1993; Carlstead, Brown, & Strawn, 1993). Always the freshest feces was collected and stored frozen at -20°C until processing and analysis. A group-specific 11-oxoetiocholanolone enzyme immunoassay (Palme & Möstl, 1997) was used, measuring 11,17-dioxoandrostanes (11,17-DOA), a group of cortisol metabolites. Schatz and Palme (2001) successfully tested this method on domestic cats (*Felis catus*) and showed the validity of 11,17-DOA as a parameter of the adrenocortical activity in felids, although a direct validation for snow leopards would have been preferable.

Data on the daily mean duration of behavior, daily mean concentration of 11,17-DOA, and daily mean temperature (see following) were compared using exact permutation tests (Colegrave, Engel, & Plowman, 2006). All statistical tests were two-tailed, with the significance level set at $p = .05$, and were run on SPSS 13.0 (2004).

RESULTS

According to the “frustrated appetitive foraging behavior hypothesis,” we expected reduced levels of stereotypic pacing and fecal glucocorticoids under the box-feeding regime compared with the control-feeding regime. For both snow leopards, however, this was not reflected in the data from our behavioral observations and physiological measurements (Table 1). Both animals showed a significant increase in locomotion under the box-feeding regime. F1 significantly reduced the duration of sleeping and showed a significant increase in the activity index during box-feeding; however, no significant differences were found in resting and other behaviors. F2 significantly reduced the duration of other behaviors during box-feeding but showed no significant differences in sleeping, resting, and the activity index between the two feeding regimes (Table 1).

The stereotypies were not evenly distributed over the course of the day. Both snow leopards performed most stereotypic pacing independent of the feeding regime during the observation period after 1700 hr (F1: box 62%, control 68%; F2: box 97%, control 86%). Stereotypic pacing also frequently occurred during the evening following an observation day in both animals, with no significant differences between the two feeding regimes (F1: $p = .50$, $n = 5$; F2: $p = .35$, $n = 7$).

TABLE 1
Effects of an Active Foraging Device by Means of Feeding Boxes (Box), Compared With a Control-Feeding Regime (Control), on the Behavior (Percentages of Mean Values \pm *SD* on Duration and Corresponding Indices) and Fecal Glucocorticoid Level (Mean Concentration \pm *SD* of 11,17-dioxoandrostanes in ng/g Feces) in 2 Adult Female Snow Leopards (*N* = 8 for Each Animal and Feeding Regime)

		<i>Sleeping</i>	<i>Resting</i>	<i>Locomotion</i>	<i>Stereotypic Pacing</i>	<i>Others</i>	<i>Activity Index</i>	<i>Stereotypy Index</i>	<i>11,17-DOA</i>
F1	Box	41.1 \pm 15.8	26.2 \pm 8.1	9.1 \pm 4.2	9.9 \pm 10.2	13.9 \pm 5.5	0.59 \pm 0.16	0.14 \pm 0.14	1522 \pm 971
	Control	57.3 \pm 6.7	24.4 \pm 5.5	2.6 \pm 0.8	6.3 \pm 6.9	9.6 \pm 2.9	0.43 \pm 0.72	0.14 \pm 0.13	916 \pm 658
	<i>p</i>	.04	.38	.01	.46	.20	.04	.84	.25
F2	Box	40.7 \pm 11.5	40.0 \pm 10.9	3.8 \pm 1.0	1.9 \pm 1.8	13.6 \pm 2.9	0.59 \pm 0.11	0.03 \pm 0.03	188 \pm 104
	Control	45.4 \pm 10.0	39.4 \pm 8.1	2.5 \pm 0.6	3.5 \pm 2.3	9.2 \pm 3.7	0.55 \pm 0.10	0.06 \pm 0.04	197 \pm 66
	<i>p</i>	.11	1.00	.04	.11	.01	.11	.11	.84

According to the “coping hypothesis,” we expected that on days with more stereotypic behavior, animals would show a lower physiological stress level. In the 2 snow leopards, however, the fecal glucocorticoid concentration was not significantly correlated with the stereotypy index on the corresponding day (F1: $p = .08$, $n = 16$; F2: $p = .74$, $n = 16$). Furthermore, according to the “coping hypothesis,” individuals who exhibit more stereotypic behavior are expected to have a lower physiological stress level. However, although the fecal glucocorticoid concentration was significantly different between the 2 snow leopards ($p < .0001$, $n_1 = n_2 = 16$), with marked day-to-day and within-individual variability, the stereotypy index was not ($p = .10$, $n_1 = n_2 = 16$).

We also examined the influence of daily mean temperature as a potentially compounding environmental factor that differs markedly from the snow leopard’s natural habitat (data obtained from the Swiss Meteorological Institute–MeteoSwiss, Zurich). In F1, a significant negative correlation between temperature and stereotypy index was found ($p = .03$, $n = 16$), whereas activity index and fecal glucocorticoid concentration were not related to temperature ($p > .05$, $n = 16$). F2 showed a significant positive correlation between temperature and fecal glucocorticoid concentration ($p = .04$, $n = 16$), whereas activity index and stereotypy index were not correlated with temperature ($p > .05$, $n = 16$).

DISCUSSION

Our results from behavioral observations and noninvasive glucocorticoid measurements in feces indicate that the 2 snow leopards did not perform successful coping behavior through exercising active foraging behavior or displaying the stereotypic pacing itself. However, the findings obtained remain inconclusive given that the small sample size and possible generalizations from our results are thus limited. Furthermore, marked interanimal differences in glucocorticoid levels, as also found in other studies on captive carnivores (Carlstead et al., 1992; Gusset, 2005; Wielebnowski, Fletchall, Carlstead, Busso, & Brown, 2002), may partly reflect the inherent variability of an individual’s ability to cope with the captive environment. There are several mutually nonexclusive explanations for these findings.

Stereotypies may be so persistent that rewarding alternative behavioral patterns have little effect (Mason, 1991), but we found no physiological evidence in the 2 snow leopards that this persistence was related to reinforcement by the stereotypic pacing itself. Similar results were obtained for other carnivore species (Carlstead, Brown, & Seidensticker, 1993; Gusset, 2005; Wielebnowski et al., 2002), collectively suggesting that stereotypic pacing cannot be regarded as successful coping behavior that ameliorates potentially inadequate housing conditions of captive carnivores by reducing their glucocorticoid levels.

A possible explanation supported by our data is that the box-feeding method did not provide the 2 snow leopards with the external stimuli they were seeking to satisfy their appetitive behavioral needs, either because the feeding boxes did not allow them to show successful foraging behavior or because the proximate cause of the stereotypic pacing was not solely found in frustrated appetitive foraging behavior. We discuss these two possibilities following.

Although the use of feeding boxes significantly reduced stereotypic pacing in tigers (*Panthera tigris*) (Jenny & Schmid, 2002), this feeding method was found to overtax the behavioral organization in margays (*Leopardus wiedii*) (Gusset, Burgener, & Schmid, 2002). Here, the use of feeding boxes did not reduce stereotypic pacing and fecal glucocorticoid levels, probably because the box-feeding method could not adequately simulate the sit-and-wait hunting strategy of small cats in the wild. Hartmann-Furter (2000), using a modified type of feeding box adapted to the hunting behavior of small cats, prevented the occurrence of stereotypes in European wildcats (*Felis s. silvestris*). Snow leopards, however, show a hunting behavior similar to tigers (Sunquist & Sunquist, 2002), so it is not clear why in contrast to tigers, the box-feeding method should not provide snow leopards with the appropriate external stimulus that would allow the appetitive behavior (foraging) to be coupled with its functional consequences (feeding).

Nevertheless, behavioral patterns involved in foraging are complex in free-ranging snow leopards (Sunquist & Sunquist, 2002), thus leaving the possibility that the feeding boxes, which can simulate only a fraction of natural hunting behavior, could not provide the stimulation an animal was seeking. This is supported by the finding that whereas overall activity significantly decreased in tigers using the box-feeding method (Jenny & Schmid, 2002), it increased in snow leopards because of a significant increase in locomotion, largely because of many unsuccessful foraging trips. Potentially, the 2 snow leopards could not exercise the desired level of control over their environment, thus possibly causing frustration and stress. This situation could be improved by providing a reliable visual or acoustic signal—preferably animated—that indicates a foraging opportunity (whether a feeding box can be opened or not) (Markowitz & Aday, 1998).

Supporting the hypothesis that stereotypic pacing found in captive carnivores is primarily caused by permanently frustrated appetitive foraging behavior (Carlstead, 1998), many other studies successfully provided a number of carnivore species with environmental enrichment related to feeding (Carlstead & Seidensticker, 1991; Carlstead, Seidensticker, & Baldwin, 1991; Forthman et al., 1992; Hartmann-Furter, 2000; Jenny & Schmid, 2002; Markowitz, Aday, & Gavazzi, 1995; Markowitz & LaForse, 1987; Shepherdson et al., 1993; Wechsler, 1994). Therefore, varying the spatial and temporal availability of food, as applied under our control-feeding regime, might have been stimulation enough to reduce—but not eliminate—stereotypic pacing compared with the conventional feeding regime, without using feeding boxes. This is supported by our finding that stereotypic pacing under both feeding regimes predominately occurred after all the

food was provided or obtained, as this temporal pattern of stereotypic pacing cannot be explained with food-anticipatory stereotypies otherwise mainly exhibited by captive carnivores (Carlstead, 1998). Nevertheless, other appetitive behavioral patterns besides foraging were also found to be related to stereotypies in captive carnivores, particularly permanently frustrated appetitive seeking of conspecifics (Carlstead & Seidensticker, 1991; Fischbacher & Schmid, 1999; Gusset et al., 2002; Jenny & Schmid, 2002). From our behavioral observations, it appears that this too could have been a compounding factor in this study. As providing a conspecific is not always possible or desirable, olfactory or auditory stimuli might prove more suitable and feasible in this regard.

Furthermore, numerous factors not necessarily or exclusively related to appetitive behavior can cause stereotypies and influence their performance (Mason, 1991). For example, we found a significant influence of temperature on behavioral and physiological measures of stress in the 2 snow leopards. High temperatures, which are atypical for the snow leopard's natural habitat (Sunquist & Sunquist, 2002), were related to increased glucocorticoid levels in F2 and to a shift in stereotypic pacing toward the cooler evening in F1 (see Fischbacher & Schmid, 1999, for more temperature effects on stereotypic pacing in captive carnivores). It is understood that a multitude of other environmental and social factors might have influenced our findings, for they also play a critical role in determining the behavioral and physiological responses of felids to captivity (Clubb & Mason, 2003; Gusset, 2003; Law, Macdonald, & Reid, 1997; Lyons, Young, & Deag, 1997; Mellen, 1991; Mellen, Hayes, & Shepherdson, 1998; Mellen & Shepherdson, 1997). Considering these factors is equally important in maintaining not only numerically and genetically but also behaviorally healthy captive populations of endangered species like snow leopards (Carlstead & Shepherdson, 1994; Shepherdson, 1994).

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REFERENCES

- Carlstead, K. (1998). Determining the causes of stereotypic behaviors in zoo carnivores: toward appropriate enrichment strategies. In D. J. Shepherdson, J. D. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 172–183). Washington, DC: Smithsonian Institution Press.

- Carlstead, K., Brown, J. L., Monfort, S. L., Killens, R., & Wildt, D. E. (1992). Urinary monitoring of adrenal responses to psychological stressors in domestic and nondomestic felids. *Zoo Biology, 11*, 165–176.
- Carlstead, K., Brown, J. L., & Seidensticker, J. (1993). Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biology, 12*, 321–331.
- Carlstead, K., Brown, J. L., & Strawn, W. (1993). Behavioral and physiological correlates of stress in laboratory cats. *Applied Animal Behaviour Science, 38*, 143–158.
- Carlstead, K., & Seidensticker, J. (1991). Seasonal variation in stereotypic pacing in an American black bear (*Ursus americanus*). *Behavioral Processes, 25*, 155–161.
- Carlstead, K., Seidensticker, J., & Baldwin, R. (1991). Environmental enrichment for zoo bears. *Zoo Biology, 10*, 3–16.
- Carlstead, K., & Shepherdson, D. (1994). Effects of environmental enrichment on reproduction. *Zoo Biology, 13*, 447–58.
- Carlstead, K., & Shepherdson, D. (2000). Alleviating stress in zoo animals with environmental enrichment. In G. P. Moberg & J. A. Mench (Eds.), *The biology of animal stress: Basic principles and implications for animal welfare* (pp. 337–354). Wallingford, UK: CAB International.
- Clubb, R., & Mason, G. (2003). Captivity effects on wide-ranging carnivores. *Nature, 425*, 473–474.
- Colegrave, N., Engel, J., & Plowman, A. B. (2006). Randomisation tests. In A. B. Plowman (Ed.), *Zoo research guidelines: Statistics for typical zoo datasets* (pp. 7–16). London: BIAZA.
- Fischbacher, M., & Schmid, H. (1999). Feeding enrichment and stereotypic behavior in spectacled bears. *Zoo Biology, 18*, 363–371.
- Forthman, D. L., Elder, S. D., Bakeman, R., Kurkowski, T. W., Noble, C. C., & Winslow, S. W. (1992). Effects of feeding enrichment on behavior of three species of captive bears. *Zoo Biology, 11*, 187–195.
- Graham, L. H., & Brown, J. L. (1996). Cortisol metabolism in the domestic cat and implications for non-invasive monitoring of adrenocortical function in endangered felids. *Zoo Biology, 15*, 71–82.
- Gusset, M. (2003). Acht Punkte zur Verbesserung der Haltungsbedingungen von Kleinkatzen in zoologischen Gärten [Eight aspects of improving the housing conditions for small cats in zoological gardens]. *Irbis, 20*, 15.
- Gusset, M. (2005). Faecal glucocorticoid level is not correlated with stereotypic pacing in two captive margays (*Leopardus wiedii*). *Animal Welfare, 14*, 157–159.
- Gusset, M., Burgener, N., & Schmid, H. (2002). Wirkung einer aktiven Futterbeschaffung mittels Futterkisten auf das stereotype Gehen und den Glukokortikoidspiegel von Margays, *Leopardus wiedii*, im Zoo Zürich [Effects of an active foraging device on the stereotypic pacing and fecal glucocorticoid level in margays, *Leopardus wiedii*, in the Zürich Zoo]. *Der Zoologische Garten N.F., 72*, 245–262.
- Hartmann-Furter, M. (2000). A species-specific feeding technique designed for European wildcats (*Felis s. silvestris*) in captivity. *Säugetierkundliche Informationen, 4*, 567–575.
- Hughes, B. O., & Duncan, I. J. H. (1988). The notion of ethological “need,” models of motivation and animal welfare. *Animal Behaviour, 36*, 1696–1707.
- Jenny, S., & Schmid, H. (2002). Effect of feeding boxes on the behavior of stereotyping Amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. *Zoo Biology, 21*, 573–584.
- Law, G., Macdonald, A., & Reid, A. (1997). Dispelling some common misconceptions about the keeping of felids in captivity. *International Zoo Yearbook, 35*, 197–207.
- Lindburg, D. G. (1988). Improving the feeding of captive felines through application of field data. *Zoo Biology, 7*, 211–218.
- Lindburg, D. G. (1998). Enrichment of captive mammals through provisioning. In D. J. Shepherdson, J. D. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 262–276). Washington, DC: Smithsonian Institution Press.

- 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*, 71–83.
- Markowitz, H., & Aday, C. (1998). Power for captive animals: Contingencies and nature. In D. J. Shepherdson, J. D. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 47–58). Washington, DC: Smithsonian Institution Press.
- Markowitz, H., Aday, C., & Gavazzi, A. (1995). Effectiveness of acoustic ‘prey’: Environmental enrichment for a captive African leopard (*Panthera pardus*). *Zoo Biology*, *14*, 371–379.
- Markowitz, H., & LaForse, S. (1987). Artificial prey as behavioral enrichment devices for felines. *Applied Animal Behaviour Science*, *18*, 31–43.
- Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide* (2nd ed.). Cambridge, UK: Cambridge University Press.
- Mason, G. J. (1991). Stereotypies: A critical review. *Animal Behaviour*, *41*, 1015–1037.
- Mellen, J. D. (1991). Factors influencing reproductive success in small captive exotic felids (*Felis* spp.): A multiple regression analysis. *Zoo Biology*, *10*, 95–110.
- Mellen, J. D., Hayes, M. P., & Shepherdson, D. J. (1998). Captive environments for small felids. In D. J. Shepherdson, J. D. Mellen, & M. Hutchins (Eds.), *Second nature: Environmental enrichment for captive animals* (pp. 184–201). Washington, DC: Smithsonian Institution Press.
- Mellen, J. D., & Shepherdson, D. J. (1997). Environmental enrichment for felids: An integrated approach. *International Zoo Yearbook*, *35*, 191–197.
- Palme, R., & Möstl, E. (1997). Measurement of cortisol metabolites in faeces of sheep as a parameter of cortisol concentration in blood. *International Journal of Mammalian Biology*, *62*(Suppl. 2), 192–197.
- Schatz, S., & Palme, R. (2001). Measurement of faecal cortisol metabolites in cats and dogs: A non-invasive method for evaluating adrenocortical function. *Veterinary Research Communications*, *25*, 271–287.
- Shepherdson, D. (1994). The role of environmental enrichment in the captive breeding and reintroduction of endangered species. In P. J. S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), *Creative conservation: Interactive management of wild and captive animals* (pp. 167–177). London: Chapman & Hall.
- 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.
- Sunquist, M., & Sunquist, F. (2002). *Wild cats of the world*. Chicago: University of Chicago Press.
- Wechsler, B. (1991). Stereotypies in polar bears. *Zoo Biology*, *10*, 177–188.
- Wechsler, B. (1994). Zur Stabilität von Bewegungstereotypien bei Eisbären [On the stability of stereotyped behavior patterns in polar bears]. *Der Zoologische Garten N.F.*, *64*, 25–34.
- Wechsler, B. (1995). Coping and coping strategies: A behavioural view. *Applied Animal Behaviour Science*, *43*, 123–134.
- Wielebnowski, N. C., Fletchall, N., Carlstead, K., Busso, J. M., & Brown, J. L. (2002). Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. *Zoo Biology*, *21*, 77–98.
- Young, K. M., Walker, S. L., Lanthier, C., Waddell, W. T., Monfort, S. L., & Brown, J. L. (2004). Noninvasive monitoring of adrenocortical activity in carnivores by fecal glucocorticoid analyses. *General and Comparative Endocrinology*, *137*, 148–165.

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