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A survey assessment of variables related to stereotypy in captive giraffe and okapi

Meredith J. Bashaw^{a,b,*}, Loraine R. Tarou^{a,b}, Todd S. Maki^a, Terry L. Maple^{a,b}

^aTECHlab, Zoo Atlanta, 800 Cherokee Avenue SE, Atlanta, GA 30315, USA ^bSchool of Psychology, Georgia Institute of Technology, 274 5th Street Atlanta, GA 30332-0170, USA

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Abstract

Stereotypic behavior has been investigated in a wide variety of animals, but little published information is available on this problem in captive exotic ungulates. A survey was used to gather information on the prevalence of stereotypic behavior in giraffe and okapi and to identify variables associated with these behaviors. Of the 71 institutions that received a survey, 69.0% responded. Data were reported for 257 individuals, including 214 giraffe (representing five subspecies) and 29 okapi. Of the animals included in the survey, 79.7% performed at least one type of stereotypic behavior. Licking of non-food objects (72.4%) and pacing (29.2%) were the most prevalent stereotypic behaviors, though other stereotypies were reported in 3.2% of the animals. The results of a logistic regression performed on the data indicated that sub species, number of hours the individuals spent indoors, access at night to conspecifics, feeding frequency, method of feeding, and type of food provided were predictors of stereotypic licking. Sub species, birth history, size of the indoor enclosure, environmental change, and type of food provided were found to be significant predictors of stereotypic pacing. In general, feeding motivation appears to be related to an oral stereotypy, whereas other environmental factors appear to be associated with a locomotor stereotypy. The results of this study suggest changes in management strategies that may be empirically studied and applied to improve the well-being of captive populations of giraffe and okapi. © 2001 Elsevier Science B.V. All rights reserved.

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^{*}Corresponding author. Tel.: +1-404-624-5682; fax: +1-404-624-5684. *E-mail address*: gt3813a@prism.gatech.edu (M.J. Bashaw).

1. Introduction

Most definitions of stereotypic behavior include three elements: these behaviors must have an invariant pattern, be regularly repeated, and serve no apparent purpose (Keiper, 1969; Marriner and Drickamer, 1994; Mason, 1991). In addition, an individual's performance of stereotypic behavior typically increases under stressful conditions (Mason, 1991). As stereotypic behaviors develop, they may become emancipated from their initial eliciting stimulus, and subsequently can be induced by any stimulus that increases general arousal (Ridley and Baker, 1982). Stereotypic behavior has been studied extensively in non-human primates (for review, see Capitanio, 1986), carnivores (for review, see Carlstead, 1998), and domestic animals (e.g. Redbo and Norblad, 1997). Though there is much debate about the causes of stereotypic behavior, one conclusion is clear: stereotypic behavior is the result of an abnormal animal–environment interaction (Carlstead, 1998). Stereotypic behavior may take many forms (for review, see Mason, 1993), and it is likely that different types of stereotypic behavior are the results of different types of abnormalities in the interaction between an animal and its environment.

Carlstead (1996) has suggested that stereotypies may be caused by the inability of a highly motivated behavior pattern to be successfully completed. Feeding behaviors are perhaps the most highly motivated of any behavior pattern, and therefore, frustrated feeding motivation is often linked to stereotypies that resemble feeding behaviors (Carlstead, 1998; Lukas, 1999). The extensive research on domestic ungulates (Redbo, 1990) supports the association between feeding motivation and the prevalence of oral stereotypies (including tongue-playing, bar biting, and licking of equipment in grazers) postulated by Mason and Mendl (1997). Redbo (1990) found these behaviors typically adjoined behaviors related to food searching, and only occurred in conditions where the animals were not at pasture. Links have been established between oral stereotypies and both feeding schedule and presence of a foraging substrate in sows (Rushen, 1985; Spoolder et al., 1995). Heifers fed a greater portion of roughage and allowed to feed for a longer duration of time devoted a much smaller proportion of their time to oral stereotypic behaviors (Redbo and Norblad, 1997). This relationship between oral stereotypies and type of food provided (Lukas, 1999; Redbo et al., 1998) and between oral stereotypies and feeding duration (Baker and Easley, 1996; Lukas, 1999; Savory and Maros, 1993; Terlouw et al., 1991; Willard et al., 1977) has also been established in horses, pigs, broiler breeders, chimpanzees (Pan troglodytes), and gorillas (Gorilla gorilla gorilla).

Despite the variety of research on domestic ungulates, the problem of stereotypy in giraffe (*Giraffa camelopardalis*) and okapi (*Okapi johnstoni*) is not well documented. During a study of social separation, two female giraffe at Zoo Atlanta were observed repeatedly licking the fences surrounding their outdoor enclosure, despite the presence of an adjacent mineral lick (Tarou et al., 2000). When they were separated from the male in their social group, a situation that appeared to cause stress, this licking increased, and one of the females began to pace. These observations suggest that fence licking and pacing are stereotypic behaviors for the giraffe at Zoo Atlanta. Koene (1999) has identified the problem of stereotypic licking in giraffe and suggested the performance of this oral stereotypic behavior is related to differences between wild and captive feeding patterns.

In the wild, giraffe spend approximately 60% of the day feeding and foraging (Ginnett and Demment, 1997; Pellew, 1984), and must use their tongues to remove tree leaves (Dagg and Foster, 1976). Some giraffe have been observed to spend time feeding every hour during the day (Dagg and Foster, 1976). Pellew (1984) observed wild Masai giraffe in Serengeti National Park, and 96% of feeding was on trees or shrubs, with Acacia species most frequently consumed during the wet season. Removal of Acacia leaves is difficult because most species have thorns (Dagg and Foster, 1976; Pellew, 1984) or stinging ants (Dagg and Foster, 1976). The difficulty of this task is not replicated in captivity, where giraffe are typically fed hay and concentrated grain supplemented by a limited supply of browse that is thornless and relatively easy to process. The ease of captive feeding may contribute to the prevalence of oral stereotypies in giraffe, as high quality feed (e.g. alfalfa) was associated with greater oral stereotypy (Koene, 1999) and provision of additional browse reduced oral stereotypy (Koene and Visser, 1999). If a discrepancy between captive and wild feeding contributes to the prevalence of oral stereotypies in these animals, then variables related to feeding should be more strongly associated with stereotypical licking than other environmental variables.

Locomotor stereotypies, including pacing, have also been observed in ungulates (e.g. Pollard and Littlejohn, 1996). Unlike carnivores, feeding in ungulate herbivores is not completely dependent on locomotor patterns, though they must move from one food source to another, they do not need to stalk or chase down those sources. It seems less likely that frustrated feeding motivation would result in locomotor stereotypies in these animals. However, it is possible that features of the captive environment influence pacing in captive ungulates, since they may limit travel opportunity. Giraffe in the wild have a home range size of 50 km or greater (Foster, 1966), but in captivity are limited to the size of their enclosures. While exhibit spaces are typically large, giraffe are frequently housed in much smaller indoor holding facilities at night and in inclement weather (Sartor, personal communication). A negative relationship between enclosure size and pacing has been suggested in horses (Winskill et al., 1995) and quantified in red deer stags (Pollard and Littlejohn, 1996). Moreover, behavioral differences have been demonstrated between indoor and outdoor enclosures in gorillas (Hoff et al., 1997) and sifakas (Propithecus verreauxi, Macedonia, 1987). Forthman (1998) has suggested that allowing greater access to exhibit space may reduce stereotypies and allow a more natural activity cycle. We hypothesized that environmental variables, including enclosure size and time spent inside, would be more strongly related to pacing than would feeding variables.

Identifying deficiencies in a captive environment that may be relevant to stereotypies can be tedious, time-consuming, and sometimes extremely difficult. Mellen (1994) suggests that the use of surveys may be the most effective way to evaluate a range of housing facilities and management strategies for a larger number of animals than could be accomplished in a single institution. McGreevy et al. (1995) and Redbo et al. (1998) successfully used survey methodology to identify factors related to stereotyped behaviors in racehorses. We conducted a survey of all AZA accredited North American zoos holding giraffe and okapi. We aimed to assess associations between feeding variables and oral stereotypies and between environmental variables and locomotor stereotypies, as well as to identify other variables that might be related to the expression of stereotypic behavior. Questions focused on the individual history, environment, and management of the animals,

in hopes that variables would be identified that could later be experimentally manipulated to reduce the performance of stereotypic behavior.

2. Methods

2.1. Materials and data collection

Surveys were mailed to each of the 71 American Association of Zoos and Aquariums (AZA) accredited North American zoological institutions known to house giraffe and/or okapi. The 16-item survey was addressed to the hoofstock department of each zoo with instructions that it be filled out by the member of the staff most familiar with the history and husbandry routines of the giraffe and okapi at the facility. The survey questions focused on subject variables, environmental variables, husbandry routine, and stereotypic behaviors performed by individual giraffe or okapi housed at each institution. These variables included: (1) species, (2) sex and age, (3) years in exhibit, (4) rearing history, (5) number of hours housed indoors per day, (6) number of hours housed outdoors per day, (7) size of indoor and outdoor holding facilities, (8) access to members of the same species or another species during the day and night, (9) whether an environmental or social change had occurred in the past year, (10) frequency of feeding per day, (11) whether they were fed by staff only, special guests, or general public, (12) food type, (13) feeder type, (14) type and number of stereotypic behaviors exhibited, (15) location of stereotypic behavior, and (16) whether attempts to reduce the behavior were successful or unsuccessful.

2.2. Data analysis

Descriptive statistics were computed on all variables. To determine which of the survey answers were the best predictors of the presence or absence of stereotypic behavior, data were analyzed using a forward logistic regression with a criterion value of 0.10 for inclusion of a variable (Tabachnick and Fidell, 2001). Each survey answer served as an independent variable in the analysis. Before performing the regression, we eliminated variables that were highly correlated with another survey response (r > 0.70) to reduce multi-collinearity in the dataset (Tabachnick and Fidell, 2001). A variable was selected for exclusion if it was less related to our hypotheses or less parsimonious than its correlated variable. Logistic regression was chosen because it takes into account correlations between predictor variables and predicts outcomes on a binary measure. In this study, we created two equations, one to predict the occurrence of stereotypic licking and one to predict stereotypic pacing.

3. Results

3.1. Demographics

Of the 71 institutions that received a survey, 49 (69.0%) responded. Data were reported for 257 individuals, including 214 giraffe (representing five subspecies) and 29 okapi. Nine

of the giraffe were reported to be hybrids. Because of the low number of okapi and lack of statistically significant differences between okapi and giraffe on predictor variables (discussed below), the data for giraffe and okapi were combined for all analyses. The majority of the individuals for which data were reported were females, comprising 65.5% of the population. Only 2.3% of all individuals were wild-born.

Most of the survey questions addressed environmental and husbandry variables. Most institutions housed their individuals both in outdoor yards and indoor holding areas. Average time spent in each area was approximately the same, with individuals spending an average of 11.3 h outdoors and 12.7 h indoors. Most individuals were housed socially with other individuals of their species. Of those surveyed, 9.7% have some access and 88.7% have full access to others of their own species during the day. At night, 29.2% have some access and 59.1% have full access to others of their own species. In addition, 13.6% were reported as having some access and 50.2% as having full access to members of other species during the day. The average size of the outdoor yards was 84,880 m² (range: 160–1,200,000 m²). At night, 9.7% have some access and 12.1% have full access to members of other species. The average size of the indoor holding areas was 95 m² (range 10–320 m²).

Several questions were related to the manner in which individuals were fed. Giraffe and okapi are not fed often during the day. Approximately 57% were reported as being fed once a day, whereas 24.5% and 18.3% were fed two and three times a day, respectively. The majority were fed browse (91.8%), hay (100%), and commercial chow (92.2%), as well as had access to a mineral lick (98.8%). Most were also fed fruits and vegetables (63.0%). According to the responses, 57.2% of the individuals are fed by staff only, 19.5% are also fed by special guests, and 23.3% are also fed by the public. All individuals included in the survey are fed with elevated feeders, however, 21.4% are also fed with ground feeders. These feeders are mostly open at the top (85.6%) allowing easy access of the food. However, some feeders were reported to have closed tops (17.1%) which presumably increase the amount of work required to obtain food.

Stereotypic behavior was prevalent across institutions, with 79.7% of animals reported as performing at least one type of stereotypic behavior. Out of these 51% showed only one type of stereotypic behavior, 26.8% showed two forms of stereotypic behavior, and 1.9% showed three or more forms of stereotypic behavior. Repetitive licking of non-food objects (72.4%, hereafter referred to as "licking") and pacing (29.2%) were the two most predominant forms of stereotypic behavior reported. More animals were reported licking on artificial (67.6%) than on natural substrates (35.9%). Other stereotypic behaviors were observed in 3.2% of the individuals, and included self-injury, head tossing, and tongue playing. Individuals were reported to perform stereotypic behavior more often indoors (35.0%) than outdoors (16.7%), and stereotypic behavior was observed equally indoors and outdoors for 28.4% of the individuals. Of the 49 institutions that returned the surveys, 51.7% had attempted to reduce or eliminate stereotypic behavior in their animals. Only 51.9% reported that their efforts were successful.

3.2. Regression analysis

Prior to regression, four survey answers were removed from the pool of predictor variables because of their high correlations with other included predictors. These were

Variable	Regression coefficient (B)	Wald statistic	d.f.	Wald P-value
Reticulated giraffe	-2.84	21.0	1	< 0.001
Masai giraffe	-3.07	9.27	1	0.002
Hours indoors	-0.13	4.40	1	0.036
Some night access to same species	1.97	9.73	1	0.002
Full night access to same species	1.88	10.39	1	0.001
Feeding frequency	0.34	6.68	1	0.010
Fed by staff only	-2.85	15.06	1	< 0.001
Fed by public	-1.80	3.52	1	0.060
Fed browse	-3.16	15.13	1	< 0.001
Closed top feeders	-4.58	18.35	1	< 0.001
Constant	-8.16	14.12	1	< 0.001

Table 1 Logistic regression analysis of stereotypic licking as a function of subject and environmental variables

number of years in the exhibit (with age, r = 0.922), number of hours outside (with number of hours inside, r = -0.999), night access to other species (with outdoor size, r = 0.701), and change in environmental and social factors (with environmental change alone, r = 0.852).

The overall model for stereotypic licking was statistically significant, $X^2(10) = 80.090$, P < 0.001, and there was a good model fit, Hosmer and Lemeshow $X^2(8) = 6.860$, P = 0.552. The model had an overall Nagelkerke $R^2 = 0.504$ and classified 82.8% of animals correctly. However, classification was better for those animals that did lick (92.7%) than those that did not (61.4%). Table 1 reports regression coefficients, Wald statistics, degrees of freedom, and significance for all variables included in the equation. Eight of the nine variables included in the model were significant (P < 0.05). Predictors positively related to licking were some or full access to members of the same species at night and feeding frequency. Negative relationships with licking were found for reticulated and Masai subspecies, hours spent indoors, being fed by staff only, being fed browse, and the use of closed-top feeders. One variable, being fed by the public, approached significance (P = 0.06).

For stereotypic pacing, the overall model was also significant, $X^2(10) = 91.725$, P < 0.001. The model had an overall Nagelkerke $R^2 = 0.579$ and had a good fit, Hosmer and Lemeshow $X^2(8) = 2.367$, P = 0.968. Unlike the licking model, the pacing model classified animals that did not pace (89.3%) more accurately than those that did pace (69.4%). However, the overall classification accuracy of 83.9% was similar to the licking analysis. Regression coefficients, Wald statistics, degrees of freedom, and significance of each of the variables in the equation are included in Table 2. A total of 10 predictors were included in the equation, but only five of them were significant (P < 0.05): giraffe, Masai giraffe, size of indoor enclosures, environmental change in the past year, and feeding chow. Of these, all but feeding chow had a negative relationship with pacing. Two other relationships approached significance, hybrid giraffe (P = 0.057, positive) and birth history (P = 0.060, negative).

Variable	Regression coefficient (B)	Wald statistic	d.f.	Wald P-value
Giraffe	-2.30	4.20	1	0.004
Angolan giraffe	19.45	0.04	1	0.848
Masai giraffe	-3.25	6.74	1	0.009
Hybrid giraffe	2.22	3.62	1	0.057
Birth history	-3.40	3.52	1	0.060
Indoor size	-0.003	24.14	1	< 0.001
Outdoor size	0.000	0.30	1	0.589
Environmental change	-3.93	5.92	1	0.015
Fed browse	9.98	0.23	1	0.632
Fed chow	1.83	4.79	1	0.029
Constant	14.39	0.02	1	0.888

Table 2 Logistic regression analysis of stereotypic pacing as a function of subject and environmental variables

4. Discussion

Of the 257 giraffe and okapi reported in the survey, 79.7% showed at least one form of stereotypy. Of these stereotypies, licking was the most common, followed by pacing. Individuals were significantly less likely to show stereotyped licking if they were Masai giraffe or reticulated giraffe, spent more hours housed indoors, lacked night access to members of the same species, were fed by staff only, received browse, and had access to feeders with closed tops. Giraffe or okapi were significantly less likely to pace if they were a giraffe of unknown subspecies or a Masai giraffe, lived in larger indoor enclosures, had experienced an environmental change in the past year, and were not fed concentrated chow. Several of the variables predicting licking were related to feeding, supporting our hypothesis that licking in captive giraffe and okapi may be related to feeding motivation. Similarly, stereotypic pacing was related to several environmental variables, supporting the hypothesis that locomotor stereotypies in giraffe and okapi may be related to constraints of the physical environment. However, two environmental variables (night access to others of the same species and number of hours indoors) were predictive of licking, while one feeding variable (being fed chow) was associated with pacing. This overlap indicates that locomotor and oral stereotypies share some motivational features.

These findings begin to extend the work on domestic ungulate stereotypy to include captive exotic animals. As in the research on cattle, there appears to be an association between feeding motivation and the prevalence of oral stereotypies (Redbo, 1990). Both feeding duration and feeding schedule have been linked to the performance of stereotypic behavior. In this study, animals being fed browse and fed with closed-top feeders were less likely to exhibit stereotypic licking. These have both been used to increase feeding bout duration in giraffe and okapi (Koene and Visser, 1999). Experimentally increased feeding duration has been associated with decreased oral stereotypies in heifers (Redbo and Norblad, 1997), pigs (Terlouw et al., 1991), and boiler breeders (Savory and Maros, 1993). Experimental manipulations designed to increase feeding duration, including presenting a foraging substrate for sows (Spoolder et al., 1995), have reduced the time

animals spend engaged in oral stereotypic behavior. The duration of feeding behavior may also be a better predictor of oral stereotypy than quantity of food in cattle (Lindstrom and Redbo, 2000).

In addition, our survey pointed to feeding frequency as a significant predictor of stereotypic licking. Specifically, animals that were fed more often during the day were more likely to exhibit stereotypic licking than animals fed less often. To our knowledge, an effect of number of feedings on stereotypy has not been addressed in ungulates, though stereotypy has been demonstrated to occur in temporal proximity to feeding bouts in both sows (Rushen, 1985) and cattle (Redbo, 1990). It is difficult to interpret the relationship between feeding schedule and stereotypic licking because the survey did not assess the quantity of food provided or feeding duration. No published studies have quantitatively measured the relationship between feeding duration and oral stereotypy in giraffe and okapi while controlling for the effects of feeding schedule and quantity of food. At Zoo Atlanta, we are currently trying to differentiate these variables by studying the provision of daily rations in enrichment devices designed to increase foraging time and effort required to obtain the same quantity of food.

Stereotypic licking was also less likely to be exhibited by animals that are fed by staff members only. Animals that are fed only by staff members probably have more definite cues associated with providing food. The presence of these cues (e.g. keeper presence at a feeding location, sounds of food being prepared or delivered) only at feeding times could create a situation in which feeding motivation is lower when the cues signaling food are not present, a phenomenon which may be related to occasion-setting (e.g. Bonardi, 1992). The association between feeding motivation and cues associated with feeding could reduce the occurrence of stereotypies related to feeding motivation when these cues are not present. Animals fed by the special guests or the public, on the other hand, may be less likely to have consistent cues associated with feeding and may have less predictable feeding schedules. Spatial and temporal variation in the presentation of food has been demonstrated to influence stereotypy, aggression, and exploratory behavior in Scottish wildcats (Hartmann, 1999), chimpanzees (Bloomsmith and Lambeth, 1995), bears (Carlstead and Seidensticker, 1991; Carlstead et al., 1991), and macaques (Waitt et al., 1999). Although these animals all obtain their food in different ways, it is possible that variation in food presentation has a general effect on stereotypy across a variety of species.

The relationship between smaller indoor enclosures and greater likelihood of pacing found in our survey is the same as that found in red deer stags (Pollard and Littlejohn, 1996). When free-ranging stags were temporarily confined in smaller pens, a greater percentage of animals performed stereotypic pacing and vertical/horizontal head movements. Furthermore, the frequencies of these movements were higher. One confounding factor in these types of studies is an increase in social density occurring when a group of animals is moved to a smaller enclosure (Judge and DeWaal, 1993). There is some evidence that suggests this increase in density or an effect of novel environment may be responsible for these changes, rather than enclosure size itself (e.g. Nash and Chilton, 1986; Line et al., 1990). Social density may be a factor in the current study, as well, since 59.1% of animals were housed with full night access to other members of their own species. However, there was no relationship between night access and pacing. Pollard and Littlejohn (1996) postulated that pacing in red deer might be related to motivation to escape, which would

account for both an inverse relationship between pacing and enclosure size and a direct relationship between pacing and social density.

Similarly, the relationship between night access to members of the same species and stereotypic licking behavior may be related to social density. Redbo et al. (1998) found that wood-chewing, an oral behavioral disturbance, was greater in horses provided full social access to one another than in horses housed with lesser degrees of contact. It is possible that increased social density, typical of night housing in smaller spaces, may produce competition for resources, especially food, which could then increase the likelihood of stereotypic licking. An experimental manipulation of enclosure size in isolated animals or with constant social density could help distinguish the effects of enclosure size and social density on pacing in giraffe and okapi.

Another environmental factor that can be used to predict the occurrence of licking is the number of hours an animal is housed indoors, which may be related to an inability to locomote as they would outdoors. Redbo (1992) found that heifers performed oral stereotypies at a much higher level when tethered than when housed in loose stalls. Similar results have been found for horses; animals that had more opportunity for exercise out of their stalls (Krzak et al., 1991) or light training (Redbo et al., 1998) were less likely to exhibit wood-chewing. Redbo et al. (1998) suggest that this period of exercise allows the horse to express an activity budget more similar to in the wild, when it would expend energy in travel. The same may be true of giraffe and okapi, reduced opportunity for exercise may lead to decreased periods of sleep and increased time available for undesirable behavior. Also, indoor enclosures tend to provide less quantity and variety of stimulation than outdoor enclosures. It has been argued that this type of stimulation is important for reducing stereotypy in general (Hutchins et al., 1984). In support of this argument, our study revealed that animals were less likely to pace if they had experienced an environmental change in the past year. It is possible that both environmental change and time outdoors expose the animals to more diverse stimuli, thereby reducing the chance they will engage in stereotypic behavior.

Animal welfare has become an increasingly important standard by which zoos are judged. Physical welfare, including the freedom from disease, long life, and the ability to reproduce, has historically been the most important component of animal welfare in captivity (Wuichet and Norton, 1995). In the latter half of the 20th century, psychological welfare has risen to equal prominence, and has even been included in recent USDA regulations for housing captive primates (Kreger, 1999). Maple (1995, p. 24) contends that "zoo professionals take seriously their obligation to minimize animal stress, boredom, trauma and disease". Measures of the psychological component of welfare, however, are difficult to establish (Mason, 1991). Frequently, it is easier to identify indicators of poor welfare than good welfare (Broom, 1991). One of the major problems with measuring psychological well-being is that all measures are inherently subjective, depending on human perspective of what is important to an animal (Mason and Mendl, 1993). Another issue is that measures of well-being vary from species to species, from individual to individual, and even in the same individual over time (Mason and Mendl, 1993). Despite these challenges, some standards have been widely accepted. An improvement in wellbeing may be indicated by reduced undesirable, stereotypic, or hyper-aggressive behaviors (those behaviors not found in the wild or found at much greater frequencies in captivity), and increased activity, control over interactions with the environment, and species-specific or "natural" behaviors (those seen in the wild) (Broom, 1991; Novak and Drewston, 1989; Wuichet and Norton, 1995). If the presence of stereotypies is indicative of a deficient animal/environment interaction, then a reduced frequency of these stereotypies may improve the well-being of captive giraffe and okapi.

5. Conclusions

Stereotypic behavior was prevalent in zoo-housed giraffe and okapi. The responses from this survey allowed us to identify variables that are predictive of stereotypic behavior in these individuals. As in other species, oral stereotypy seemed to be influenced more by feeding variables than environmental variables, whereas locomotor stereotypy seemed to be more strongly influenced by environmental variables. Factors thought to affect feeding duration and feeding schedule appear to be related to oral stereotypy, but more work is needed to isolate the effects of these variables. The method in which food is presented also affects or al stereotypy. Two variables that could be related to social density (smaller indoor enclosure and night access to conspecifics) were associated with increased levels of stereotypic behavior. Finally, the importance of variation in stimuli was emphasized by the decreased likelihood of licking when animals spent less time indoors or had been exposed to environmental change in the past year. The results of this survey suggest changes in housing and management strategies that may ultimately reduce the performance of stereotypic behavior in zoo-housed giraffe and okapi, thereby improving their well-being. An experimental evaluation of these variables will provide a more complete understanding of the relationships between environment and behavior in zoo-housed ungulates.

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