

Socio-ecological factors correlate with levels of stereotypic behavior in zoo-housed primates



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ABSTRACT

Stereotypic behavior often indicates poor welfare. It may develop when the animal's ability to carry out appropriate behavioral responses is limited, despite a high motivation to express them. Behavioral motivations vary across species. Consequently, under similar captive conditions, the sustained inability of animals to express certain behaviors is likely to affect some species more than others. We used a phylogenetic comparative approach to evaluate the socio-ecological factors affecting the manifestation of stereotypic behavior in 24 species of zoo-housed primates. We examined the relationship between two stereotypic behaviors: hair-pulling and pacing, and the species' natural socio-ecological factors and captivity conditions. The degree of stereotypic behaviors was unaffected by phylogenetic relatedness between species. Stereotypic hair-pulling behavior levels were positively correlated with natural group size. Stereotypic pacing levels were positively correlated with the animals' natural day journey length. These findings suggest large-group and wide-ranging primate species are more prone to suffer in captivity. Our findings facilitate the detection of species that are more susceptible to behaving stereotypically in captivity. We suggest that providing appropriate social stimuli, and increasing the complexity of the captive environment rather than enlarging it, are both attainable and expected to improve the animals' welfare.

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1. Introduction

Stereotypic behavior is widespread among captive animals (Mason and Latham, 2004). It often reflects poor welfare (D'Eath et al., 2009), since it is related to other markers of poor welfare such as negative emotional states (Pomerantz et al., 2012a,b) and stress-induced abnormal brain functions (Lewis et al., 2006). Stereotypic behavior has been suggested to stem from a chronic lack of opportunity to respond appropriately to internal or external stimuli (i.e. to carry out the appropriate behavioral responses), despite a high motivation to do so (Mason and Burn, 2011).

Some motivations are controlled by negative feedback loops (e.g. an animal will stop running after successfully escaping danger). However, when these negative feedback loops fail, the animal may remain in a state of high motivation, which can lead to frustration-related stress, and consequently to the development of stereotypic behavior (the frustrated motivation hypothesis) (Jones et al., 2011; Rushen and Mason, 2006). For instance,

maternally-deprived rhesus macaques (*Macaca mulatta*) are thought to self-clasp due to insufficient tactile stimulation from their mothers. Introducing a 'surrogate mother' for the young monkeys to clasp ameliorates this condition (Novak et al., 2006).

The motivations of animals to exhibit certain behaviors are products of natural selection to the environment in which they have evolved (Broom, 2011; Dawkins, 1990). Therefore, animals of different species vary in their motivations to exhibit certain behaviors. Thus, the continuous inability of certain animals to express certain behaviors is likely to affect more greatly those species which are more motivated to express them, and possibly lead to the development of stereotypic behavior in these species more than in others. Indeed, wide-ranging carnivore species exhibit more stereotypic locomotor behavior in zoos compared to species with smaller natural home ranges (Clubb and Mason, 2007, 2003). This implies that wide-rangers are predisposed to be more negatively affected by the reduced space of their enclosures.

Clubb and Mason (2003, 2007) are the only researchers to date to have employed a phylogenetic comparative approach to assess stereotypic behavior in captive animals. Phylogenetic comparative methods are used to test hypotheses with data regarding multiple species, while controlling for phylogenetic non-independence (similarities between related taxa because of shared traits from a common ancestor) (Mason, 2010). Modern phylogenetic

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comparative methods can also quantify the degree to which traits are affected by shared ancestry, and vary the weight ascribed to phylogeny accordingly (Hernández et al., 2013). Clubb and Mason (2003, 2007) gathered literature data on pacing in carnivores and examined the factors that affect the proportion of time spent pacing. Their study incorporated data only from individuals that paced stereotypically (i.e. they ignored individuals that did not behave stereotypically). Here, we used a similar approach to evaluate the factors affecting the manifestation of two types stereotypic behaviors in 24 species of zoo-housed primates. We directly observed all animals and therefore have quantitative observational data for both stereotyping and non-stereotyping individuals.

Captive primates exhibit a wide range of stereotypic behaviors (e.g. Lutz et al., 2003; Pomerantz et al., 2012a,b). Indeed, we identified over 20 different types of repetitive, unvarying and apparently functionless (e.g. Mason, 1991) behaviors (results not shown). We chose to focus on the two most prominent stereotypic behaviors we observed during the study: hair-pulling, which was observed in 18 of the 24 species; and pacing, which was expressed by 12 species. Hair-pulling and pacing are well-known stereotypic behaviors (e.g. Lutz et al., 2003; Honess et al., 2005). Both of these behaviors are common and relate to an animal's welfare, and have thus been widely studied (e.g. Lutz et al., 2003; Honess et al., 2005). We predicted that the levels of stereotypic behavior would be higher in species whose biological needs are addressed worst in captivity, while controlling for captivity-related factors.

Hair-pulling has been linked to social rather than ecological factors in the primates' natural habitats (Reinhardt, 2005). In particular, grooming is a fundamental social activity in primates (Rosenblum et al., 1966; Tiddi et al., 2012), and it was suggested to be the 'source behavior' of hair-pulling (i.e. hair-pulling is derived from grooming) (Honess et al., 2005). Barton (1985) considers self- and social-grooming as complementary behaviors. Therefore, in the absence of sufficient social-grooming, an animal may repeatedly self-groom to the point of pulling its own hair. Hair-pulling is prevalent in singly-housed primates whose social needs are severely neglected (Reinhardt, 2005). This strengthens the hypothesis that it is related to an unattended need to be groomed. Although zoo-housed primates are usually socially-housed, we suggest that the socially restrictive environment (relative to the wild) promotes the development of hair-pulling due to frustrated motivations for social grooming.

Group size is positively correlated with the frequency of social grooming in wild primates (Dunbar, 1991). Individuals from primate species with large natural groups may thus be more motivated to socially groom; and, accordingly, could be more frustrated by the relatively small number of individuals in their captive group. Moreover, rates of self-grooming have been shown to increase in larger wild primate groups (Isbell and Young, 1993). Therefore, we predicted that primate species with larger natural groups would show higher levels of hair-pulling.

Regarding the second stereotypic behavior we investigated – pacing – in accordance with Clubb and Mason (2003, 2007), we predicted that stereotypic pacing levels would be higher in primate species with naturally wide home-ranges and longer day journeys, since these species are assumed to be more motivated to range, and therefore would be worse affected by the limited space in zoos.

Using a phylogenetic comparative approach, we sought to identify the factors that are correlated with stereotypic behavior levels and thus to detect those primate species whose welfare is most compromised by captive constraints. The prospective outcomes of this study are expected to contribute to our understanding of the development of abnormal behavior and, by emphasizing the major factors that should be addressed, can be used to improve captive primate welfare.

2. Methods

2.1. Evaluation of levels of stereotypic behavior

One of us (OP) observed 49 groups belonging to 24 diurnal primate species (214 observed adult individuals), housed in six Israeli zoos, between November 2009 and July 2010 (Table 1). Observations were uniformly spread across time among groups to control for potential temporal and seasonal effects (e.g. across the diel cycle and not synchronized with feeding times). All observations were conducted from 07:30 h to 17:00 h in the primate exhibition yards. Each group was observed 24 times (20 min per observation) using instantaneous scan sampling (Martin and Bateson, 1993). Stereotypic pacing and hair-pulling were recorded at 30-s intervals (Marriner and Drickamer, 1994). Stereotypic pacing was defined as walking in a fixed pattern repeatedly (including repetitive brachiation along the same route); and hair-pulling was defined as repeatedly pulling out hair from the body using a hand. Animals were also observed between scans in order to detect bouts of pacing and hair-pulling. If those bouts continued during the scan (i.e. 'on the beep' (Martin and Bateson, 1993)), then the animals were scored as behaving stereotypically.

The behavior of each individual was recorded in each scan. The total number of stereotypic pacing and hair-pulling events recorded during each observation, was then divided by the number of scans (i.e. 40), and the number of observed individuals (total number of stereotypic behaviors/(40_{scans} × N_{individuals})). For example, in a group of 10 subjects pacing could potentially be recorded up to 400 times (if all animals presented this behavior during every scan). Thus, 400 divided by 40 (scans), then by 10 (individuals), equals one (i.e. 100% stereotypic pacing). Next, a mean of the percentage of scans engaged in pacing and in hair-pulling was averaged for each group across the 24 observations and used as our response variable. For species housed in more than one zoo we averaged stereotypic behavior levels across all groups (i.e. a mean of means), as a preliminary analysis had not detected differences between zoos in stereotypic behavior levels.

We conducted additional analyses using data only from those individuals that exhibited hair pulling and/or pacing. These analyses were performed in order to allow a more accurate comparison to Clubb and Mason (2003, 2007), who examined only individuals that behaved stereotypically (since they used literature data, from which data on non-stereotyping individuals could not be reliably ascertained). For these analyses, we averaged the percentage of scans in which stereotypic behavior was observed (once for hair-pulling and once for pacing) across the stereotyping individuals within each group. Where there were stereotyping individuals in more than one group per species, we calculated a mean of means, in order to derive final species estimates.

Only socially-stable groups without new constant environmental enrichment were observed, in order to eliminate transient novel effects.

Our predictors were captivity-related variables and socio-ecological and body mass data (Table 1).

2.2. Captivity-related factors

We gathered data concerning captive conditions from the zoo records in order to control for variation in captive settings that could explain apparent species differences in stereotypic behavior levels (Table 1). For each species we calculated the average enclosure size (m²), meal frequency (number of meals received daily), and the number of enrichments provided per week (any kind of temporary manipulanda that are not included in the feeding regime). We predicted that stereotypic behavior levels would be negatively correlated with all of the captivity-related factors.

Table 1

Predictor variables: number of groups observed per species, number of individuals in each species (first column: mean number of group members, including unobserved juveniles, second column: total number of observed adults), average enclosure size, average number of meals (per normal day), average enrichments provided (per week), mean natural home range size (ha), mean natural day journey length (m) mean natural group sizes, and mean body mass (male–female average, g). References are in parentheses.

Species	# of groups	# of individuals	Enclosure size	# of meals	# of enrichments	Home-range size	Day journey	Group size	Body mass
<i>Alouatta caraya</i>	1	7, 5	150.0	2	0.0	5.9 ^a	400 ^a	7.3 ^d	5012.5 ^e
<i>Ateles paniscus</i>	1	8, 6	43.0	1	0.0	206.0 ^a	2400 ^a	20.3 ^d	3430.0 ^e
<i>Callithrix geoffroyi</i>	2	5, 7	19.0	2	1.0	23.3 ^f	1230 ^f	6.8 ⁿ	793.0 ⁱ
<i>Callithrix jacchus</i>	3	2, 6	6.0	5	1.5	11.7 ^a	880 ^a	8.2 ^d	347.5 ^e
<i>Cebus apella</i>	2	9.5, 14	197.5	2.5	2.0	344.0 ^a	2100 ^a	15.1 ^d	2589.0 ^e
<i>Chlorocebus pygerythrus</i>	2	5, 10	23.0	1.5	0.5	70.4 ^a	1200 ^a	25.6 ^b	4623.6 ^j
<i>Colobus angolensis</i>	2	5.5, 11	922.5	2	0.8	400.0 ^b	1300 ^a	11.7 ^d	9670.0 ^e
<i>Erythrocebus patas</i>	1	4, 4	40.0	3	1.5	3000.0 ^a	3200 ^a	31.0 ^d	7376.0 ^e
<i>Eulemur fulvus</i>	3	4.33, 13	120.0	2	0.0	48.6 ^c	550 ^b	8.2 ^d	1400.0 ^k
<i>Gorilla gorilla</i>	1	6, 4	450.0	4	6.0	2540.0 ^a	860 ^a	15.8 ^d	120,975.0 ^e
<i>Hylobates lar</i>	2	2.5, 5	74.0	2.5	0.0	34.2 ^a	1600 ^a	3.8 ^d	5550.0 ^e
<i>Lemur catta</i>	2	6, 12	69.0	2	0.8	14.4 ^c	957 ^b	15.9 ^d	2090.0 ^e
<i>Macaca nemestrina</i>	1	6, 6	45.0	1	0.0	355.0 ^a	1800 ^a	40.2 ^d	4456.0 ^e
<i>Macaca nigra</i>	2	6.5, 6	175.0	4	2.0	260.0 ^a	2400 ^a	22.1 ^d	3452.0 ^e
<i>Macaca silenus</i>	2	8, 9	185.0	3	1.5	50.7 ^a	1600 ^a	18.1 ^d	5902.0 ^l
<i>Mandrillus sphinx</i>	2	3.5, 7	70.0	3	1.0	3080.0 ^a	3500 ^a	84.0 ^d	11,500.0 ^e
<i>Pan troglodytes</i>	3	8.66, 20	850.0	4	6.0	1790.0 ^a	3800 ^a	49.2 ^d	60,433.2 ^e
<i>Papio hamadryas</i>	3	9.33, 25	900.0	2	1.0	2800.0 ^a	11 000 ^a	37.8 ^b	12,020.0 ^e
<i>Pongo pygmaeus</i>	3	1.66, 5	300.0	2	5.0	170.0 ^a	500 ^a	1.8 ^d	54,229.0 ^e
<i>Saguinus oedipus</i>	4	3.33, 11	19.0	2.5	1.0	15.7 ^a	1900 ^a	5.3 ^d	327.1 ^e
<i>Saimiri sciureus</i>	1	10, 10	38.0	1	0.0	149.0 ^a	1800 ^a	43.1 ^d	578.7 ^e
<i>Trachypithecus obscurus</i>	1	10, 10	1800	3	1.5	33.0 ^b	755 ^b	13.7 ^b	6912.0 ^j
<i>Varecia rubra</i>	2	2, 4	175.0	2.5	1.0	57.7 ^g	772 ^b	8.3 ^d	3510.0 ^m
<i>Varecia variegata</i>	3	1.33, 4	300.0	4	1.5	110.2 ^c	718 ^b	8.3 ^d	2705.5 ^e

^a Nunn et al. (2004).

^b Nunn and van Schaik (2001).

^c Wich and Nunn (2002).

^d Nunn (2002).

^e Boddy et al. (2012).

^f Passamani and Rylands (2000).

^g Vasey (2000).

^h Martinez (2010).

ⁱ Marino (1998).

^j Isler et al. (2008).

^k Stephan et al. (1981).

^l Barton (2001).

^m Jiwani (2005).

ⁿ Chiarello and de Melo (2001).

2.3. Socio-ecological factors and body mass

Data pertaining to socio-ecological factors were taken primarily (87.5% of our data points) from the comprehensive comparative database of Charles L. Nunn (http://www.people.fas.harvard.edu/~nunn/comparative_data.html) (Table 1). Body masses were taken mainly from Boddy et al. (2012). Data that were unavailable in Nunn's or Boddy's databases were taken from other literature sources (Table 1). Similar to the stereotypic behavior data, we averaged the socio-ecological data of the studied individuals. We recorded home-range size (ha), day journey length (m), and group size (mean number of individuals, including juveniles). Mean body mass (g, averaged between the sexes) was additionally included in the analyses as it correlates with a range of ecological and behavioral factors (Clubb and Mason, 2003, 2007).

In order to further test our hypothesis that differences between wild and captive conditions generate stereotypic behavior, we created an additional variable by dividing mean captive group sizes (mean number of individuals, including unobserved juveniles) by the correspondent mean wild group sizes (hereafter, group size ratio). We did not repeat this for home-range, since, in all cases, the zoo enclosure sizes were negligible compared to the natural home-range size. We were unable to create a ratio variable for day journey length since we did not measure the distance traveled in the zoos. We predicted that we would find a negative

correlation between group size ratio and the levels of stereotypic behaviors.

2.4. Analyses

Data were log-transformed to better comply with the assumptions of parametric tests. Model selection was by means of backwards stepwise elimination based on *P* values. We used multiple regression and analyses of co-variance to examine the influence of the various factors. To estimate and correct for the effects of phylogenetic relatedness between species we used the species-level phylogeny of Chatterjee et al. (2009). Using phylogenetic generalized least square (PGLS) regression, we examined the strength of phylogenetic non-independence using the maximum likelihood value of the scaling parameter λ (Pagel, 1999) implemented in the R package Caper (Orme et al., 2012). Pagel's λ is a multiplier of the off-diagonal elements of the variance–covariance matrix, which provides the best fit of the Brownian motion model to the tip data, and ranges between zero (no phylogenetic signal) and one (phylogenetic signal that depends on branch lengths as in analysis of phylogenetically-independent contrasts). We then corrected for the effects on shared ancestry using the maximum value of λ . For a comprehensive review of comparative methods and their use in ecological and welfare studies, see Mason (2010). All analyses were

Table 2
Average values per species of the proportion of scans in which stereotypic hair-pulling or pacing were detected.

Species	Stereotypic hair-pulling ^a	Stereotypic pacing ^a	Stereotypic hair-pulling ^b	Stereotypic pacing ^b
<i>Alouatta caraya</i>	0.04	0	0.21 (1)	0 (0)
<i>Ateles paniscus</i>	0.53	0.59	2.92 (1)	3.33 (1)
<i>Callithrix geoffroyi</i>	0.048	0	0.16 (2)	0 (0)
<i>Callithrix jacchus</i>	0	0	0 (0)	0 (0)
<i>Cebus apella</i>	0.06	1.14	0.42 (1)	2.98 (4)
<i>Chlorocebus pygerythrus</i>	0.91	0.51	3.31 (3)	2.03 (2)
<i>Colobus angolensis</i>	0.27	0	0.41 (2)	0 (0)
<i>Erythrocebus patas</i>	0.37	2.24	1.46 (1)	8.96 (1)
<i>Eulemur fulvus</i>	0	0	0 (0)	0 (0)
<i>Gorilla gorilla</i>	0.31	0	1.25 (1)	0 (0)
<i>Hylobates lar</i>	0	0.97	0 (0)	2.30 (2)
<i>Lemur catta</i>	0	0.13	0 (0)	0.42 (1)
<i>Macaca nemestrina</i>	0.42	0	2.5 (1)	0 (0)
<i>Macaca nigra</i>	0.72	0	2.22 (2)	0 (0)
<i>Macaca silenus</i>	0.11	0.01	0.47 (2)	0.10 (1)
<i>Mandrillus sphinx</i>	0.32	0.07	1.13 (2)	0.54 (1)
<i>Pan troglodytes</i>	0.04	1.07	0.30 (3)	4.76 (2)
<i>Papio hamadryas</i>	0.20	0	1.61 (3)	0 (0)
<i>Pongo pygmaeus</i>	0	0	0 (0)	0 (0)
<i>Saguinus oedipus</i>	0.11	0.07	0.45 (3)	0.63 (1)
<i>Saimiri sciureus</i>	0.17	0.08	1.35 (1)	0.42 (2)
<i>Trachypithecus obscurus</i>	0.16	0	0.78 (2)	0 (0)
<i>Varecia rubra</i>	0	0.05	0 (0)	0.42 (1)
<i>Varecia variegata</i>	0.03	0	0.10 (1)	0 (0)

The total number of individuals that exhibited the stereotypic behaviors is noted in parentheses.

^a % of scans, all observed individuals.

^b Only individuals expressing the behavior.

two-tailed, and carried out using R version 2.14.0 (R Development Core Team, 2011).

3. Results

We identified 26 behaviors that fit the ‘classical’ definition of stereotypic behavior (Mason, 1991), although most of these were expressed in relatively few groups. For example, head twirling (the third most prominent stereotypic behavior) was exhibited in only six of the observed species, and somersault only in one. Individuals from 18 of the 24 observed species (75%) exhibited stereotypic hair-pulling, while individuals from 12 of the 24 species (50%) exhibited stereotypic pacing. The primates pulled hair for, on average, $0.2 \pm 0.05\%$ (mean \pm SE) of the scans, and paced stereotypically for, on average, $0.3 \pm 0.11\%$ (mean \pm SE) of the scans (Table 2). There was no correlation between the levels of the two stereotypic behaviors across species ($R^2 = 0.02$, $P = 0.56$). Thirty-two of the 214 observed adult individuals, pulled their hair (1.17 ± 0.23 , mean \pm SE proportion of the scans), and 19 paced (2.24 ± 0.74 , mean \pm SE proportion of the scans) (Table 2).

The maximum likelihood value of lambda in all of the following analyses was not significantly different from zero, indicating that the degree of stereotypic behavior is not affected by phylogenetic relatedness.

3.1. Stereotypic hair-pulling and group size

The minimum adequate model explained 27.2% of the proportion of scans in which individuals pulled hair stereotypically. It included a significant relationship between mean stereotypic hair-pulling (including data from all the observed animals) and natural group size (slope: 0.11 ± 0.03 , $P = 0.008$) (Fig. 1). Body mass and captivity related factors were dropped from our best model.

Using group size ratio in the analysis, instead of absolute means of wild group size, yielded a minimum adequate model which included a significant negative correlation between the mean proportion of scans in which stereotypic hair-pulling was observed

and group size ratio (slope: -0.12 ± 0.05 , $P = 0.04$) (Fig. 2). As in the previous analysis, body mass and captivity-related factors were dropped from our best model.

When taking only those individuals that pulled hair into account, we found a significant positive correlation between mean proportion of scans in which stereotypic hair-pulling was detected and natural group size (slope: 0.31 ± 0.12 , $P = 0.02$, $N = 18$, $R^2 = 0.30$). We also found a significant negative correlation between mean proportion of scans with stereotypic hair-pulling (using data only from hair-pullers) and group size ratio (slope: -0.37 ± 0.16 , $P = 0.03$, $N = 18$, $R^2 = 0.25$).

Mean proportion of scans with stereotypic hair-pulling was uncorrelated with both mean day journey length (slope: 0.04 ± 0.06 , $P = 0.53$, $N = 24$), and mean home-range size (slope: 0.03 ± 0.03 , $P = 0.29$, $N = 24$).

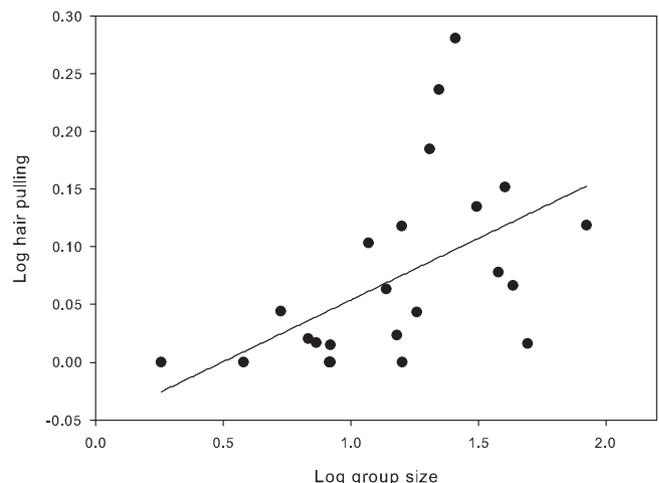


Fig. 1. Correlation between log natural group size and log stereotypic hair-pulling, $N = 24$, $R^2 = 0.27$.

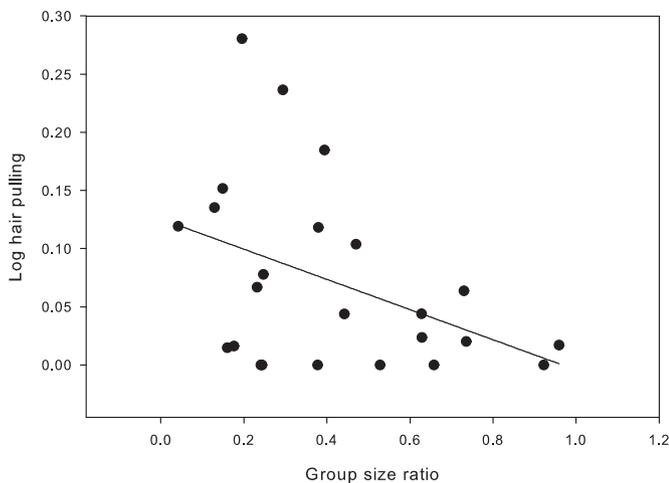


Fig. 2. Correlation between group size ratio (captive/wild) and log stereotypic hair-pulling, $N=24$, $R^2=0.17$.

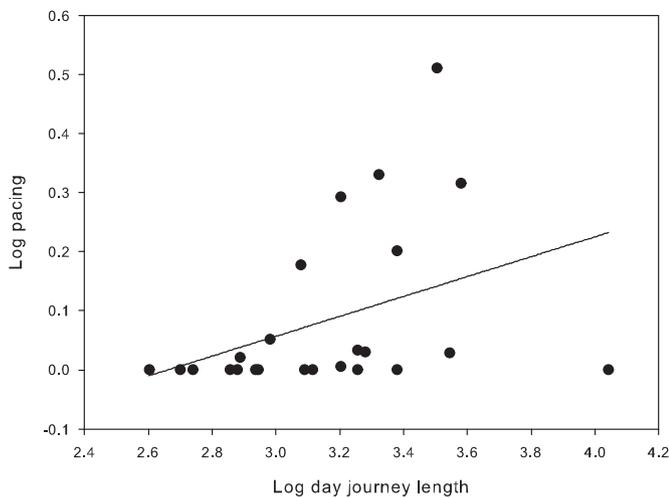


Fig. 3. Correlation between log day journey length (m) and log stereotypic pacing, $N=24$, $R^2=0.15$.

3.2. Pacing and ranging-related ecological factors

This minimum adequate model ($N=24$ species) explained 15% of the proportion of scans showing pacing. The mean proportion of scans showing stereotypic pacing was marginally non-significantly correlated with day journey length (slope: 0.17 ± 0.08 , $P=0.06$) (Fig. 3). Home-range size, body mass and captivity-related factors were dropped from our best model.

Similarly, when taking only those individuals that paced into account, we found that the mean proportion of scans with stereotypic pacing was marginally non-significantly correlated with day journey length (slope: 0.77 ± 0.36 , $P=0.06$, $N=12$, $R^2=0.31$).

We did not find any significant correlation between mean stereotypic pacing and mean natural group size (slope: 0.01 ± 0.25 , $P=0.97$, $N=24$), or with mean group size ratio (slope: -0.09 ± 0.12 , $P=0.44$, $N=24$).

4. Discussion

4.1. Hair-pulling and group size

Sociality has a central role in primate lives (e.g. Novak and Suomi, 1991). A major feature of group living in primates is social

grooming, which facilitates social bonding (Dunbar, 2010). Social grooming was further found to reduce anxiety in primates, a process possibly mediated by increased tolerance among group members (Aureli and Yates, 2010). Therefore, the degree of social grooming is considered a key factor affecting fitness (Silk, 2007). Moreover, data indicate that when an individual has not been groomed for some time, this lowers the level of endorphins in its brain and increases its motivation to be groomed; while, correspondingly, grooming increases the level of endorphins in the brain and alleviates the motivation to groom (Fabre-Nys et al., 1982; Martel et al., 1995). Accordingly, capuchin monkeys (*Cebus apella*) showed higher preferences for social companionship over food, demonstrating the high motivation for social contact (Dettmer and Fragaszy, 2000).

Primate species with larger natural groups pulled their hair more in captivity than species with smaller natural groups. This finding was evident when we used natural group sizes and group size ratio, and also when we included only hair-pulling individuals in the analyses. We suggest that socially-related motivations are central to primate welfare, and the frustration resulting from the inability of the animal to address these motivations in captivity promotes the development of stereotypic behavior.

The frustrated motivation hypothesis suggests that stereotypic behaviors may develop due to the continuous elicitation of highly motivated 'source behaviors' that the animal is unable to express (e.g. Würbel et al., 1996; Jones et al., 2011). Pathological intensification of normal grooming (the 'source behavior') may result in hair-pulling behavior (Honest et al., 2005). Thus, when an animal's motivation to groom is inadequately fulfilled it may become frustrated and develop stereotypic hair-pulling. We predicted that primates with large natural group sizes would show higher levels of hair-pulling, since they are known to devote more time to social and self-grooming (e.g. Dunbar, 1991; Isbell and Young, 1993). We therefore suggest that individuals from species with large natural groups are more motivated to engage in social or self-grooming, and are, therefore, more frustrated due to the relatively low availability of social grooming in captive settings. Consequently, individuals from these species are more likely to develop hair-pulling behavior, and stereotyping individuals belonging to species with large natural groups are more prone to show this behavior.

4.2. Pacing and day journey lengths

In agreement with Clubb and Mason's (2003, 2007) findings for carnivores, primate species with longer daily travel distances tended to pace more. This result was seen both when including all of the observed animals, and also when using data only from pacers. Pacing may thus simply represent an urge to range. Animals may be motivated to range in order to obtain more food (Isbell, 1991), or to compensate for increased intra- and inter-specific resource competition (i.e. food and mates) (Li et al., 2010; Koenig, 2002). Thus, the motivation to range seems fundamental to the fitness of the animal. However, the confined zoo environment prevents the animals from addressing these highly-motivated ranging behaviors. Consequently, stereotypic pacing may appear (Carlstead, 1996), especially in species with large natural ranges (Clubb and Mason, 2003, 2007).

In addition, rather than due to the frustrated motivation to travel longer distances, primates may pace due to frustrated motivations for cognitive challenges. Clubb and Mason (2003, 2007) suggested that there is a significant gap in the cognitive challenges (such as decision-making and navigation) that animals are faced with in the wild in comparison to in captivity; and that 'the important 'missing variables' in captivity could actually be the stimuli and the challenges that are encountered when ranging widely in the wild'. While individuals in the wild constantly need

to respond to the changes in their surroundings, and react adaptively, their captive conspecifics experience a considerably more constant environment. For example, primates (and other taxa) use spatial memory in order to navigate in their territory (Kappeler, 2000). This enables them to recall the location of types of food, quantity and stage of ripeness, and thus to choose to travel further (Cunningham and Janson, 2007) to more productive sites despite these being more distant than less productive ones (Janson and Byrne, 2007). The cognitive skills that are needed in order to survive are therefore assumed to be more developed in species that travel longer distances, compared to those that move less. Indeed, ranging-related factors were found to be positively correlated with indices of brain size among primates (Clutton-Brock and Harvey, 1980; Milton, 1988; Dunbar, 1992; Sawaguchi, 1988; Deane et al., 2000), suggesting higher cognitive abilities in wide-rangers. For example, the patas monkey (*Erythrocebus patas*) has a mean home-range size of 30 km² in the wild. In comparison, the group observed in the current study had a “home-range” of only 0.00004 km². Patas monkeys cover large areas in the search for food, and use navigational skills in order to avoid predators (Nakagawa, 1999; Isbell, 1998). These qualities require constant decision-making and high spatial-memory abilities, which are largely not needed in the captive surroundings.

In regard to the current study, it should be taken into account that since some of the observed species are represented by just one group, further research, employing larger-scale studies, is needed in order to validate these suggestions.

4.3. Animal husbandry

Our findings have two main implications for the welfare of zoo-housed primates. First, by employing comparative methods we were able to identify those species that are more susceptible to the negative effects of captive life. In a reality of limited financial means, this knowledge may allow zoos to reach informed decisions as to how to best allocate their resources in order to meet the motivational demands of naturally large-grouped species and species that travel long distances. Second, our results highlight the important factors that need to be addressed when designing enclosures and incorporating environmental enrichment within zoo-housed primate groups. In particular, we suggest focusing on creating more opportunities for positive social interactions for the animals. Where possible, it is recommended to house groups in numbers similar to those reported in the wild. Indeed, social companionship of compatible conspecifics is a potent contributor to enhanced well-being (Honeess et al., 2012). Due to the obvious limitations in this respect, however, other alternatives should be considered. For example care-givers and trainers can improve the social lives of captive primates by positively interacting with them, and thereby address the animals' high motivation for social contact (e.g. Dorey et al., 2009). This can be achieved either through unstructured positive interactions between the animals and their care-givers (Baker, 2004), and/or through positive reinforcement training programs (Pomerantz and Terkel, 2009). Both of these techniques have been shown to increase positive social behaviors and reduce abnormal ones.

Furthermore, rather than simply increasing enclosure size (which is often impractical), we suggest investing in the complexity of the enclosure. More complex environments have been shown to be related to lower levels of stereotypic behavior and to an increase in the expression of natural behavioral repertoires (Mallapur et al., 2002). Among captive primates the complexity of the captive environment is more important in promoting locomotion (thus addressing the motivation to range) than the actual enclosure size (Kessel and Brent, 1996). Indeed, simply enlarging the primates' enclosure size has been shown to be ineffective in

reducing levels of stereotypic behavior (Honeess and Marin, 2006). Instead, we suggest that the animals' opportunities to express ranging behaviors be increased by incorporating modular structures within the enclosure, allowing for easy and frequent change of the environment. Moreover, scattering and hiding food in unpredictable locations promotes the search for food, which is a major motivator for animals to range (Isbell, 1991), and has been found to have a positive effect on their welfare (Young, 1998).

In conclusion, by employing comparative methods we were able to show that group size and day journey lengths in the wild are major predictors of stereotypic behavior among zoo-housed primates. This finding facilitates detection of the more ‘susceptible’ species, as well as enabling the decision-makers to focus on specific environmental factors in order to improve the primates' psychological welfare.

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