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Abnormal behaviour in captive sooty mangabeys

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Abstract

*The influence of several factors on abnormal behaviour was investigated in 46 singly housed sooty mangabeys (*Cercocebus atys*) (eight nursery-reared, 38 mother-reared), including self-injurious, self-directed, stereotypic locomotion, and faeces/urine-related behaviours (SIB, SDB, SL, FUR, respectively). An analysis of behavioural assessments spanning a mean of four years per subject showed that 83% displayed at least one form of AB during that time, with SL being the most common (mean of 3.06% of observation sessions and displayed by 59% of subjects) and SIB the least common (mean of 0.09% of all observation sessions and displayed by 20% of subjects). Like other primate species, displaying AB was influenced by the percent of life spent singly housed and by nursery-rearing during infancy. However, unlike some other primates, there was no influence of the number of yearly sedations or room relocations on AB; also, females were more likely to display AB than male mangabeys. To investigate the effects of nursery-rearing further, we compared the eight nursery-reared, singly housed subjects with eight nursery-reared subjects that were socially housed since the age of three years. While nursery-reared subjects in single housing displayed SL and FUR in higher proportions than those in social housing, subjects from both environments displayed SIB and SDB in equal proportions, suggesting that they are persistent forms of AB for nursery-reared mangabeys even after long-term social housing. To reduce future incidence of AB in captive mangabeys, we recommend minimising nursery-rearing and the duration of single-housing whenever feasible or avoiding them altogether.*

Keywords: *abnormal behaviour, animal welfare, nursery-rearing, single-housing, sooty mangabey, stereotypic behaviour*

Introduction

The term abnormal behaviour refers to behaviours that are species-atypical in form or frequency, repetitive and/or functionless, and potentially physically harmful (Erwin & Deni 1979; Walsh 1982; Mason 1991; Lutz *et al* 2003). Abnormal behaviour is often categorised as either whole-body locomotor stereotypies (eg pacing, flipping) or self-directed behaviour (eg eye-poking, bizarre body posture, digit sucking; Novak 2003). Self-injurious behaviour (SIB) is considered an extreme form of self-directed behaviour and includes behaviours that have the potential to cause serious injury, such as head banging and self-biting. Accordingly, SIB is widely regarded as an indicator of poor psychological welfare (Novak 2003). Animals may engage in abnormal behaviour as a way to cope with stressors and alleviate anxiety, out of frustration, compulsion, or habit (Mason 1991; Tiefenbacher *et al* 2005); however, it is generally accepted that well-being is compromised in animals that express abnormal behaviour because these behaviours often occur in contexts where the animals lack physical space, sensory and social stimulation, and/or control over their environment (Mason 1991). Maximising psychological welfare is important not only for the animals' sakes, but to enhance the quality of research, as animals that display abnormal behaviour are physiologically and cognitively different from those that do not; for example, they tend to have dysregulation of the systems regulating response to stress and anxiety and slower procedural and reversal learning (Tiefenbacher *et al* 2000, 2004, 2005; Tanimura *et al* 2008). Thus, it is important for researchers using animal models to reduce and/or avoid conditions that contribute to engagement in abnormal behaviour, as it can directly impact the measures in their studies.

As natural hosts of the Simian Immunodeficiency Virus (SIV), sooty mangabeys (*Cercocebus atys*) are an important animal model for Acquired Immune Deficiency Syndrome (AIDS) research. The Yerkes National Primate Research Center (YNPRC) houses a colony of sooty mangabeys, a subset of which is singly housed, to participate in IACUC-approved research protocols. Although much is known about mangabey social and reproductive behaviour (eg Bernstein 1971; Ehardt 1988a,b; Gust & Gordon 1991,

1993; Gust 1995; Range 2005), we know little about the behaviour and welfare of singly housed mangabeys. Thus, we investigated the prevalence of various forms of abnormal behaviour in 46 singly housed mangabeys and the influence of various factors on the occurrence of abnormal behaviour in these subjects, including overall time spent in single-housing, the frequency of sedations and room changes per year, sex, and rearing history. Subjects were not housed in particular configurations and did not undergo particular procedures for the purposes of the current study; instead, we used behavioural records collected while subjects were living at the YNPRC in various circumstances. To investigate the long-term effects of nursery-rearing on abnormal behaviour further, we assessed the presence of abnormal behaviour in eight additional sooty mangabeys that were nursery-reared and singly housed for the first three years of their lives, as required by a research protocol in the early 1990s, and then housed socially for the next 15 years (at the time of sampling).

A primary contributor to abnormal behaviour is adverse early life experience, which often takes the form of repeated or permanent separation from the mother during infancy and/or early juvenility. Studies have shown that permanent maternal separation and subsequent nursery-rearing is associated with abnormal behaviour in adulthood in a variety of primate species; for example: rhesus macaques (*Macaca mulatta*) (Harlow & Harlow 1962; Erwin *et al* 1973; Lutz *et al* 2003; Novak 2003; Rommeck *et al* 2009a,b; Vandeleest *et al* 2011), pigtail macaques (*Macaca nemestrina*) (Bellanca & Crockett 2002), baboons (*Papio hamadryas*) (Brent & Hughes 1997; Lutz *et al* 2012), chimpanzees (*Pan troglodytes*) (Walsh 1982; Maki *et al* 1993; Pazol & Bloomsmith 1993; Kalcher *et al* 2008). Furthermore, the earlier the infant is separated and/or the longer the separation bouts last can increase the likelihood and severity of abnormal behaviour later in life (Kalcher *et al* 2008; Latham & Mason 2008). Corroborating these findings, Gottlieb and colleagues (2013) found that singly housed rhesus macaques exhibited less abnormal behaviour for every year they spent living outdoors in large social groups prior to being singly housed. Together, these findings show that it is not only the rearing experience *per se*, but also the timing of adverse early experience that contributes to the development of abnormal behaviour in adulthood.

Underlying that relationship is a variety of physiological perturbations that occur as the animal develops under adverse conditions. The context of nursery-rearing generally involves being raised indoors in close contact with humans with limitations in physical space, enrichment, and social feedback from conspecifics (Capitanio *et al* 2006). Compared to mother-reared primates, nursery-reared animals show life-long differences in brain structures, neurochemistry, and cognition (eg Sánchez *et al* 1998; Spinelli *et al* 2009), immune function and survival rates (eg Lewis *et al* 2000; Lubach & Coe 2006), and a variety of other behavioural differences (eg Champoux *et al* 1992; Dettling *et al* 2002; Bastian *et al* 2003; Kalcher-Sommersguter *et al* 2011). In addition, it appears that prolonged heightened activation of the hypothalamic-pituitary-adrenal (HPA) axis during early adverse experiences lead to HPA axis hypofunctionality, as reflected by reduced basal cortisol levels and blunted reactivity to stressors later in life (Clark 1993; Capitanio *et al* 2005; Sánchez 2006; for a review including studies with different results, see Novak *et al* 2013). While it remains unclear how HPA axis hypofunctionality influences the likelihood of an animal's engagement in abnormal behaviour, it appears that when this process occurs in an animal with a certain genotype, the likelihood of engaging in abnormal behaviour increases (Champoux *et al* 2002; Novak *et al* 2013).

Some animals without adverse early life experiences also develop abnormal behaviour. Often, these animals live in an indoor laboratory setting (single-, paired- or group-housed), since, as mentioned previously, these are animals that generally lack extensive physical space, have reduced sensory and social stimulation, and have little control over their environment. Consequently, many studies investigate the link between abnormal behaviour and single-housing, which is the housing situation for many laboratory-housed animals (according to a 2007 survey, 27% of all laboratory-housed primates in the US are singly housed out of 35,863 animals reported in the survey; Baker *et al* 2007). Although social restriction and spatial confinement are usually confounded in single-housing, it appears that social restriction plays an independent role in the development of self-directed abnormal behaviour, whereas it is predominantly confinement that contributes to the development of stereotypic locomotion (eg pacing, flipping; Draper & Bernstein 1963; Ridley & Baker 1982; Bellanca & Crockett 2002; Vandeleest *et al* 2011). Stereotypic locomotion is often reported as the most frequently observed form of abnormal behaviour in singly housed primates (eg Jorgensen *et al* 1998; Seier *et al* 2011, 2013) and it is often linked with the amount of time spent in single-housing and the age at which animals begin living in single-housing (Bellanca & Crockett 2002; Lutz *et al* 2003, 2012).

Other factors associated with abnormal behaviour expression are some events associated with research use of the animals and the animal's sex. Primates living in a laboratory setting are sometimes moved to different rooms, which involves a sudden change in environment and neighbours. Some studies find an effect of such room relocations on the occurrence of abnormal behaviour (Rommeck *et al* 2009a; Gottlieb *et al* 2013), while others do not (Lutz *et al* 2003; Novak 2003). Sedating primates for a clinical or research purpose is also associated with abnormal behaviour (eg Crockett *et al* 2000; Lutz *et al* 2003, 2012; Novak 2003; Vandeleest *et al* 2011). Finally, abnormal behaviour appears to be more prevalent in singly housed males than in females in macaques and baboons (eg Bayne *et al* 1995; Brent & Hughes 1997; Lutz *et al* 2003; Gottlieb *et al* 2013), but more common in female than male vervet (*Chlorocebus pygerythrus*) monkeys (Seier *et al* 2011).

Since abnormal behaviour is difficult to treat once it develops (Line *et al* 1991; Novak *et al* 1998) and various forms of abnormal behaviour often co-occur (eg Gottlieb

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et al 2013), it is important to minimise abnormal behaviour risk factors to support both the psychological well-being of laboratory animals and the quality of the research for which they serve. For macaque species, these include minimising or avoiding social isolation during the infant and juvenile period, reducing the time spent in single-housing and the number of sedations and room changes they experience while in single-housing. Thus, we investigated whether these factors influence abnormal behaviour in sooty mangabeys that were housed at the YNPRC. We categorised abnormal behaviours as self-injurious (SIB), self-directed (SDB), stereotypic locomotion (SL), and faeces/urine-related behaviour (FUR).

As seen in macaque species, we expected stereotypic locomotion to have been displayed more frequently than the other forms of abnormal behaviour and that subjects which displayed stereotypic locomotion would have also displayed at least one other form of abnormal behaviour. Additionally, we expected subjects that engaged in abnormal behaviour would have a relatively high percent of life in single-housing and number of sedations and room changes per year, to be male, and to have a history of nursery-rearing (as opposed to mother-rearing) in the first two years of life compared to those that did not engage in abnormal behaviour. In a separate analysis, we investigated the long-term effects of nursery-rearing by comparing the eight nursery-reared mangabeys that were singly housed with eight nursery-reared mangabeys that were socially housed for over 15 years. Of these subjects, we expected a greater number of singly housed subjects to have displayed abnormal behaviours than those that were socially housed.

Materials and methods

Subjects and housing

Singly housed subjects

Of approximately 200 sooty mangabeys in the YNPRC colony, n = 46 were singly housed during the study period (31 male, 15 female [none of which were pregnant or lactating]; 38 mother-reared, eight nursery-reared) and ranged in age from 7 to 26 years (mean age 16.8 years). The subjects were housed in stainless steel cages (varying from 6.0 to 9.9 square feet of floor space, which met cage size requirements in the United States) at the YNPRC in rooms in which they could see and hear conspecifics. Six of the eight nursery-reared, singly housed subjects lived in single-housing their whole lives (7–18 years; mean of 13.7 years) and the remainder (two nursery-reared and 38 mother-reared) were housed socially in indoor-outdoor enclosures prior to moving to pair- or single-housing. The YNPRC pair-houses animals whenever possible; however, we exclusively used data that were collected when subjects were singly housed due to social incompatibility and/or the requirements of a research protocol. Subjects were assigned to protocols involving SIV-related research, as sooty mangabeys are natural carriers of the virus and do not become immunocompromised (Silvestri *et al* 2007). All protocols were approved by the facility's Institutional Animal Care and Use Committee and all aspects of management and research use conformed to US federal regulations and guidelines. Monkey chow (LabDiet Monkey Diet 5037, PMI Nutrition International, St Louis, MO, USA) was distributed twice daily, water was available *ad libitum*, each cage included a perch and a manipulable object, and other enrichment was distributed daily in the forms of fresh produce, grain, foraging devices, and destructible enrichment.

Socially housed subjects

Eight sooty mangabeys (five male, three female; all nursery-reared and between 18–19 years old at initiation of data collection) were housed at the YNPRC in social groups of varying sizes and compositions. These subjects were nursery-reared and then singly housed until the ages of 2–3 years due to a research protocol conducted in the early 1990s. Once single-housing was no longer required, these subjects were systematically socialised and introduced to large, indoor-outdoor, compound-housed social groups comprising of 15–20 adult males and females, juveniles, and infants (indoor quarters: 54–101 m^2; outdoor quarters: 1,524–3,049 m^2). At the time of sampling for the present study, the three female subjects still lived in the mixed-sex and mixed-age compound-housed group and the five male subjects lived in bachelor groups comprising 3–19 adult males in run-housing (76–152 m^2), with the exception of one male which was temporarily housed individually in an indoor-outdoor run (25 m^2; this subject was also housed individually in a run or cage setting for three years prior to the start of this study, though the other 12 years of his life were spent living socially). The five male subjects had lived in large, compound-housed, mixed-sex and age groups for at least one year prior to living in bachelor groups, three of which lived in compound-housed groups for over ten years, including the temporarily individually housed male subject. Monkey chow was distributed twice daily, water was available *ad libitum*, and feeding enrichment consisting of fresh fruit, vegetables and seeds was distributed daily. The compound was equipped with various shade structures, climbing structures, fire hose, and toys; runs were equipped with perches, plastic barrels, fire hose, and toys.

Data collection

Singly housed subjects

The YNPRC Behavioural Management Unit (BMU) functions to monitor and enhance animal welfare by the use of social housing, environmental enrichment and animal training methods. In addition, BMU uses a standardised assessment protocol to monitor the behaviour of all primates in single-, panel-, and pair-housing and provides treatment for animals that exhibit behavioural problems (for panel-housed monkeys, a perforated panel was placed in the wall adjoining two cages allowing limited physical interaction between two monkeys). This protocol involves: identifying animals that exhibit abnormal behaviour, determining its level of severity (rate and duration of the behaviour), administering treatment for certain behavioural problems (treatments such as enrichment devices, environmental or

Table 1 Ethogram of abnormal behaviour (AB).

AB category	Behaviour	Definition
Self-injurious behaviour (SIB)	Self-biting	Closing teeth rapidly and with force on self (with or without breaking the skin; may cause bruising)
	Other SIB	Any self-directed behaviour that results in an injury (breaking skin and/or bruising) or has the potential to result in injury (eg self-slapping, head banging against the cage)
Self-directed behaviour (SDB)	Hair pluck	Directed pulling out of one's own hair with teeth or fingers
	Floating limb	Raising a limb in the air; animal does not appear in control of limb; animal sometimes threatens and/or bites the limb
	Bizarre posture	Holding a seemingly uncomfortable or unnatural body position
	Oral SDB	Oral contact with one's own body (eg digit sucking)
	Eye SDB	Manual contact with one's own eyes (eg eye-poking, saluting, eye-covering)
	Locomotor SDB	Any self-directed, repetitive and ritualistic behaviour not involving whole-body locomotion (eg, self-clasping, rocking)
Stereotypic locomotion (SL)	Stereotypic locomotion	Repetitive locomotion patterns involving whole-body movement (eg, pacing, flipping, circling)
Faeces/Urine-related (FUR)	Faeces smear	Smearing or rubbing faecal material onto a surface or coprophagy
	Urine drink	Licking or drinking of urine either directly from penis or pooled on a surface
	Regurgitate-reingestion[†]	Vomiting food and/or liquid and reingesting vomited material

[†] Regurgitate-reingestion was included in the FUR category because the behaviour was only recorded once; thus, it did not warrant its own category and did not clearly fit into the other categories (see Table 3).

social changes, and desensitisation training), evaluating treatment, and modifying treatment as needed.

To monitor the animals, a trained observer walked through each animal room approximately three times per week at various times of day, observing each animal (spending about 10 min in the room) and recording the occurrence of any abnormal behaviour using a one-zero sampling technique (see Table 1). The observers were trained to be a neutral presence in the room, avoiding eye contact and refraining from interaction with the animals during the observation session. The assessment was not started until the observer was in the room for several minutes and the animals appeared to stop responding to the presence of the observer. This data collection procedure allows BMU to monitor a large number of animals in a time-effective manner.

For the present study, we used the data regarding the 'occurrence' and 'frequency of observations sessions' during which each type of abnormal behaviour was recorded for each subject between August 2006 and November 2011 (a period of 5.3 years). We included observations sessions in which subjects were panel-housed, as it is considered a form of single-housing (National Research Council 2011), but not when subjects were pair-housed. Ten subjects experienced intermittent panel-housing throughout the study period. By the end of the study period, the duration subjects had lived in single-housing ranged from six months to 18.5 years (mean 8.9 years). Because the subjects varied in the amount of time spent in single-housing, data collection ranged across subjects from six months to 5.3 years, with a mean duration of 4 years and mean (± SEM) total of 577 (± 33) observation sessions per subject (total: 26,543 observation sessions). Because observers spent approximately 10 min collecting data during each observation period and because their mere presence may have influenced whether the subjects engaged in abnormal behaviour, it is likely there is an underestimation of number of subjects that engaged in abnormal behaviours and the frequency of observations sessions in which they did so. However, we regard the duration of time that subjects were observed — an average of four years per subject — as sufficient for the purposes of determining: i) whether subjects engaged in each type of abnormal behaviour at least once; and ii) the relative frequencies with which subjects engaged in each category of abnormal behaviour (SIB, SDB, SL, and FUR).

Socially housed subjects

We did not have a similar dataset for the eight nursery-reared subjects living in social housing because the BMU does not use the same assessment protocol for animals housed socially in large enclosures. Instead, for the purposes of the present study, we observed each of these subjects opportunistically and recorded the occurrence of abnormal behaviour *ad libidum* at a minimum of three times per week over a period of 22 months (July 2011–May 2013; see Table 1). In addition, staff familiar with these animals were asked to note the presence or absence of each type of abnormal behaviour (see Table 1) for each subject and their responses corroborated our findings. Thus, we gathered data on presence or absence of abnormal behaviour for the eight nursery-reared, socially housed subjects.

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Data analysis

Abnormal behaviours were categorised as self-injurious (SIB; eg self-biting, head banging), self-directed (SDB; eg hair plucking, bizarre posturing, floating limb, eye-poking, digit sucking, rocking), stereotypic locomotion (SL; eg pacing, circling, flipping), or faeces/urine-related (FUR; eg faeces smearing, urine drinking, regurgitating and re-ingesting) abnormal behaviour (Table 1). All subjects, both singly and socially housed, were categorised as having displayed or not displayed each type of abnormal behaviour at least once (ie presence or absence).

Singly housed subjects

First, we analysed general patterns in the types of abnormal behaviour displayed: we compared the frequency of observation sessions that each category of abnormal behaviour was recorded across subjects with Wilcoxon signed rank tests and we used two-tailed Spearman's rank correlations to assess co-morbidities in the occurrence of each form of abnormal behaviour ($\alpha = 0.0167$). Next, we used Mann-Whitney *U* tests to examine whether subjects that displayed abnormal behaviour in each category differed from those that did not in the percent of life spent in single-housing and the number of sedations and room changes they experienced per year ($\alpha = 0.05$). Table 2 shows the characteristics of the singly housed subjects with regard to these variables. We chose not to include age and the age first singly housed as factors of interest because both variables were significantly negatively correlated with percent of life in single-housing ($r = -0.35$; $r = -0.93$, respectively; $P \leq 0.05$). Next, we used Fisher's exact tests to compare the proportions of subjects that did and did not display abnormal behaviour in each category across sex and rearing history (mother- or nursery-reared; $\alpha = 0.05$). We report moderate to high effect sizes ($\varphi > 0.3$) and relative risks greater than 2.

Socially housed subjects

To examine the long-term effects of nursery-rearing on abnormal behaviour, we compared the occurrence of abnormal behaviour between eight nursery-reared subjects that were singly housed and eight nursery-reared subjects that were socially housed from three years of age (they were housed socially for 15 years at the time of sampling). We used Fisher's exact tests to compare the proportions of nursery-reared subjects that displayed each category of abnormal behaviour across housing type (single or social), again reporting moderate to high effect sizes ($\varphi > 0.3$) and relative risks greater than 2.

Results

General patterns

Singly housed subjects

Thirty-eight of the 46 singly housed subjects displayed abnormal behaviour at least once (83% of subjects). Despite this high proportion, abnormal behaviour was not frequently recorded for most subjects: 80% of singly housed subjects displayed abnormal behaviour in fewer than 10% of the observation sessions (37 of 46 subjects; eight of which never displayed abnormal behaviour). Seventeen of the 38 subjects displayed abnormal behaviour in less than 1% of the observation sessions and twelve subjects displayed abnormal behaviour in 1–9.9% of observation sessions.

Table 2 Characteristics of the 46 singly housed subjects with regard to the quantitative factors included in data analysis.

Factor	Mean (± SEM)	Range
Percent of life in single-housing	56.2 (± 3.95)	2–100
Number of sedations per year	7.16 (± 0.5)	2.7–17.1
Number of room changes per year	0.89 (± 0.05)	0.38–1.97

Table 3 The number of subjects that displayed each type of abnormal behaviour and the frequency of observation sessions during which each type of abnormal behaviour was recorded across the singly housed subjects (n = 46) and across 5.3 years (a total of 26,543 observation sessions).

Category	Behaviour	Subjects (n)	Observation sessions recorded (n)
SIB	Self-biting	8	22
	Other SIB	1	1
	Any form of SIB	9	23
SDB	Hair pluck	2	2
	Floating limb	1	1
	Bizarre posturing	0	0
	Oral SDB	3	16
	Eye SDB	0	0
	Locomotor SDB	17	64
	Any form of SDB	18	84
SL	Stereotypic locomotion	27	822
FUR	Faeces smear	23	367
	Urine drink	10	33
	Regurgitate-reingest	1	1
	Any form of FUR	28	401

The specific types of abnormal behaviour are not mutually exclusive (eg an animal may have displayed both hair pluck and locomotor SDB but was only counted once as having displayed any form of SDB).

Nine of the 46 subjects displayed SIB on at least one occasion (20% of subjects; two of the nine self-biters wounded themselves at least once, each subject requiring one instance of minor veterinary intervention). Eighteen subjects displayed SDB (39% of subjects), 27 displayed SL (59% of subjects), and 28 displayed FUR (61% of subjects) on at least one occasion (Table 3). SL was the most frequently recorded form of abnormal behaviour in terms of the percent of observation sessions in which it was recorded, followed by FUR, SDB, and finally SIB. Table 3 shows the number of singly housed subjects that displayed each type of abnormal behaviour and the number of obser-

Table 4 The mean (± SEM) and range in the percent of observation sessions during which subjects were recorded as displaying each category of abnormal behaviour (AB).

Category	Mean (± SEM) percent of observation sessions during which subjects were recorded as displaying each AB category (n = 46)[†]	Range
SIB	0.09 (± 0.05)%	0–2%
SDB	0.35 (± 0.16)%[‡]	0–7%
SL	3.06 (± 0.93)%[§]	0–29%
FUR	1.83 (± 0.70)%[#]	0–21%

[†] Mean percent of observation sessions that each form of AB was recorded did not differ by much when we removed the subjects that never displayed AB (SIB: 0.11; SDB: 0.42; SL: 3.70; FUR: 2.21).
[‡] SDB recorded more frequently than SIB ($P = 0.006$); Wilcoxon signed rank test.
[§] SL recorded more frequently than SIB and SDB (each $P < 0.001$); Wilcoxon signed-rank test.
[#] FUR recorded more frequently than SIB ($P < 0.001$); Wilcoxon signed rank test.

vation sessions that each type of abnormal behaviour was recorded across subjects.

As most subjects displayed abnormal behaviour in fewer than 10% of observation sessions, the overall mean percent of observation sessions during which each form of abnormal behaviour was recorded were relatively low (see Table 4). Wilcoxon signed rank tests showed that the mean percent of observation sessions during which SL was recorded (3.05%) was significantly higher than SIB and SDB (0.35 and 0.09%, respectively; $P < 0.001$); FUR (1.83%) was higher than SIB ($P < 0.001$); and SDB was higher than SIB ($P = 0.006$). Two-tailed Spearman's rank correlations showed that the subjects that displayed SL were more likely to display SIB ($rho = 0.414$, $P = 0.004$) and SDB ($rho = 0.492$, $P = 0.001$) than those that did not display SL. Those that displayed SDB were also more likely to display SIB, as well ($rho = 0.391$, $P = 0.007$).

Socially housed subjects

Seven of eight socially housed, nursery-reared subjects displayed abnormal behaviour. Five of eight subjects displayed SIB (self-biting), six of eight subjects showed SDB (two engaged in bizarre posture, one showed floating limb, and three displayed locomotor SDB), and one of eight subjects displayed SL and FUR (urine drinking). Other SIB (eg head banging), oral SDB (eg digit sucking), eye SDB, faeces smear, and regurgitate-reingestion were never observed in the socially housed subjects.

Factors influencing abnormal behaviour

Singly housed subjects: percent of life in single-housing, number of sedations per year, and number of room changes per year

Subjects were categorised as either displaying or not displaying each category of abnormal behaviour (ie presence or absence) and we compared these groups on the percent of life spent in single-housing, number of sedations experienced per year, and number of room changes per year using Mann-Whitney *U* tests. Table 5 shows the means and medians of each factor of interest in these groups. The percent of life in single-housing was higher in subjects that displayed abnormal behaviour than for those that did not, significantly so for SIB, SDB, SL, and for subjects that displayed any form of abnormal behaviour (all categories pooled; mean percent of life in single-housing: SIB vs no SIB: 87 vs 49%, $P < 0.001$; SDB vs no SDB: 67 vs 49%, $P = 0.019$; SL vs no SL: 68 vs 39%, $P = 0.001$; FUR vs no FUR: 61 vs 48%, $P = 0.083$; any AB vs no AB: 61 vs 35%, $P = 0.008$). To ensure that these differences were not driven by the nursery-reared, singly housed subjects (n = 8; all of which displayed some form of abnormal behaviour and seven of which spent a majority or all of their lives in single-housing), we re-ran these comparisons without those subjects and found the same pattern of results. There were no differences in number of sedations per year (means ranging between 7–8) and room changes per year (means ranging between 0.82–0.99) for subjects that displayed each category of abnormal behaviour and those that did not (see Table 5).

Singly housed subjects: sex and rearing history

Next, we looked at whether the proportions of subjects that did or did not display each category of abnormal behaviour differed across sex and rearing history using Fisher's exact tests (including moderate to high effect sizes, $\varphi > 0.3$, and relative risks greater than 2). Females tended to display abnormal behaviour in higher proportions than males, although only significantly so when all categories of abnormal behaviour were pooled ($P = 0.04$, $\varphi = 0.32$; Table 6). Although Fisher's exact test showed no difference in the proportion of males and females that displayed SIB, SIB subjects were 2.5× more likely to be female than male (13% of males and 33% of females displayed SIB; see Table 6). Subjects that were nursery-reared showed SIB and SDB in higher proportions than those that were mother-reared (SIB: $P < 0.001$, $\varphi = 0.64$; SDB: $P = 0.03$, $\varphi = 0.34$; Table 6) and SIB subjects were 9.4× more likely to be nursery-reared than mother-reared and SDB subjects were 2.3× more likely to be nursery-reared than mother-reared. The difference in proportions of nursery- and mother-reared subjects that displayed SL approached significance ($P = 0.07$).

Nursery-reared subjects: housing type (single vs social)

A comparison of nursery-reared subjects that were singly housed with those that were socially housed showed that the proportions of subjects that displayed SIB and SDB in each housing type were not significantly different: six of eight singly housed and five of eight socially housed subjects displayed SIB; six of eight singly housed and the same proportion of socially housed subjects displayed SDB. A higher proportion of nursery-reared, singly housed subjects displayed SL than did nursery-reared, socially housed subjects: seven of eight singly housed and one of eight socially housed subjects displayed SL ($P = 0.01$, $\varphi = 0.75$); thus, nursery-reared subjects that displayed SL were 6.8× more likely to be singly than socially housed. In addition, although Fisher's exact test showed no difference in proportions of nursery-reared subjects that displayed FUR, they

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Table 5 Means and medians of the percent of life spent in single-housing (%LifeSH), number of sedations per year (#Sed/yr), and number of room changes per year (#RC/yr) for subjects that displayed each category of abnormal behaviour (AB) and those that did not (of the 46 subjects, n = 9 displayed SIB; n = 18 displayed SDB; n = 27 displayed SL; n = 28 displayed FUR; and n = 38 displayed any AB).

	SIB	No SIB	SDB	No SDB	SL	No SL	FUR	No FUR	Any AB	No AB
Mean%LifeSH	87	49	67	49	68	39	61	48	61	35
Median%LifeSH	98†	45	74†	47	72†	38	70	43	65†	35
Mean#Sed/yr	8	7	8	7	7	7	7	8	7	8
Median#Sed/yr	6	7	6	7	7	7	6	8	7	8
Mean#RC/yr	0.83	0.90	0.90	0.88	0.82	0.99	0.87	0.92	0.90	0.84
Median#RC/yr	0.93	0.90	0.87	0.91	0.82	0.91	0.83	0.94	0.90	0.93

† $P < 0.02$; Mann-Whitney *U* tests.

Table 6 Proportion of males and females, mother- and nursery-reared, and singly and socially housed subjects that displayed each category of abnormal behaviour (AB).

		SIB	SDB	SL	FUR	Any AB
Sex	Males (n = 31)	0.13	0.32	0.55	0.52	0.74
	Females (n = 15)	0.33	0.53	0.67	0.80	1.0‡
Rearing history (singly housed)	Mother-reared subjects (n = 38)	0.08	0.32	0.53	0.63	0.79
	Nursery-reared (n = 8)	0.75†	0.75†	0.88	0.50	1.0
Housing type (nursery-reared)	Singly housed, nursery-reared subjects (n = 8)	0.75	0.75	0.88‡	0.50	1.0
	Socially housed, nursery-reared subjects (n = 8)	0.63	0.75	0.13	0.13	0.88

† $P < 0.05$, $\varphi > 0.3$; Fisher's exact test, one-tailed.
‡ $P < 0.05$, $\varphi > 0.3$; Fisher's exact test, two-tailed.

were 3.8× more likely to be singly housed than socially housed: four of eight singly housed and one of eight socially housed subjects displayed FUR ($\varphi = 0.41$).

Discussion

A large proportion of the singly housed mangabeys displayed some form of abnormal behaviour at least once during the sampling period (83% of subjects; the sampling period spanned a mean of four years per subject). This is similar to what has been reported for singly housed rhesus macaques at one facility (89% of subjects; Lutz *et al* 2003). Despite a relatively high proportion displaying some form of abnormal behaviour, it was not frequently observed, overall: 80% of the subjects displayed abnormal behaviour in fewer than 10% of the observation sessions (mean [± SEM] of 577 [± 33] observation sessions per subject). It is possible that the prevalence and frequency of abnormal behaviours are underestimated due to the presence of an observer in the room and/or the modest duration of data collection during each observation session. However, even if underestimated, we consider the duration of time the animals were observed (an average of over four years per subject) to be sufficient for our purpose, which was to determine the presence or absence of abnormal behaviour in each subject and the relative frequencies with which they engaged in each category of abnormal behaviour.

Stereotypic locomotion (SL) was the most commonly observed form of abnormal behaviour in the singly housed sooty mangabeys, as is commonly reported for singly housed macaque species (eg Bellanca & Crockett 2002; Lutz *et al* 2003). The second most commonly observed category of abnormal behaviour was FUR, followed by SDB, and finally SIB (see Tables 3 and 4). Nine of 46 singly housed mangabeys displayed SIB (~20%), each in fewer than 2% of the sessions in which they were observed (two of these subjects self-wounded). While SIB was observed relatively infrequently compared to the other forms of abnormal behaviour, the proportion of the singly housed population that displayed SIB at least once was somewhat higher than that of singly housed macaque populations, which varies between 5–15% of subjects (Bayne *et al* 1995; Novak 2003; Novak *et al* 2013). This indicates that singly housed mangabeys may be at a higher risk for developing self-injurious behaviour than are singly housed macaque species.

An assessment of the co-morbidity between forms of abnormal behaviour suggested that singly housed mangabeys that engage in one form of abnormal behaviour are likely to engage in other forms, as well. Co-morbidity was evident in subjects that displayed SIB, SDB, and SL. These findings correspond with what has been reported for singly housed rhesus macaques (eg Lutz *et al* 2003; Rommeck *et al* 2009a; Gottlieb *et al* 2013) and suggest that most animals that

engage in abnormal behaviour do so in a variety of ways. In fact, recent research shows that the tendency to engage in abnormal behaviour may be related to personality and temperament, in addition to rearing history and time spent in single-housing (Vandeleest *et al* 2011; Gottlieb *et al* 2013).

As seen in many other species, the singly housed mangabeys that displayed abnormal behaviour had spent significantly more time in single-housing than those that did not. Specifically, the subjects that engaged in SIB, SDB, and SL had spent over half of their lives in single-housing (between 67–85% of their lifetimes, on average), whereas the subjects that did not engage in those forms of abnormal behaviour spent less than half of their lives in single-housing (between 39–50% of their lifetimes, on average; see Table 5). This indicates that the overall time spent in single-housing contributes to the development of a variety of forms of abnormal behaviour in sooty mangabeys, including most prominently, self-biting, locomotor self-directed behaviour (eg self-clasping, rocking), and stereotypic locomotion (eg pacing, flipping; see Table 3). Because this variable was strongly correlated with the age at which the animals were first singly housed ($r = –0.93$), we are not able to parse out their independent contributions to the development of abnormal behaviour. However, as is the case for macaques (eg Lutz *et al* 2003; Novak 2003), it is likely that when both of these factors occur together, risk for abnormal behaviour development is compounded.

Contrary to some studies of macaques in single-housing, we found that the number of times subjects were sedated and moved to different rooms per year did not differ between singly housed mangabeys that displayed abnormal behaviour and those that did not. However, because we saw very little variation in the number of yearly sedations and, in particular, room changes in the present sample (see Table 2), we are not able to decipher whether these two factors did not reach a level to negatively impact their welfare or whether sooty mangabeys simply do not react to these changes in a way that is similar to some singly housed macaque populations (eg Gottlieb *et al* 2013). The influence of these factors on abnormal behaviour in sooty mangabeys requires further study.

Unlike macaques and baboons, female mangabeys were more likely than males to engage in SIB (2.5× more likely), they were observed displaying FUR behaviours more often than males, and they displayed more abnormal behaviours overall. Like vervet monkeys (Seier *et al* 2011), our findings indicate that female mangabeys may be more susceptible to displaying abnormal behaviour than male mangabeys. This is contrary to the pattern of greater susceptibility among male macaques and baboons (Bayne *et al* 1995; Brent & Hughes 1997), and may indicate a species difference.

As expected, nursery-rearing appears to be a significant risk factor for abnormal behaviour in sooty mangabeys, particularly SIB and SDB. Of the singly housed subjects, those that engaged in SIB and SDB were much more likely to be nursery-reared than mother-reared (relative risks 9.4 and 2.3, respectively). The impact of nursery-rearing on abnormal behaviour was particularly striking when we compared the nursery-reared subjects that were singly housed with those that were socially housed: SIB and SDB were just as likely to be displayed by subjects that had been living socially for over 15 years as it was for subjects that were living in single-housing (over half of the nursery-reared subjects in each housing situation showed SIB and SDB). This shows that SIB and SDB are extremely persistent forms of abnormal behaviour in nursery-reared mangabeys, and later social housing in large indoor-outdoor facilities does not eliminate these behaviours. It also provides additional evidence that separation from conspecifics during infancy and early juvenility results in lasting physiological changes that may predispose such individuals to developing and maintaining abnormal behaviour (Tiefenbacher *et al* 2005). Since engaging in SIB reduces the heart rate and anxiety of rhesus macaques, and also might release endogenous opioids thereby reinforcing the behaviour (Novak 2003; Tiefenbacher *et al* 2003, 2005), primates may continue to engage in SIB in the long term to cope with acute environmental stressors and/or they remain long-term behaviour patterns due to past physiological reinforcement (Mason 1991).

Interestingly, SIB cases occasionally develop in mother-reared, singly housed monkeys and many nursery-reared monkeys never develop SIB. In our sample, three of 38 mother-reared, singly housed subjects developed SIB — each of them began living in single-housing between 2 and 3.4 years of age and spent between 61–85% of their lives in single-housing. In addition, five of the 16 nursery-reared subjects in this study never displayed SIB (two were singly housed and three were socially housed). This underscores the idea that interactions between particular temperaments (eg nervousness), personalities (eg active), and genotypes with particular environmental experiences that alter neuroanatomy, neurochemistry, and/or neuroendocrine systems may lead some individuals to engage in abnormal behaviours while others do not (Miller *et al* 2004; Chen *et al* 2010; Vandeleest *et al* 2011; Spinelli *et al* 2012; Gottlieb *et al* 2013; Novak *et al* 2013).

Two forms of abnormal behaviour that were infrequently or never recorded in the nursery-reared, socially housed subjects, SL and FUR, seem to have been minimised by social housing in large outdoor facilities. Similarly, stereotypic pacing was less common than self-directed behaviours in group-housed baboons (Brent & Hughes 1997). In our sample, only one of eight nursery-reared, socially housed subjects exhibited SL and, interestingly, this subject had spent the most time housed individually in either a run or cage setting (between 3 and 4 years) compared to the other socially housed subjects. These findings support the idea that SL and SIB have different aetiologies: SL stemming from confinement in a relatively small space with little sensory and social stimulation, and SIB stemming from social restriction during infancy and/or juvenility (Ridley & Baker 1982).

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Animal welfare implications and conclusion

Identifying factors associated with abnormal behaviour in sooty mangabeys is an important step toward promoting their psychological well-being and their value as research subjects. Our analysis suggests that avoiding nursery-rearing and single-housing can reduce the likelihood of abnormal behaviour development in sooty mangabeys. Therefore, we recommend reducing the durations of nursery-rearing and single-housing as much as possible, or to avoid them all together, if possible. When it is not possible to avoid nursery-rearing or single-housing, we recommend providing increased space, a complex enrichment programme, and positive reinforcement training to minimise the development of abnormal behaviour. Our findings that nursery-rearing and single-housing influence the expression of abnormal behaviour are in agreement with findings from other primate species (eg Maki *et al* 1993; Brent & Hughes 1997; Bellanca & Crockett 2002; Lutz *et al* 2003; Gottlieb *et al* 2013). On the other hand, the number of yearly sedations and relocations to different rooms did not impact the expression of abnormal behaviour in sooty mangabeys, although further research on these factors is needed. Also, there appears to be a species difference in how sex affects the expression of abnormal behaviour, as female sooty mangabeys were more likely to display abnormal behaviour than males (it is the males of other singly housed primate species that tend to show more abnormal behaviour). The present analysis along with evidence from other species indicates that duration spent in single-housing and nursery-rearing are reliable predictors of abnormal behaviour. In order to enhance both animal welfare and the quality of the research for which the animals serve, we encourage investigators and managers to look for alternatives to single-housing and nursery-rearing. It is important for studies like this one to inform decisions regarding the management of captive primates with the goal of maximising psychological well-being.

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References

Baker KC, Weed JL, Crockett CM and Bloomsmith MA 2007 Survey of environmental enhancement programs for laboratory primates. *American Journal of Primatology 69*: 377-394. http://dx.doi.org/10.1002/ajp.20347

Bastian ML, Sponberg AC, Suomi SJ and Higley DJ 2003 Long-term effects of infant rearing condition on the acquisition of dominance rank in juvenile and adult rhesus macaques (*Macaca mulatta*). *Developmental Psychobiology 42*: 44-51. http://dx.doi.org/10.1002/dev.10091

Bayne K, Haines M, Dexter S, Woodman D and Evans C 1995 Nonhuman primate wounding prevalence: a retrospective analysis. *Lab Animal 24*: 40-44

Bellanca RU and Crockett CM 2002 Factors predicting increased incidence of abnormal behavior in male pigtail macaques. *American Journal of Primatology 58*: 57-69. http://dx.doi.org/10.1002/ajp.10052

Bernstein IS 1971 The influence of introductory techniques on the formation of captive mangabey groups. *Primates 12*: 33-44. http://dx.doi.org/10.1007/BF01730380

Brent L and Hughes A 1997 The occurrence of abnormal behavior in group housed baboons. *American Journal of Primatology 42*: 96-97 (Abstract)

Capitanio JP, Mason WA, Mendoza SP, DelRosso L and Roberts JA 2006 Nursery rearing and biobehavioral organization. In: Sackett GP, Ruppenthal GC and Elias K (eds) *Nursery Rearing of Nonhuman Primates in the 21st Century* pp 191-214. Springer: New York, USA. http://dx.doi.org/10.1007/978-0-387-25640-5_11

Capitanio JP, Mendoza SP, Mason WA and Maninger N 2005 Rearing environment and hypothalamic-pituitary-adrenal regulation in young rhesus monkeys (*Macaca mulatta*). *Developmental Psychobiology 46*: 318-330. http://dx.doi.org/10.1002/dev.20067

Champoux M, Bennett A, Shannon C, Higley JD, Lesch KP and Suomi SJ 2002 Serotonin transporter gene polymorphism, differential early rearing, and behavior in rhesus monkey neonates. *Molecular Psychiatry 7*: 1058-1063. http://dx.doi.org/10.1038/sj.mp.4001157

Champoux M, Byrne E, DeLizio R and Suomi S 1992 Motherless mothers revisited: rhesus maternal behavior and rearing history. *Primates 33*: 251-255. http://dx.doi.org/10.1007/BF02382755

Chen G-L, Novak MA, Meyer JS, Kelly BJ, Vallender EJ and Miller GM 2010 TPH2 5'- and 3'-regulatory polymorphisms are differentially associated with HPA axis function and self-injurious behavior in rhesus monkeys. *Genes Brain and Behavior 9*: 335-347. http://dx.doi.org/10.1111/j.1601-183X.2010.00564.x

Clark AS 1993 Social rearing effects on HPA axis activity over early development and in response to stress in rhesus monkeys. *Developmental Psychobiology 26*: 433-446. http://dx.doi.org/10.1002 /dev.420260802

Crockett CM, Shimoji M and Bowden DM 2000 Behavior, appetite, and urinary cortisol responses by adult female pigtailed macaques to cage size, cage level, room change, and ketamine sedation. *American Journal of Primatology 52*: 63-80. http://dx.doi.org/10.1002/1098-2345(200010)52:2<63::AID-AJP1>3.0.CO;2-K

Dettling AC, Feldon J and Pryce CR 2002 Early deprivation and behavioral and physiological responses to social separation/novelty in the marmoset. *Pharmacology Biochemistry and Behavior 73*: 259-269. http://dx.doi.org/10.1016/S0091-3057(02)00785-2

Draper WA and Bernstein IS. 1963 Stereotyped behavior and cage size. *Perceptual and Motor Skills 16*: 231-234. http://dx.doi.org/10.2466/pms.1963.16.1.231

Ehardt CL 1988a Absence of strongly kin-preferential behavior by adult female sooty mangabeys (*Cercocebus atys*). *American Journal of Physical Anthropology 76*: 233-243. http://dx.doi.org/10.1002/ajpa.1330760212

Ehardt CL 1988b Affiliative behavior of adult female sooty mangabeys (*Cercocebus atys*). *American Journal of Primatology 15*: 115-127. http://dx.doi.org/10.1002/ajp.1350150205

Erwin J, Mitchell G and Maple T 1973 Abnormal behavior in non-isolate-reared rhesus monkeys. *Psychological Reports 33*: 515-523. http://dx.doi.org/10.2466/pr0.1973.33.2.515

Erwin J and Deni R 1979 Strangers in a strange land: abnormal behaviors or abnormal environment? In: Erwin J, Maple TL and Mitchell G (eds) *Captivity and Behavior, Primates in Breeding Colonies, Laboratories, and Zoos* pp 1-28. Van Nostrand Reinhold: New York, USA

Gottlieb DH, Capitanio JP and McCowan B 2013 Risk factors for stereotypic behavior and self-biting in rhesus macaques (*Macaca mulatta*): animal's history, current environment, and personality. *American Journal of Primatology 75*: 995-1008. http://dx.doi.org/10.1002/ajp.22161

Gust DA 1995 Moving up the dominance hierarchy in young sooty mangabeys. *Animal Behaviour 50*: 15-21. http://dx.doi.org/10.1006/anbe.1995.0216

Gust DA and Gordon TP 1991 Male age and reproductive behaviour in sooty mangabeys, *Cercocebus torquatus atys*. *Animal Behaviour 41*: 277-283. http://dx.doi.org/10.1016/S0003-3472(05)80479-8

Gust DA and Gordon TP 1993 Conflict resolution in sooty mangabeys. *Animal Behaviour 46*: 685-694. http://dx.doi.org/10.1006/anbe.1993.1245

Harlow HF and Harlow MK 1962 Social deprivation in monkeys. *Scientific American 207*: 136-146. http://dx.doi.org/10.1038/scientificamerican1162-136

Jorgensen MJ, Kinsey JH and Novak MA. 1998. Risk factors for self-injurious behavior in captive rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology 45*: 187 (Abstract)

Kalcher E, Franz C, Crailsheim K and Preuschoft S 2008 Differential onset of infantile deprivation produces distinctive long-term effects in adult ex-laboratory chimpanzees (*Pan troglodytes*). *Developmental Psychobiology 50*: 777-788. http://dx.doi.org/10.1002/dev.20330

Kalcher-Sommersguter E, Preuschoft S, Crailsheim K and Franz C 2011 Social competence of adult chimpanzees (*Pan troglodytes*) with severe deprivation history: I. An individual approach. *Developmental Psychology 47*: 77-90. http://dx.doi.org/10.1037/a0020783

Latham NR and Mason GJ 2008 Maternal deprivation and the development of stereotypic behavior. *Applied Animal Behavior Science 110*: 84-108. http://dx.doi.org/10.1016/j.applanim.2007.03.026

Lewis MH, Gluck JP, Petitto JM, Hensley LL and Ozer H 2000 Early social deprivation in nonhuman primates: long-term effects on survival and cell-mediated immunity. *Society of Biological Psychiatry 47*: 119-126. http://dx.doi.org/10.1016/S0006-3223(99)00238-3

Line SW, Morgan KN and Markowitz H 1991 Simple toys do not alter the behavior of aged rhesus monkeys. *Zoo Biology 10*: 473-484. http://dx.doi.org/10.1002/zoo.1430100606

Lubach GR and Coe CL 2006 Immunological consequences of nursery rearing. In: Sackett GP, Ruppenthal GC and Elias K (eds) *Nursery Rearing of Nonhuman Primates in the 21st Century*. pp 135-168. Springer: New York, USA. http://dx.doi.org/10.1007/978-0-387-25640-5_9

Lutz C, Well A and Novak M 2003 Stereotypic and self-injurious behavior in rhesus macaques: a survey and retrospective analysis of environment and early experience. *American Journal of Primatology 60*: 1-15. http://dx.doi.org/10.1002/ajp.10075

Lutz CK, Linsenbardt KA, Williams PC and Sharp RM 2012 Abnormal behavior in captive baboons (*Papio hamadryas* spp). *American Journal of Primatology 74(S1)*: 36 (Abstract)

Maki S, Fritz J and England N 1993 An assessment of early differential rearing conditions on later behavioral development in captive chimpanzees. *Infant Behavior and Development 16*: 373-381. http://dx.doi.org/10.1016/0163-6383(93)80042-7

Mason GJ 1991 Stereotypies: a critical review. *Animal Behaviour 41*: 1015-1037. http://dx.doi.org/10.1016/S0003-3472(05)80640-2

Miller G, Bendor J, Tiefenbacher S, Yang H, Novak MA and Madras BK 2004 A mu-opioid receptor single nucleotide polymorphism in rhesus monkey: association with stress response and aggression. *Molecular Psychiatry 9*: 99-108. http://dx.doi.org/10.1038/sj.mp.4001378

National Research Council 2011 *Guide for the Care and Use of Laboratory Animals, Eighth Edition*. The National Academies Press: Washington, DC, USA

Novak MA 2003 Self-injurious behavior in rhesus macaques: new insights into its etiology, physiology, and treatment. *American Journal of Primatology* 59: 3-19. http://dx.doi.org/10.1002/ajp.10063

Novak MA, Kinsey JH, Jorgensen MJ and Hazen TJ 1998 Effects of puzzle feeders on pathological behavior in individually housed rhesus monkeys. *American Journal of Primatology 46*: 213-227. http://dx.doi.org/10.1002/(SICI)1098-2345(1998)46:3<213::AID-AJP3>3.0.CO;2-L

Novak MA, Hamel AH, Kelly BJ, Dettmer AM and Meyer JS 2013 Stress, the HPA axis, and nonhuman primate well-being: a review. *Applied Animal Behavior Science 143*: 135-149. http://dx.doi.org/10.1016/j.applanim.2012.10.012

Pazol KA and Bloomsmith MA 1993 The development of stereotyped body rocking in chimpanzees (*Pan troglodytes*) reared in a variety of nursery settings. *Animal Welfare* 2: 113-129

Range F 2005 Female sooty mangabeys (*Cercocebus torquatus atys*) respond differently to males depending on the male's residence status-preliminary data. *American Journal of Primatology 65*: 327-333. http://dx.doi.org/10.1002/ajp.20119

Ridley RM and Baker HF 1982 Stereotypy in monkeys and humans. *Psychological Medicine 12*: 61-72. http://dx.doi.org/10.1017/S0033291700043294

Rommeck I, Anderson K, Heagerty A, Cameron A and McCowan, B 2009a Risk factors and remediation of self-injurious and self-abuse behavior in rhesus macaques. *Journal of Applied Animal Welfare Science 12*: 61-72. http://dx.doi.org/10.1080/10888700802536798

Rommeck I, Gottlieb DH, Strand SC and McCowan B 2009b The effects of four nursery rearing strategies on infant behavioral development in rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory Animal Science 48*: 395-401

Sánchez MM 2006 The impact of early adverse care on HPA axis development: nonhuman primate models. *Hormones and Behavior 50*: 623-631. http://dx.doi.org/10.1016/j.yhbeh.2 006.06.012

https://doi.org/10.7120/09627286.23.2.167 Published online by Cambridge University Press

Sánchez MM, Hearn EF, Do D, Rilling JK and Herndon JG 1998 Differential rearing affects corpus callosum size and cognitive function of rhesus monkeys. *Brain Research 812*: 38-49. http://dx.doi.org/10.1016/S0006-8993(98)00857-9

Seier J, de Villiers C, van Heerden J and Laubscher R 2011 The effect of housing and environmental enrichment on stereotyped behavior of adult vervet monkeys (*Chlorocebus aethiops*). *Lab Animal 40*: 218-224. http://dx.doi.org/10.1038/laban0711-218

Silvestri G, Paiardini M, Pandrea I, Lederman MM and Sodora DL 2007 Understanding the benign nature of SIV infection in natural hosts. *The Journal of Clinical Investigation 117*: 3148-3154. http://dx.doi.org/10.1172/JCI33034

Spinelli S, Chefer S, Suomi SJ, Higley JD, Barr CS and Stein E 2009 Early-life stress induces long-term morphologic changes in primate brain. *Archives of General Psychiatry 66*: 658-665. http://dx.doi.org/10.1001/archgenpsychiatry.2009.52

Spinelli S, Schwandt M, Lindell SG, Heilig M, Suomi SJ, Higley JD, Goldman D and Barr CS 2012 The serotonin transporter gene linked polymorphic region is associated with the behavioral response to repeated stress exposure in infant rhesus macaques. *Development and Psychopathology 24*: 157-165. http://dx.doi.org/10.1017/S0954579411000745

Tanimura Y, Yang MC and Lewis MH 2008 Procedural learning and cognitive flexibility in a mouse model of restricted, repetitive behavior. *Behavioral Brain Research 189*: 250-256. http://dx.doi.org/10.1016/j.bbr.2008.01.001

Tiefenbacher S, Marinus LM, Davenport MD, Poulioti AL, Kaufman M, Fahey MA, Novak MA and Meyers JS 2003 Evidence for endogenous opioid involvement in the expression of self-injurious behavior in rhesus monkeys. *American Journal of Primatology 60*: 103 (Abstract)

Tiefenbacher S, Novak M, Jorgensen, MJ and Meyer JS 2000 Physiological correlates of self-injurious behavior in captive, socially-reared rhesus monkeys. *Psychoneuroendocrinology 25*: 799-817. http://dx.doi.org/10.1016/S0306-4530(00)00027-5

Tiefenbacher S, Novak MA, Marinus LM, Chase WK, Miller JA and Meyer JS 2004 Altered hypothalamic-pituitary-adrenocortical function in rhesus monkeys (*Macaca mulatta*) with self-injurious behavior. *Psychoneuroendocrinology 29*: 501-515. http://dx.doi.org/10.1016/S0306-4530(03)00068-4

Tiefenbacher S, Novak MA, Lutz CK and Meyer JS 2005 The physiology and neurochemistry of self-injurious behavior: a nonhuman primate model. *Frontiers in Bioscience 10*: 1-11. http://dx.doi.org/10.2741/1500

Vandeleest JJ, McCowan B and Capitanio JP 2011 Early rearing interacts with temperament and housing to influence the risk for motor stereotypy in rhesus monkeys (*Macaca mulatta*). *Applied Animal Behavior Science 132*: 81-89. http://dx.doi.org/10.1016/j.applanim.2011.02.010

Walsh S, Bramblett CA and Alford PL 1982 A vocabulary of abnormal behaviors in restrictively reared chimpanzees. *American Journal of Primatology 3*: 315-319. http://dx.doi.org/10.1002/ajp.13 50030131