

## Experimentally evaluating the function of self-directed behaviour in two adult mandrills (*Mandrillus sphinx*)

A Leeds\*<sup>†‡</sup> and KE Lukas<sup>†‡</sup>

<sup>†</sup> Cleveland Metroparks Zoo, 3900 Wildlife Way, Cleveland, OH 44109, USA

<sup>‡</sup> Case Western Reserve University, 10900 Euclid Avenue, Cleveland, OH 44106, USA

\* Contact for correspondence and requests for reprints: cal@clevelandmetroparks.com

### Abstract

Given the difficulties of conducting regular endocrine and veterinary assessments of animals, behavioural observations are often the most commonly used tool to assess the welfare of animals in human care. Behavioural measures, inexpensive and convenient to collect, also have their challenges, such as ensuring the behaviours of interest are reliable indicators of an animal's internal state. Welfare assessments include both positive and negative indicators, and a commonly used indicator of negative welfare is self-directed behaviour (SDB). SDB has been described as a behavioural indicator of stress through observation and experimentation; however, this pattern is not universal despite assumptions otherwise. The purpose of this study was to experimentally evaluate the use of SDB as an indicator of negative welfare in mandrills (*Mandrillus sphinx*) with the goal of understanding the function of SDB in relation to stress. Using a touchscreen-mediated cognitive task, the mandrills were observed to self-scratch significantly more often during incorrect than correct trials; however, rates of SDB did not vary between increasingly difficult testing conditions. The mandrills had individual variation in their use of body-shakes and yawns under negative and positive conditions that mirror similar variation observed in other primates. This study provides experimental evidence that self-scratching in mandrills can be used as a behavioural indicator of anxiety and that welfare assessments for animals in human care need to account not only for species' differences, but also for individual differences.

**Keywords:** animal behaviour, animal welfare, mandrill, primate cognition, self-directed behaviour, zoo

### Introduction

Assessing animal welfare through behavioural observation is a common practice that relies upon the use of validated behavioural measures. Self-directed behaviour (SDB), which includes self-scratching, body-shaking and yawning, are common behaviours used in assessing the stress and, ultimately, welfare of primates in human care (Chelluri *et al* 2013; Kranendonk & Schippers 2014; Herrelko *et al* 2015). Stress is generally viewed as the perception of an uncontrollable and/or unpredictable stimulus that exceeds the immediate coping capacity of the individual (Koolhaas *et al* 2011). Primates have been observed to increase SDB in contexts associated with uncertainty and unpredictability, such as the proximity of a dominant individual (eg Castles *et al* 1999), following agonistic encounters that may result in further aggression (eg Romero *et al* 2009), and when the spatial density of social groupings increase (Cordoni & Palagi 2007; Ross *et al* 2010; Caperos *et al* 2011). Furthermore, long-tailed macaques (*Macaca fascicularis*) were observed to decrease SDB following the administration of anxiolytic (anti-anxiety) drugs and increase SDB following the administration of anxiogenic (anxiety-inducing) drugs (Schino *et al* 1996).

Given these findings, SDB has long been considered a universal behavioural indicator of anxiety (for a review, see Maestripieri *et al* 1992), and has been used in welfare evaluations of primates in human care (eg Chelluri *et al* 2013; Kranendonk & Schippers 2014; Herrelko *et al* 2015). However, several studies provide evidence that SDB may not be a universal indicator of stress in primates. Hamadryas baboons (*Papio hamadryas*) showed no change in self-scratching when confined to smaller enclosures, a common experimental test of anxiety (Judge *et al* 2006). In addition, salivary cortisol did not correlate with self-scratching in the same species (Pearson *et al* 2015) or in olive baboons (*Papio hamadryas anubis*; Higham *et al* 2009). Marmosets (*Callithrix jacchus*) similarly had no change in self-scratching when administered an anxiogenic drug, held in isolation, or exposed to an artificial predator (Kato *et al* 2014) and, interestingly, were observed to have increased self-scratching rates during play (Neal & Caine 2016). However, another marmoset species (*Callithrix penicillata*) exhibited decreased frequency of self-scratching in the presence of an artificial predator when administered an anxiolytic drug (Barros *et al* 2000). An additional factor that is rarely considered is the presence of ectoparasites. A recent study of wild Japanese macaques (*Macaca fuscata*) found

that lice density was a better predictor of self-scratching than social stress (Duboscq *et al* 2016), though this is likely not a common factor for primates in human care. Given the mixed observations of SDB in primates and the limited number of controlled experimental studies, researchers interested in using SDB as a behavioural measure of stress should ensure that SDB has been appropriately validated in their respective study species prior to use.

Mandrills (*Mandrillus sphinx*) are a prominent species in zoos, yet have received limited empirical evaluation of their behaviour and welfare. Similar to other species, there appears to be an unclear relationship between stress and SDB as self-scratching in mandrills has been observed to both increase (Schino & Marini 2012) and remain unchanged following social stress (Peignot *et al* 2004). In addition, body-shaking and yawning have not been evaluated in mandrills though they are included in behavioural studies (Setchell & Wickings 2005). Cognitive challenges, as part of ongoing cognitive studies, have been used to validate the function of SDB in primate species. Chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla gorilla*) have been shown to increase their self-scratching following an incorrect choice compared to a correct choice during a touchscreen-mediated task (Wagner *et al* 2016). In addition, changes in task difficulty have been shown to affect SDB in chimpanzees (Leavens *et al* 2001), orangutans (*Pongo pygmaeus*; Elder & Menzel 2001), lion-tailed macaques (*Macaca silenus*), squirrel monkeys (*Saimiri sciureus*) and capuchin monkeys (*Cebus paella*; Judge *et al* 2011). At Cleveland Metroparks Zoo, USA, a bachelor mandrill group was the focus of a long-term behavioural monitoring and cognition study. The purpose of this analysis was to test the function of SDB in the mandrills using a touchscreen-mediated cognitive task, similar to previous research on apes (Wagner *et al* 2016). Specifically, this study evaluated the use of self-scratching, body-shaking and yawning, three common mandrill SDBs, across three levels of task difficulty and between correct and incorrect trials. It was hypothesised that if SDB is a behavioural indicator of stress in mandrills, the mandrills' rate of SDB would increase with task difficulty and that the rate would be greater during incorrect compared to correct trials.

## Materials and methods

### Study animals

The methodology of this study was approved by the Animal Care and Use Committee of Cleveland Metroparks Zoo (CMZ). Participation by the subjects was voluntary. Subjects were two adult male mandrills (M1, eight years; M2, 13.5 years) living as a bachelor group at CMZ, Cleveland, OH, USA. Both males had lived together for approximately three years at the time of the study. Both subjects had been participating in touchscreen cognition testing sessions for approximately 18 months prior to the start of the study.

### Testing and analysis

Testing occurred while subjects were on exhibit between 0800 and 0900h, three days per week. Data for this study were collected between February and August 2016. Using a random number generator, 33 days were randomly selected and testing sessions for that day were filmed using an iPad mini 2 (Apple, Cupertino, CA, USA) for later analysis. Tests were conducted using a 32-inch LCD touchmonitor (Elo Touchsystems, Menlo Park, CA, USA). The screen was operated by AL who stood next to the screen and provided food rewards to the mandrills following successfully completed trials. The dominant male, M1, underwent testing with M2 present. Due to the dominance structure of the group (M1 dominant to M2), M2 tested with M1 shifted into an adjacent room or transfer stairwell to minimise any potential aggressive or displacement behaviour towards M2 during testing. M1's shifting was voluntary and rewarded with food items from his scheduled diet. The males had auditory and olfactory access to each other when M1 was in the stairwell and visual access when in the adjacent room. Separation lasted no more than 10 min. Separation training is a routine aspect of zoo animal care, and helps facilitate a variety of management practices, including positive reinforcement training and ensuring that special diet items or medicines are consumed by the intended individual. At CMZ, the mandrills separate voluntarily for regular training and husbandry purposes as part of their daily routine.

The mandrills were tested using a list sequencing task. In each trial, the subjects were asked to select symbols on the screen in a consistent, pre-determined order. If a symbol was selected out of order, a 'buzz' tone was played and the screen turned white for 5 s. If a trial was completed successfully — that is all symbols were selected in the correct order — the mandrill was provided a small food reward which was preceded by a 'ding' tone. Each testing session consisted of 40 trials. The subjects completed three task difficulties. The easy condition was a two-item list (50% probability of success), the medium condition a three-item list (16.5% probability of success) and the hard condition a four-item list (4.1% probability of success). Subjects completed ten testing sessions for each difficulty level (30 total sessions per mandrill).

All occurrence sampling was used to record the rates of SDB during each trial from the recordings. The SDB coded were:

- Self-scratch: Any self-touching involving the ends of the digits, including both gentle and rough contact (Baker & Aureli 1997; Leavens *et al* 2001). Individual scratches were noted to begin with the movement of hand or foot in a single direction in contact with a continuous body part and ending when contact with the body ended and/or when the direction of the scratch changed (Wagner *et al* 2016).
- Body-shake: A quick side-to-side shaking of the whole body (Schino *et al* 1996).
- Yawn: A broad opening of the mouth along with a long inspiration followed by a brief expiration (Provine *et al* 1987).

To control for variation in trial length, the rate of each SDB per second per trial was calculated by dividing the number of SDBs per trial by trial length in seconds (for mean trial length by subject and testing level, see Table 1). The average rate across all trials per testing session was then calculated by summing the values and dividing by the number of trials per session. Due to the small sample size, analysis was conducted for each subject separately using non-parametric repeated measures tests. The test statistic was generated using a Monte Carlo sampling method (10,000 permutations) per the recommendations of Colegrave *et al* (2006) for small sample size studies. *Post hoc* comparisons used a Bonferroni correction ( $\alpha = 0.017$ ). All statistics were conducted with SPSS V.24 (IBM, Chicago, IL, USA).

## Results

To confirm that testing difficulty differed across conditions, subject performance (percentage of successfully completed trials) was compared across each difficulty level using Friedman's ANOVA (Table 1). There was a significant difference in performance across task difficulties. *Post hoc* comparisons using Wilcoxon signed-rank tests revealed that increasing task difficulty resulted in a decrease in performance. The rate of SDB for each subject was then compared across task difficulty using Friedman's ANOVA with Wilcoxon signed-rank tests for *post hoc* comparisons. SDB did not differ across testing difficulty for either subject (Table 2). Given this, the subsequent analysis combined data from the three task difficulties. The rate of self-scratching, yawning and body-shaking were then compared between correct and incorrect trials using Wilcoxon signed-rank tests (Figure 1). For both subjects, self-scratching occurred significantly more during incorrect than correct trials. M1 yawned significantly more during incorrect trials; however, M2 was never observed to yawn during testing. M1's rate of body-shaking did not differ between conditions but M2's rate was significantly more frequent during incorrect trials.

## Discussion

The purpose of this study was to test experimentally the function of SDB in mandrills using methods that have been applied successfully to the study of other primate species. The first hypothesis predicted that SDB would increase with task difficulty. It was found that task difficulty did not affect the rate of SDB. This result is surprising given the difference in probability of successfully completing a trial (easy = 50%, medium = 16.5%, hard = 4.1%), however, the same outcome was reported in a study of gorillas and chimpanzees participating in the same cognitive task as the present study (Wagner *et al* 2016). This may indicate that the rate of SDB does not correlate with perceived stress of the stimuli but rather that a minimum threshold of perceived stress elicits SDB. Alternatively, although each task was significantly more challenging, the mandrills' might not have perceived the tasks as being more challenging, despite the difference in the percentage of correct and incorrect trials. An additional variable may be the reward system. The

**Table 1** Statistical analysis of mandrill performance across task difficulty.

Factor	Subject	
	M1	M2
<i>Mean (<math>\pm</math> SEM) trial length (s)</i>		
Two-item list	4.62 ( $\pm$ 0.12)	5.35 ( $\pm$ 0.08)
Three-item list	5.66 ( $\pm$ 0.12)	6.85 ( $\pm$ 0.15)
Four-item list	5.89 ( $\pm$ 0.06)	7.21 ( $\pm$ 0.09)
<i>Mean (<math>\pm</math> SEM) percentage of correct trials</i>		
Two-item list	87.75 ( $\pm$ 1.74)	89.00 ( $\pm$ 1.63)
Three-item list	72.25 ( $\pm$ 2.65)	68.25 ( $\pm$ 2.84)
Four-item list	47.75 ( $\pm$ 3.42)	45.50 ( $\pm$ 2.52)
<i>Friedman's ANOVA</i>		
$\chi^2$	18.2	20.0
df	2	2
P-value	< 0.001*	< 0.001*
<i>Post hoc comparisons</i>		
<i>List comparison (2 to 3)</i>		
z-value	-2.81	2.81
P-value	0.002**	0.002**
<i>List comparison (3 to 4)</i>		
z-value	-2.66	-2.81
P-value	0.008**	0.001**

\* Statistically significant at  $P < 0.05$ ;

\*\* *Post hoc* comparisons statistically significant at  $P < 0.025$ .

task itself may be perceived by the mandrills differently at each testing level, but the perceived stress from the cognitive challenge may be less than the perceived stress of not receiving a reward, leaving the differences between testing difficulties to be a non-factor. Further study is needed to better understand the relationship between rate of SDB and perceived intensity of a stressor, as well as how testing methodology may affect the behaviour of participants.

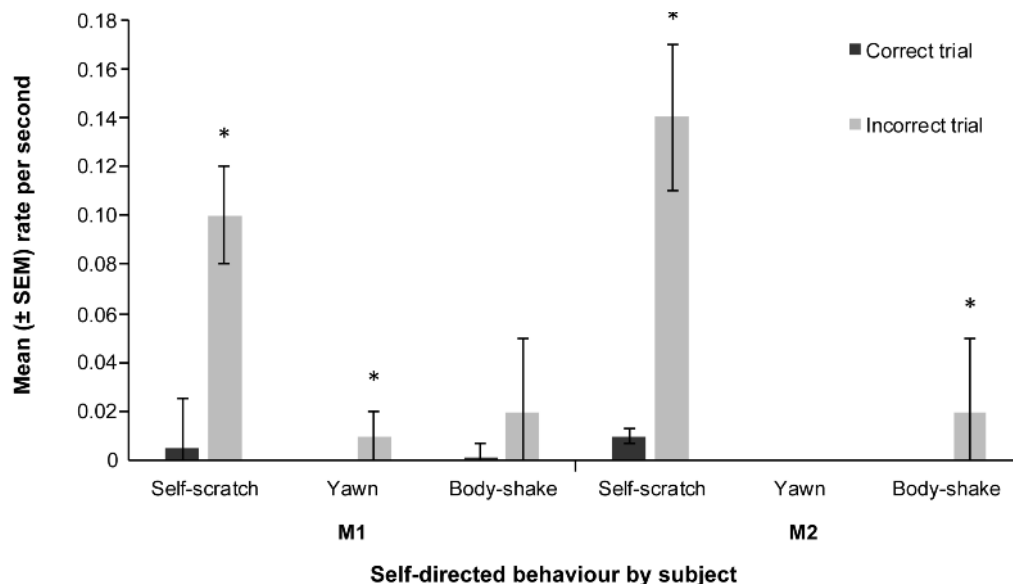
The second hypothesis predicted that SDB would be more frequent during incorrect compared to correct trials. Both subjects' self-scratching increased significantly during incorrect compared to correct trials, similar to previous evaluations of chimpanzees and gorillas (Yamanashi & Matsuzawa 2010; Wagner *et al* 2016). This provides some evidence that in mandrills, self-scratching may be a behavioural indicator of stress, depending on the context of the behaviour. However, it should be noted that this study had a limited sample size and may not have population-level significance. Further experimental evaluation of this kind will require multi-institutional collaboration as these two

**Table 2** Statistical analysis of mandrill self-directed behaviour across task difficulty.

Subject	SDB	Mean ( $\pm$ SEM) two-item rate per second	Mean ( $\pm$ SEM) three-item rate per second	Mean ( $\pm$ SEM) four-item rate per second	$\chi^2$	df	P-value
M1	Self-scratch	0.03 ( $\pm$ 0.06)	0.02 ( $\pm$ 0.05)	0.02 ( $\pm$ 0.05)	1.24	2	0.565
	Yawn	0.0004 ( $\pm$ 0.003)	0.002 ( $\pm$ 0.005)	0.005 ( $\pm$ 0.009)	6.00	2	0.046 <sup>†</sup>
	Body-shake	0.00 ( $\pm$ 0.0)	0.006 ( $\pm$ 0.02)	0.009 ( $\pm$ 0.03)	3.50	2	0.256
M2	Self-scratch	0.04 ( $\pm$ 0.07)	0.05 ( $\pm$ 0.07)	0.05 ( $\pm$ 0.07)	0.60	2	0.827
	Yawn	0.00 ( $\pm$ 0.0)	0.00 ( $\pm$ 0.0)	0.00 ( $\pm$ 0.0)	0.00	2	1.000
	Body-shake	0.00 ( $\pm$ 0.0)	0.003 ( $\pm$ 0.02)	0.015 ( $\pm$ 0.04)	9.50	2	0.012 <sup>‡</sup>

<sup>†</sup> Post hoc comparisons with Bonferroni correction ( $P = 0.017$ ) were non-significant (2 to 3,  $z = -1.83$ ;  $P = 0.68$ ; 3 to 4,  $z = -0.98$ ;  $P = 0.33$ ; 2 to 4,  $z = -2.10$ ;  $P = 0.035$ ).

<sup>‡</sup> Post hoc comparisons with Bonferroni correction ( $P = 0.017$ ) were non-significant (2 to 3,  $z = -1.00$ ;  $P = 0.32$ ; 3 to 4,  $z = -2.03$ ;  $P = 0.042$ ; 2 to 4,  $z = -2.03$ ;  $P = 0.042$ ).

**Figure 1**

The mean rate per second of self-directed behaviour by subject during correct and incorrect trials (asterisks note significance). Self-scratching was significantly more frequent during incorrect than correct trials for both subjects (M1,  $z = -3.15$ ;  $P = 0.001$ ; M2,  $z = -4.167$ ;  $P < 0.001$ ). M1 had a significant increase in the rate of yawns during incorrect trials ( $z = -3.06$ ;  $P < 0.001$ ) but M2's yawning did not differ ( $z = 0.00$ ;  $P = 1.00$ ). M1 had no difference in his rate of body-shakes between trials ( $z = -1.36$ ;  $P = 0.214$ ) but M2 body shook significantly more frequently during incorrect trials ( $z = -2.20$ ;  $P = 0.032$ ).

mandrills are, to the authors' knowledge, the only mandrills participating in touchscreen-mediated cognitive testing in North America. This also provides evidence that self-scratching is not an indicator of positive arousal in mandrills, which has been reported in other species (Neal & Caine 2016), given that there was a significantly lower frequency of self-scratching during correct trials where a food reward was provided.

This study found individual differences in the use of body-shaking and yawning. Studies of primate SDB have often focused on free-living or laboratory populations and thus have reported data from large sample sizes. Unfortunately, due to these large sample sizes, individual variation in

SDB is not often reported. Interestingly, Yamanashi and Matsuzawa (2010) found similar individual variation in self-scratching by chimpanzees participating in cognitive tests, and in a recent review of physiological stress responses of vertebrates, Cockrem (2013) points to the necessity of assessing individual differences in stress responses. Future research, specifically research focused on individual animal welfare, should closely examine individual variation to ensure the behaviours recorded are relevant to each individual. In addition, although body-shaking and yawning are often described collectively in the same context as self-scratching, they have been evaluated individually significantly less often (Baker &



Aureli 1997; Leone *et al* 2014). More experimental studies of body-shaking and yawning, with larger samples sizes, are needed to better understand these behaviours in the context of stress and animal welfare.

Although individuals will respond to stressors in their own way (Cockrem 2013), when properly validated, the measurement of SDB can serve as a useful indicator that an individual is experiencing stress. From an applied perspective, primate caregivers should be cognisant of contexts in which SDB increases. Acute episodes of SDB may indicate successful coping for short-term stress and thus not represent a welfare concern. Long-term episodes, however, may indicate a welfare concern for that individual. That said, SDB is only one behavioural indicator of stress. Similar to the manner in which this study found individual variation in the use of specific SDB, primates may also use other behaviours as an expression of stress (eg stereotypic behaviour, increased aggression, decreased activity). Proper monitoring and assessment will allow caregivers to identify which behaviours are significant for each individual in their care.

### Animal welfare implications and conclusion

This study provides evidence that self-scratching is a behavioural expression of stress in mandrills, which corroborates data on mandrill self-scratching following agonistic interactions (Schino & Marini 2012). However, further evaluation is needed to better understand stress thresholds that elicit this behaviour. The use of body-shaking and yawning was found to vary by individual. Studies often group individual SDBs together for analysis but this study provides evidence that individual SDB expression may vary and each behaviour should be analysed separately. This finding also supports the need for an individual-based approach to animal welfare research. Lastly, as the study of experimental primate cognition continues to expand in zoos, the opportunity to validate behavioural indicators of stress in novel species increases, the results of which will further inform behaviour-based welfare studies.

### Acknowledgements

The authors would like to acknowledge Avery Zhou, Claire Thiele, Caitlin Gaffney, Julie Good, Dr Elena Less and Tad Schoffner for their assistance with this project. The authors would also like to thank Laura Bernstein-Kurtycz and two anonymous reviewers for providing helpful feedback on this manuscript. In addition, the authors are grateful to Dr Christopher Kuhar and the Cleveland Zoological Society for supporting the mandrill research programme at Cleveland Metroparks Zoo and to Dr Steve Ross for providing the cognition software used in this study.

### References

- Baker KC and Aureli F** 1997 Behavioural indicators of anxiety: An empirical test in chimpanzees. *Behaviour* 134: 1031-1050. <https://doi.org/10.1163/156853997X00386>
- Barros M, Boere V, Huston JP and Tomaz C** 2000 Measuring fear and anxiety in the marmoset (*Callithrix penicillata*) with a novel predator confrontation model: Effects of diazepam. *Behavioural Brain Research* 108: 205-211. [https://doi.org/10.1016/S0166-4328\(99\)00153-9](https://doi.org/10.1016/S0166-4328(99)00153-9)
- Caperos JM, Sanchez S, Palaez F, Fidalgo A and Morcillo A** 2011 The effect of crowding on the social behavior of the cooperatively breeding cotton-top tamarins (*Saguinus oedipus*). *International Journal of Primatology* 32: 1179-1189. <https://doi.org/10.1007/s10764-011-9534-7>
- Castles DL, Whiten A and Aureli F** 1999 Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour* 58: 1207-1215. <https://doi.org/10.1006/anbe.1999.1250>
- Chelluri GI, Ross SR and Wagner KE** 2013 Behavioral correlates and welfare implications of informal interactions between caretakers and zoo-housed chimpanzees and gorillas. *Applied Animal Behaviour Science* 147: 306-315. <https://doi.org/10.1016/j.applanim.2012.06.008>
- Cockrem JF** 2013 Individual variation in glucocorticoid stress responses in animals. *General and Comparative Endocrinology* 181: 45-58. <https://doi.org/10.1016/j.ygcen.2012.11.025>
- Colgrave N, Engel J and Plowman AB** 2006 Randomization tests. In: Plowman AB (ed) *Zoo Research Guidelines: Statistics for Typical Zoo Datasets* pp 7-16. BIAZA: London, UK
- Cordoni G and Palagi E** 2007 Response of captive lowland gorillas (*Gorilla gorilla gorilla*) to different housing conditions: Testing the aggression-density and coping models. *Journal of Comparative Psychology* 121: 171-180. <https://doi.org/10.1037/0735-7036.121.2.171>
- Duboscq J, Romano V, Sueur C and MacIntosh AJJ** 2016 Scratch that itch: Revisiting links between self-directed behaviour and parasitological, social and environmental factors in a free-ranging primate. *Royal Society Open Science* 3: 160571. <https://doi.org/10.1098/rsos.160571>
- Elder CM and Menzel CR** 2001 Dissociation of cortisol and behavioral indicators of stress in an orangutan (*Pongo pygmaeus*) during a computerized task. *Primates* 42: 345-357. <https://doi.org/10.1007/BF02629625>
- Herrelko ES, Buchanan-Smith HM and Vick SJ** 2015 Perception of available space during chimpanzee introductions: Number of accessible areas is more important than enclosure size. *Zoo Biology* 34: 397-405. <https://doi.org/10.1002/zoo.21234>
- Higham JP, Maclarnon AM, Heistermann M, Ross C and Semple S** 2009 Rates of self-directed behaviour and faecal glucocorticoid levels are not correlated in female wild olive baboons (*Papio hamadryas anubis*). *Stress* 12: 526-532. <https://doi.org/10.3109/10253890902756565>

- Judge PG, Evans DW, Schroepfer KK and Gross AC** 2011 Perseveration on a reversal-learning task correlates with rates of self-directed behavior in nonhuman primates. *Behavioural Brain Research* 222: 57-65. <https://doi.org/10.1016/j.bbr.2011.03.016>
- Judge PG, Griffaton NS and Fincke AM** 2006 Conflict management by hamadryas baboons (*Papio hamadryas hamadryas*) during crowding: A tension-reduction strategy. *American Journal of Primatology* 68: 993-1006. <https://doi.org/10.1002/ajp.20290>
- Kato Y, Gokan H, Oh-Nishi A, Suhara T, Watanabe S and Minamimoto T** 2014 Vocalizations associated with anxiety and fear in the common marmoset (*Callithrix jacchus*). *Behavioural Brain Research* 275: 43-52. <https://doi.org/10.1016/j.bbr.2014.08.047>
- Koolhaas JM, Bartolomucci A, Buwalda B, de Boer SF, Flügge G, Korte SM, Meerlo P, Murison R, Olivier B, Palanza P, Richter-Levin G, Sgoifo A, Steimer T, Stiedl O, van Dijk G, Wöhr M and Fuchs E** 2011 Stress revisited: A critical evaluation of the stress concept. *Neuroscience and Biobehavioral Reviews* 35: 1291-1301. <https://doi.org/10.1016/j.neubiorev.2011.02.003>
- Kranendonk G and Schippers EP** 2014 A pilot study on the effects of a change in behavioural management on the behaviour of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science* 160: 127-137. <https://doi.org/10.1016/j.applanim.2014.09.008>
- Leavens DA, Aureli F, Hopkins WD and Hyatt CW** 2001 Effects of cognitive challenges on self-directed behaviors by chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 55: 1-14. <https://doi.org/10.1002/ajp.1034>
- Leone A, Ferrari PF and Palagi E** 2014 Different yawns, different functions? Testing social hypotheses on spontaneous yawning in *Theropithecus gelada*. *Science Reports* 4: 4010. <https://doi.org/10.1038/srep04010>
- Maestripieri D, Schino G, Aureli F and Troisi A** 1992 A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour* 44: 967-979. [https://doi.org/10.1016/S0003-3472\(05\)80592-5](https://doi.org/10.1016/S0003-3472(05)80592-5)
- Neal SJ and Caine NG** 2016 Scratching under positive and negative arousal in common marmosets (*Callithrix jacchus*). *American Journal of Primatology* 78: 216-226. <https://doi.org/10.1002/ajp.22498>
- Pearson BL, Reeder DM and Judge PG** 2015 Crowding increases salivary cortisol but not self-directed behavior in captive baboons. *American Journal of Primatology* 77: 462-467. <https://doi.org/10.1002/ajp.22363>
- Peignot P, Jankowski F and Anderson JR** 2004 On self-scratching in captive mandrills (*Mandrillus sphinx*). *Folia Primatologica* 75: 160-164. <https://doi.org/10.1159/000078307>
- Provine RR, Hamernik HB and Curchack BC** 1987 Yawning: Relation to sleeping and stretching in humans. *Ethology* 76: 152-160. <https://doi.org/10.1111/j.1439-0310.1987.tb00680.x>
- Romero T, Colmenares F and Aureli F** 2009 Testing the function of reconciliation and third-party affiliation in hamadryas baboons (*Papio hamadryas hamadryas*). *American Journal of Primatology* 71: 60-69. <https://doi.org/10.1002/ajp.20619>
- Ross SR, Wagner KE, Schapiro SJ and Hau J** 2010 Ape behavior in two alternating environments: Comparing exhibit and short-term holding areas. *American Journal of Primatology* 72: 951-959. <https://doi.org/10.1002/ajp.20857>
- Schino G and Marini C** 2012 Self-protective function of post-conflict bystander affiliation in mandrills. *PLoS One* 7: e38936. <https://doi.org/10.1371/journal.pone.0038936>
- Schino G, Perretta G, Taglioni AM, Monaco V and Troisi A** 1996 Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety* 2: 186-191. [https://doi.org/10.1002/\(SICI\)1522-7154\(1996\)2:4<186::AID-ANX15>3.0.CO;2-M](https://doi.org/10.1002/(SICI)1522-7154(1996)2:4<186::AID-ANX15>3.0.CO;2-M)
- Setchell JM and Wickings J** 2005 Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology* 111: 25-50. <https://doi.org/10.1111/j.1439-0310.2004.01054.x>
- Wagner KE, Hopper LM and Ross SR** 2016 Asymmetries in the production of self-directed behavior by chimpanzees and gorillas during a computerized cognitive test. *Animal Cognition* 19: 343-350. <https://doi.org/10.1007/s10071-015-0937-2>
- Yamanashi Y and Matsuzawa T** 2010 Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: Individual differences in self-directed behaviours during cognitive tasks. *Animal Welfare* 19: 25-30