

Research article

Personality and social dynamics of zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*)

Elena Račevska, Catherine M. Hill

Anthropology Centre for Conservation, Environment and Development, Department of Social Sciences, Oxford Brookes University, Oxford, UK
Correspondance: Elena Račevska; elenaracevska@gmail.com

Keywords:

animal behaviour, ape, captive management, Gorilla Behaviour Index, primate, social network.

Article history:

Received: 13 November 2016
Accepted: 4 May 2017
Published online: 31 July 2017

Abstract

Western lowland gorillas (*Gorilla gorilla gorilla*) are among the most studied nonhuman primates. However, managing them in captivity is not without its challenges. Understanding individual differences between gorillas, as well as differences in group dynamics, may be of high value for more efficient captive management. The capacity to predict behaviour may be especially useful, particularly in terms of affiliative and aggressive behaviours. For these reasons, we designed a brief study that investigates the relationship between gorilla personality and social dynamics. Our study was conducted in Paignton Zoo Environmental Park (UK), in May 2015. Behavioural observations were carried out on an all-male gorilla group, comprising one silverback and four maturing blackbacks. Behaviour was recorded using scan sampling, with an instantaneous recording technique. Simultaneously, we used all occurrence sampling to record social behaviours of interest: affiliative behaviour (social resting, social playing) and agonistic behaviour (displacement, aggressive behaviour), with the initiator and the recipient recorded for each event. Additionally, the main gorilla keeper rated each gorilla on the Gorilla Behavior Index (GBI), a personality assessment instrument that identifies four personality factors - Extroverted, Dominant, Fearful, and Understanding. Gorillas with higher scores on the Extroverted factor exhibited higher proportions of social behaviour in their activity budgets, and were more likely to be chosen to rest near. Individuals with higher Dominant scores were less likely to be displaced, while higher Understanding scores were correlated with a lower likelihood of initiating aggressive interactions, and a higher proportion of solitary behaviour. To better understand the relationship between gorilla personality and behaviour, we recommend the use of a hierarchical approach to studying personality. We anticipate that a higher level of specificity will enable more accurate predictions of behaviour, thereby providing a useful tool for gorilla captive management.

Introduction

Gorillas (*Gorilla spp.*) are among the most studied primate taxa in terms of ecology, social structure, and behaviour (Tutin 2003). However, despite considerable available information, gorilla captive management can be challenging. Even in cases whereby conditions in captivity adhere to the known requirements of gorilla behavioural ecology, not all arising issues, or their solutions, are universally applicable to the captive population. Information on specific group idiosyncrasies, as well as knowledge of individual animals, is necessary for improving captive management.

Gorillas occur in a variety of social arrangements. Wild gorillas live in structurally diverse groups, from multi-female or multi-male groups, to all-male bachelor groups and solitary males (Watts 2003). However, captive gorilla groups are often restricted in size and structure by limitations in space and resources. All-male gorilla groups are often formed in captivity as a way of housing surplus males (Harcourt 1988). These groups are typically established while the males are still young, as is the case in the wild (Robbins et al. 2004). This

allows individuals to more easily form affiliative relationships with others. Aggressive behaviours are generally rare in groups assembled this way (Stoinski et al. 2004b), but tend to be common in groups formed by grouping maturing males with a silverback (Stoinski et al. 2004a).

Individual animals often behave in ways that distinguish them from others of their species. When such differences are consistent over time, they can be referred to as personalities (Lowe and Bradshaw 2001). Personality research of captive animals holds great potential as a management tool. Most studies of nonhuman animal personality are, just as those carried out on human participants, based on trait theory. Also known as dispositional theory, trait theory postulates that behaviour exhibits a certain degree of consistency over time and that personality is stable across situations (Pervin 1980; for more information on cross-situational trait consistency and within-person variability please refer to Pervin 1994; Fleeson 2004). The personality model most widely used to describe human personality is the Five-Factor Model (John et al. 1994). It proposes five broad personality factors, bipolar in their nature: Neuroticism, Agreeableness, Extraversion, Openness,

Table 1. Demographic characteristics of the study group of western lowland gorillas (N=5).

	Gorilla 1	Gorilla 2	Gorilla 3	Gorilla 4	Gorilla 5
Name	Pertinax	Kivu	Kiondo	N'Dowe	Matadi
Studbook ID	0792	1707	1706	1746	1745
Gender	Male	Male	Male	Male	Male
Born	13 April 1982	27 November 2002	11 October 2002	22 September 2003	23 March 2003
Rearing history	Hand-reared	Hand-reared	Hand-reared	Hand-reared	Parent-reared
Arrived at the zoo	1997	2007	2007	2008	2010
Group status	Current silverback	Blackback	Taking over as silverback	Blackback	Blackback
Family relations		Half-brother to Gorilla 4	Full brother to Gorilla 4	Full brother to Gorilla 3; Half-brother to Gorilla 2	

and Conscientiousness. Nonhuman animal personality literature suggests that three of the factors (Extraversion, Neuroticism, and Agreeableness) hold across most studies (Gosling and John 1999).

Gold and Maple (1994) created the “Gorilla Behaviour Index” (GBI), a personality inventory that is a modified version of the inventory developed by Stevenson-Hinde and Zunz (1978). It identifies four personality factors: Extroverted, Dominant, Fearful, and Understanding. Three of those are relatable to factors proposed by the Five-Factor Model for humans: Extroverted to Extraversion, Fearful to Neuroticism, and Understanding to Agreeableness (Gosling and John 1999). The factor Dominant is without a human counterpart at the factor-level, but corresponds to the Assertiveness facet of Extraversion (Goldberg 1999).

Sociality in nonhuman animals is a subject that raises interest beyond that of animal behaviour research. This is especially true when it comes to nonhuman primates. Their social networks can be described as assortative, meaning that individuals preferentially connect to others of the same class (Brent et al. 2011). Age and sex often determine the frequency and quality of interactions, and time spent together can be used to distinguish “bonded” and “not-bonded” pairs. Wild gorillas often live in large groups comprising three to 42 members (Gold 1997a), while group size in captivity typically ranges between two and 10 individuals, with an average of 4.45 (Gold 1997b). Gorilla social structure seems to be constructed upon a few strong to moderate ties and many additional weak ties (Maryanski 1987). The strongest bond is between a silverback and resident females, while a silverback’s ties to blackback males are typically weak, as are the ties between blackbacks. Cliques are rare and often short-lived, but gorilla groups are, nevertheless, stable. Gorillas are believed to lead “individual-centered lives” (Maryanski 1987), and social interactions are not densely interwoven.

Previous studies have revealed correlations between primate personality and behaviour (e.g. Capitanio 1999; Pederson et al. 2005). The aims of the present study were to examine gorilla personality and social dynamics, and the relationship between them.

Materials and methods

We conducted our research in Paignton Zoo Environmental Park, Paignton, UK, in May 2015. The observed western lowland gorillas (*Gorilla gorilla gorilla*) belonged to an all-male group comprising five males: one silverback and four blackbacks. They were housed in an indoor-outdoor enclosure, and allowed to move freely between the two parts during the day. There was an additional, off-

show part of the enclosure, consisting of five dens in which each of the gorillas was housed during the night. Gorillas were fed an all-vegetable diet four times a day. We obtained their demographic information from the keepers and further supplemented it from the gorilla studbook (Dewarwildlife 2015) (Table 1). We received ethics approval from the Faculty of Humanities and Social Sciences, Oxford Brookes University, prior to beginning data collection. All actions were carried out in compliance with the International Primatological Society (IPS) Guidelines for the Use of Nonhuman Primates in Research.

We collected behavioural observations for each of the five gorillas for 25 consecutive days. We observed them twice a day in bouts of two hours, one in the morning and one in the afternoon, with a two-hour break between the observation sessions. We used scan sampling with instantaneous recording at five-minute intervals, and collected a total of 520 hours of observations (104 hours for each individual), totalling 6,250 observations (1,250 observations per gorilla). We scored gorilla behaviour using an ethogram (Supplement 1), which we developed on the basis of previous gorilla behaviour research (Ogden et al. 1991).

Alongside behavioural observations, we recorded the group social dynamics. We were interested in the following behaviours: 1) social resting (sitting or lying in direct proximity to another gorilla); 2) social playing (chasing, slapping or wrestling); 3) displacement (causing another gorilla to change its location by moving towards it); and 4) aggressive behaviour (any aggressive display directed towards another gorilla (i.e. slapping, poking, elbowing, hair pulling, pushing, shoving, or wrestling when not in a play or sexual context). Using all occurrence sampling, we registered every incidence of these behaviours upon their every manifestation. We also documented the initiator and the recipient.

In order to maximise the validity of personality ratings, we asked the main gorilla keeper (the keeper who, at the time of data collection, had the highest frequency of working at the section, as well as participation in and frequency of feeding and training) to rate each gorilla using the GBI (Gold and Maple 1994). The GBI is a personality assessment instrument consisting of 25 behaviourally based adjectives (Supplement 2). We left out one of the items (motherly) due to its representation of a female-exclusive trait, thus being irrelevant in the context of an all-male group. The scale identifies four personality factors: Extroverted, Dominant, Fearful, and Understanding, and has previously been used in the construction of personality profiles, utilised to aid management decisions for captive western lowland gorillas.

Each of the GBI items was presented with a scale ranging from 1 (“The item is weakly represented, or it is not present at all”) to 5 (“The item is very strong and conspicuous, approaching the

extreme"). To enable cross-study comparisons, we calculated factor loadings in the same way as in previous studies (Gold and Maple 1994; Kuhar et al. 2006): adjectives with a positive (+) loading were added, while those with a negative (-) loading were subtracted (Supplement 3). We divided the total sum by the total number of adjectives within each factor.

We analysed behavioural and personality data in SPSS 17.0 (SPSS Inc., 2008). We computed the correlations between personality factors and behaviours within the social network using randomisation tests in R, Package "coin" (Hothorn et al. 2006).

Results

Behavioural observations

We observed gorillas performing 18 behaviours. We subtracted the time each animal spent out of sight prior to the analyses. To allow easier comparisons of behavioural data with those obtained from other instruments, we assigned the observed behaviours to nine categories: 1) passive solitary (sitting, lying, standing still, self-grooming, elimination); 2) active solitary (terrestrial movement, locomotor play, object play); 3) passive social (social resting, looking at other gorillas); 4) active social (social playing); 5) feeding (feeding, drinking, foraging); 6) aggressive; 7) abnormal (thumb-sucking, hair-plucking, homosexual behaviour, coprophagy); 8) keeper-directed (looking at keeper); and 9) visitor-directed (looking at visitors). Gorilla activity budgets are shown as percentages of time each animal spent performing behaviours of the nine categories in Table 2.

Table 2. Individual gorilla activity budgets (N=5) and group means (M), shown as percentages of time spent performing different behaviours.

Behaviour category*	Gorilla					M
	1	2	3	4	5	
Passive solitary	69.79	52.27	46.19	46.32	45.20	51.95
Active solitary	5.90	5.70	9.56	8.55	10.61	8.06
Total solitary	75.69	57.97	55.75	54.87	55.81	60.01
Passive social	0.08	2.76	1.12	2.96	0.76	1.54
Active social	0.00	1.22	0.08	1.19	0.00	0.49
Total social	0.08	3.98	1.20	4.15	0.76	2.03
Aggressive	0.00	0.33	0.40	0.42	0.42	0.31
Abnormal	0.00	0.73	4.42	1.01	0.08	1.25
Feeding-related	22.25	26.09	30.04	31.16	35.97	29.10
Keeper-directed	0.08	4.80	2.97	7.87	4.67	4.08
Visitor-directed	1.86	5.29	5.22	0.51	2.29	3.03

*Passive solitary behaviour: sitting, lying, standing still, self-grooming; Active solitary behaviour: terrestrial movement, locomotor play, object play; Passive social behaviour: social resting, looking at other gorillas; Active social behaviour: social playing; Feeding behaviour: feeding, drinking, foraging, elimination; Keeper-related behaviour: looking at keepers; Visitor-related behaviour: looking at visitors.

Gorilla Behaviour Index (GBI)

We found individual differences between gorillas on all four factors of the GBI. Gorilla 2 was assigned the highest score on the Extroverted factor, and Gorilla 1 the lowest. Gorilla 3 scored the highest on the Dominant factor, and Gorilla 1 the lowest. Gorillas 1 and 2 scored the highest on the Fearful factor, and Gorilla 4 the lowest. Finally, Gorilla 1 was assigned the highest score on the Understanding factor, and Gorilla 5 the lowest (Table 3).

To test whether personality factors and behaviours were correlated, we ranked gorillas on each of the GBI factors, and in each of the 11 behavioural categories, and calculated Spearman rank correlation coefficients using randomisation tests (Table 4).

Results indicate that gorillas with higher scores on the Extroverted factor exhibited more active social behaviours, as well as being overall socially more active. Gorillas with higher scores on the Understanding factor were more likely to engage in passive solitary behaviours.

Social Dynamics

Social resting

Observed gorillas greatly differed in their tendency to rest near another individual. While Gorilla 1 was not observed to social rest at all, Gorillas 2 and 4 spent a substantial amount of time resting together. Furthermore, there were differences with respect to initiating or receiving this type of close contact and in this case Gorilla 4 was the initiator in more than half of those situations. Gorilla 2 came to rest near Gorilla 3 on three occasions, but Gorilla 3 did not approach Gorilla 2 or another gorilla at all during the observation periods. Gorillas 4 and 5 were also observed resting together, with both of them initiating this behaviour.

Play

In terms of playing, differences are evident not only in participation in this social activity, but also in its initiation. Gorillas 2 and 4 played with each other the most, with Gorilla 4 being the initiator for the majority of play instances. Gorilla 4 also played with Gorilla 5, but in this case, Gorilla 5 initiated more play sessions than did Gorilla 4. Gorilla 2 initiated a few play behaviours with Gorilla 3, but this was not reciprocated as Gorilla 3 was only observed initiating one play event with Gorilla 5. Gorilla 1 was never observed playing with another individual.

Aggressive behaviour

Aggressive behaviour had a relatively low prevalence, though each individual was observed in this type of interaction with at least two others. Gorilla 5 was involved in the highest number of aggressive encounters, most often with Gorilla 4. Overall, Gorilla 4 was the recipient of aggression a little more often than he was the initiator. Gorilla 2 was observed in aggressive encounters with Gorilla

Table 3. Individual results for each gorilla (N=5) on the GBI, along with factor means and standard deviations.

	Gorilla					M	SD
	1	2	3	4	5		
Extroverted	0.43	2.29	1.43	2.14	1.29	1.52	0.746
Dominant	2	2.33	4	3.33	3.33	2.99	0.816
Fearful	4.25	4.25	2.25	2	3.75	3.30	1.095
Understanding	2.86	2.43	1.86	1.57	1.43	2.03	0.602

5 most frequently, being the initiator and the recipient almost equally as often. Gorilla 3 initiated few aggressive encounters, and was on the receiving end even less often. Gorilla 1 was most often aggressive towards Gorillas 5 and 3, but in both cases only as a result of previously being cornered by these gorillas. On one occasion, he was also on the receiving end of aggressive behaviour by Gorilla 2, after previously being displaced by him.

Shortly before our study, the gorilla group had begun to undergo a change in hierarchy. Gorilla 3 had started to take over as the group leader, which caused some disturbance to group dynamics. As the tension in the group was high, it is possible that gorillas were exhibiting a higher frequency of aggressive behaviours than they typically would, which was corroborated by the keepers. These instances of aggression could be better understood when combined with data on gorilla displacement patterns.

Displacement

Each individual within the study group has a place within the group hierarchy, but as the dynamics started to shift, gorillas started to assert their changing dominance status through an increase in either initiating or receiving displacements. This was particularly evident between the silverback (Gorilla 1) and the

maturing blackback trying to take over group leadership (Gorilla 3). The disproportion of displacement instances was most evident between these individuals. Although Gorilla 3 also often displaced Gorilla 2, those events differed in their nature. Displacing Gorilla 1 involved chasing, posturing and prolonged gazes in his direction, which made Gorilla 1 wary of Gorilla 3 at all times. In contrast, displacing Gorilla 2 was always relatively peaceful.

To test whether these social behaviours were correlated with personality, we performed randomised tests in R (2013). Table 6 shows Spearman rank correlation coefficients between initiating or receiving these behaviours, and the GBI scores.

Discussion

In this study, we examined differences in gorilla personality (as measured via GBI) and social dynamics. Previous studies of gorilla personality have indicated that extroversion decreases with age (Kuhar et al. 2006), which corresponds to a decrease in affiliative behaviours (Stoinski et al. 2004a; Stoinski et al. 2013). Our study supports those results, as the silverback (Gorilla 1), who is much older than the other males (Table 1) was assigned the lowest Extroverted score: about 1.5 standard deviation below the group

Table 4. Spearman rank correlation coefficients between gorilla personality, as measured by the Gorilla Behaviour Index (GBI), and behaviour category (BC).

BC	Extroverted		Dominant		Fearful		Understanding	
	r	p	r	p	r	p	r	p
Passive solitary	-0.10	0.95	-0.67	0.26	0.67	0.26	1	0.01**
Active solitary	-0.21	0.73	0.79	0.14	-0.58	0.33	-0.87	0.09
Total solitary	-0.30	0.67	-0.67	0.27	0.87	0.09	0.90	0.08
Passive social	0.90	0.08	0.36	0.62	-0.56	0.39	-0.30	0.68
Active social	0.97	0.03*	0.08	0.83	-0.13	0.80	0.10	0.90
Total social	0.97	0.03*	0.29	0.61	-0.39	0.46	-0.21	0.73
Aggressive	0.32	0.60	0.54	0.37	-0.68	0.20	-0.95	0.07
Abnormal	0.60	0.35	0.82	0.13	-0.72	0.17	-0.30	0.69
Feeding	0	1	0.82	0.13	-0.56	0.39	-0.90	0.08
Keeper-oriented	0.80	0.13	0.21	0.77	-0.46	0.43	-0.50	0.45
Visitor-oriented	0.31	0.61	0.26	0.65	0.34	0.50	0.15	0.83

Table 5. Number of instances of different social behaviours between the gorillas (N=5), along with their initiators and recipients.

	Social resting		Recipient				
	Gorilla		1	2	3	4	5
Initiator	1	-	0	0	0	0	0
	2	0	-	3	10	0	
	3	0	0	-	0	0	
	4	0	23	0	-	2	
	5	0	0	0	3	-	
Play			Recipient				
	Gorilla		1	2	3	4	5
	1	-	0	0	0	0	0
	2	0	-	2	6	0	
	3	0	0	-	0	1	
Initiator	4	0	14	0	-	5	
	5	0	0	1	3	-	
			Recipient				
	Gorilla		1	2	3	4	5
	1	-	0	1	0	0	1
Initiator	2	1	-	0	1	4	
	3	1	2	-	3	1	
	4	0	1	1	-	5	
	5	1	4	0	6	-	
	Displacing			Recipient			
Gorilla			1	2	3	4	5
1		-	0	0	0	0	1
2		1	-	0	0	0	0
3		19	10	-	5	0	
Initiator	4	0	0	0	-	0	
	5	1	0	0	2	-	

Table 6. Spearman rank correlation coefficients between gorillas' scores on Gorilla Behaviour Index (GBI) and initiation/receptiveness of social interactions.

	Extroverted		Dominant		Fearful		Understanding	
	r	p	r	p	r	p	r	p
Social resting - initiator	0.718	0.17	0	1	-0.34	0.49	-0.41	0.49
Social resting - recipient	1	0.01**	0.21	0.77	-0.21	0.73	-0.1	0.94
Play - initiator	0.8	0.13	0.21	0.77	-0.46	0.43	-0.5	0.44
Play - recipient	0.9	0.08	0.05	1	-0.10	0.90	-0.3	0.68
Aggression - initiator	0.05	1	0.76	0.20	-0.63	0.25	-0.98	0.03*
Aggression - recipient	0.1	0.95	-0.05	1	-0.15	0.83	-0.7	0.23
Displacement - initiator	-0.31	0.67	0.53	0.38	0.05	0.90	-0.15	0.83
Displacement - recipient	-0.1	0.95	-0.96	0.03*	0.67	0.26	0.7	0.24

* P<0.05; ** P<0.01

average (Table 3). This is also reflected in his social interactions; he was not observed to engage in any affiliative interactions (Tables 5). Interestingly, neither was he sought out for such interactions by the other males. Since males over 13 years of age are seldom found living in bachelor groups (Harcourt 1988), it is possible that this gorilla's age is the reason for his apparent social exclusion. Gorilla males mature between 11 and 13 years of age, and can become silverbacks around the age of 13 (Czekala and Robbins 2001), so it is no surprise that one of the maturing males (Gorilla 3) has already started to assert his dominance.

The present group reached its final composition in 2010 (Table 1). It was built around a silverback by slowly introducing the young males. This is not the most usual way of forming all-male groups in captivity (Stoinski et al. 2004a), as all-male groups are most commonly constructed from young males only, thus resembling the wild situation (Gatti et al. 2004; Robbins et al. 2004). This results in a high number of affiliative relationships within the group, as well as a relatively low rate of aggressive interactions (Stoinski et al. 2004b). During their teenage years, gorillas can be challenging to manage regardless of their group's social structure, as this is a period of increased frequency of display and dominance behaviours (Stoinski et al. 2004a; Stoinski et al. 2013), which, according to hormonal data, begin to decline when gorillas enter their 20s (Stoinski et al. 2002). These findings suggest that teenage male gorillas have not yet reached social maturity, despite being physically mature, which also corresponds to data obtained in the wild (Breuer et al. 2009).

In previously recorded cases of all-male groups built around a silverback, the silverback was almost two standard deviations below the group average on the Understanding factor (Kuhar et al. 2006). The same result was not obtained in the present study, as the silverback's Understanding score was more than one standard deviation above the group average (Table 3). This was accompanied by a Dominant score of more than one standard deviation below the group average (Table 3). Low dominance and high understanding were reflected in the aggressive and displacement encounters of which this gorilla was the recipient more often than he was the initiator (Table 5). These results show some support for previously described age differences in gorilla personality, but temporal stability of gorilla personality and observed individual differences are yet to be confirmed. Previous studies suggest that a gorilla's age is the primary predictor of social behaviour (Stoinski et al. 2013). A much-needed longitudinal assessment of the GBI is currently under way, as reported in Kuhar et al. (2006).

Another variable that has been shown to affect group dynamics is rearing history. Hand-rearing often results in animals lacking

social skills, which can leave individuals on the group periphery, and thus more exposed to aggression and more prone to depression (Porton et al. 2006). Hand-reared gorillas exhibit more solitary play, self-directed behaviours and regurgitation and reingestion, as well as inappropriate aggressive behaviours (Olson and Gold 1985; Meder 1989; Gold 1992). As all but one gorilla in this study was hand-reared, the current sample does not allow for detailed comparisons and definite conclusions regarding the impact of hand-rearing, but we find this to be worthy of further investigation.

The connection between personality and behaviour is complex. When personality is used to predict human behaviour, facets are often more useful than their broader, underlying factors. They have been revealed as significant predictors in cases where broad personality factors were not (King et al. 2008), or increased the amount of behaviour variance explained, while also offering a more detailed understanding of the behaviour in question (Paunonen and Ashton 2001). Moreover, personality traits have in some cases explained almost double the amount of criterion variance explained by broad factors (Mershon and Gorsuch 1988). It should therefore be expected that using broad measures in studies of gorilla personality reveals only a few significant relationships. Results of Gold's original research (1992) mostly identified a positive correlation of the Extroverted factor with affiliative behaviours. Kuhar et al. (2006) confirmed those findings, while also detecting a positive correlation between the Extroverted scores and initiation of contact aggression. In our study, gorillas scoring higher on the Extroverted factor were more likely to be chosen to rest near. High scores on this factor were, however, not correlated with aggressive behaviour, as was the case in previous research (Kuhar et al. 2006). The Extroverted scores were also found to be associated with a higher proportion of active social and overall social behaviour (Table 6). This is not surprising, since gregariousness is a facet of the Extroversion factor found in humans (Costa and McCrae 1995), of which this factor is an equivalent in nonhuman animals.

Gorillas scoring higher on the Dominant factor were less likely to be displaced, which is in accordance with previous studies (Kuhar et al. 2006) which have reported higher dominance associated with a lower likelihood of displacing others. However, this was not repeated in our study. Gorillas with higher Understanding scores were less likely to initiate aggressive interactions, which also supports previous findings (Kuhar et al. 2006). Moreover, we found the Understanding scores to be positively correlated to proportion of passive solitary behaviour (Table 6). This may sound contradictory at first, as this factor is the equivalent of

the Agreeableness factor described for humans (Gold and Maple 1994), which is associated with getting along better with others, being sensitive to others' needs, and experiencing less social rejection (Bierman 2003). It is also associated with a higher social responsiveness (Tobin et al. 2000) and better control of negative emotions in times of conflict (Jensen-Campbell and Graziano 2001). The study gorilla group was, at the time of behavioural observations, going through a change in hierarchy, causing disturbance to their normal routine. It could, therefore, be argued that gorillas with higher Understanding scores—which made them more in-tune to others' current states, as well as more in control of their own negative emotions—withdrawed socially, and therefore exhibited more solitary behaviours.

Even when the relationships between personality and behaviour are significant, the effect sizes can be relatively low. Shifting the research focus to different personality indicators may reveal new information. Using personality to predict behaviour could focus on the qualitative states in which discrete behaviours are performed, rather than the frequency of those behaviours (Pederson et al. 2005; Kuhar et al. 2006). Behaviour may be influenced by changes in group conditions and environment (Gold and Maple 1994), so measuring gorilla reactions to novel objects and strangers, as well as their startle responses and greeting reactions, may be useful in combination with the GBI (Kuhar et al. 2006). This approach, used successfully in canine personality research (Svartberg and Forkman 2002), would provide a measure of the shyness-boldness trait of gorilla temperament (Réale et al. 2007).

Another possible direction for future research is to build a detailed instrument that would enable the measurement of personality on a more specific level. Discrete behaviours form personality traits, and covarying traits form facets that comprise personality factors (Costa and McCrae, 1995). Studying personality at a facet level (e.g. King et al. 2008; Weiss et al. 2011) or even trait level (Ashton 1998; Pausonon 1998) could enable better prediction of specific behaviours, due to their trait-specific criterion-valid variance. More detailed personality measures built upon larger pools of items (e.g. Hominoid Personality Questionnaire, Weiss et al. 2009), and generated in a bottom-up approach from species' behavioural repertoires (e.g. Uher and Asendorpf 2008), could be useful in gorilla personality research, and a hierarchical approach may enable more detailed analyses that could result in a better understanding of the personality-behaviour relationship.

Conclusions

In this study, we showed that gorilla behaviour is correlated with personality ratings. Higher scores on the Extroverted factor were associated with a higher likelihood of being chosen to rest near, as well as exhibiting higher proportions of social behaviour. Gorillas scoring higher on the Dominant factor were less likely to be displaced, while those with higher Understanding scores were less likely to initiate aggressive interactions, and exhibit a higher proportion of passive solitary behaviour. To better predict behaviour for improved captive management, other instruments could be used alongside the GBI. We recommend the construction of a more detailed instrument which would enable a hierarchical study of gorilla personality. We believe such an approach would result in a better understanding of the relationship between gorilla personality and behaviour.

Acknowledgements

The authors would like to thank Paignton Zoo Environmental Park for endorsing this project. We would also like to thank the anonymous reviewers for their comments. We thank I. Tomić for his feedback on the early versions of this paper. We thank M. Račevska, D. Račevski, D. Račevska, and B. Tomić for supporting the project. We gratefully acknowledge all participating humans and gorillas - our study would have not been possible without them.

References

- Ashton M.C. (1998) Personality and job performance: The importance of narrow traits. *Journal of Organizational Behavior* 19: 289–303.
- Bierman K.L. (2003) Peer rejection: Developmental processes and intervention strategies. New York: The Guilford Press.
- Brent L.J., Lehmann J., Ramos-Fernández G. (2011) Social network analysis in the study of nonhuman primates: A historical perspective. *American Journal of Primatology* 73(8): 720–730.
- Breuer T., Breuer-Ndoundou Hockemba M., Olejniczak C., Parnell R.J., Stokes E. (2009) Physical maturation, life-history classes, and age estimates of free-ranging western gorillas – insights from Mbeli Bai, Republic of Congo. *American Journal of Primatology* 71: 106–119.
- Capitaino J.P. (1999) Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology* 47: 299–320.
- Costa P.T., McCrae R.R. (1992) Four ways five factors are basic. *Personality and Individual Differences* 13(6): 653–665.
- Czekala N., Robbins M.M. (2001) Assessment of reproduction and stress through hormone analysis in gorillas. In: Robbins M.M., Sicotte P. Stewart, K.J. (eds). *Mountain gorillas: three decades of research at Karisoke*. Cambridge, UK: Cambridge University Press.
- Dewarwildlife (2015) Accessed 16 July 2015 <http://www.dewarwildlife.org/jrdavis-gorilla-studbook/>
- Fleeson W. (2004) Moving personality beyond the person-situation debate: The challenge and the opportunity of within-person variability. *Current Directions in Psychological Science* 13(2): 83–87.
- Gatti S., Levrero F., Menard N., Gautier-Hion A. (2004) Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoue, Republic of Congo. *American Journal of Primatology* 63: 111–123.
- Gold K.C. (1992) Nonsocial behavior of captive infant gorillas. *American Journal of Primatology* 26: 65–72.
- Gold K.C., Maple T.L. (1994) Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology* 13(5): 509–522.
- Gold K. (1997a) Social structure - overview. In: Ogden J., Wharton D. (eds). *Management of gorillas in captivity*. Silver Spring, MD: Gorilla Species Survival Plan Husbandry Manual. Gorilla Species Survival Plan and Atlanta/Fulton County Zoo, Inc.
- Gold K. (1997b) Group size and composition. In: Ogden J., Wharton D. (eds). *Management of gorillas in captivity*. Silver Spring, MD: Gorilla Species Survival Plan Husbandry Manual. Gorilla Species Survival Plan and Atlanta/Fulton County Zoo, Inc.
- Goldberg L.R. (1999) A broad-bandwidth, public domain, personality inventory measuring the lower-level facets of several five-factor models. *Personality psychology in Europe* 7(1): 7–28.
- Gosling S.D., John O.P. (1999) Personality dimensions in nonhuman animals: a cross-species review. *Current Directions in Psychological Science* 8: 69–75.
- Harcourt A.H. (1979) The social relations and group structure of wild mountain gorillas, in: Hamburg D., McCown E. (eds.). *The behavior of great apes*. Menlo Park, CA: Benjamin/Cummings.
- Harcourt A.H. (1988) Bachelor groups of gorillas in captivity: the situation in the wild. *Dodo* 25: 54–61.
- Hothorn T., Hornik K., van de Wiel M., Zeileis A. (2006) A Lego System for Conditional Inference. *The American Statistician* 60(3): 257–263.
- Jensen-Campbell L.A., Graziano W.G. (2001) Agreeableness as a moderator of interpersonal conflict. *Journal of Personality* 69: 323–361. doi:10.1111/1467-6494.00148
- John O.P., Caspi A., Robins R.W., Moffitt T.E., Stouthamer-Loeber M. (1994) The "Little Five": Exploring the nomological network of the Five Factor Model of personality in adolescent boys. *Child Development* 65: 160–178.
- Kuhar C.W., Stoinski T.S., Lukas K.E., Maple T.L. (2006) Gorilla behavior index revisited: age, housing and behavior. *Applied Animal Behaviour Science* 96(3): 315–326.
- Lowe S.E., Bradshaw J.W.S. (2001) Ontogeny of individuality in the domestic cat in the home environment. *Animal Behaviour* 61: 231–237.
- Maryanski A.R. (1987) African ape social structure: is there strength in weak ties? *Social Networks* 9(3): 191–215.
- McKinley J., Buchanan-Smith H., Bassett L., Morris K. (2003) Training common marmosets (*Callithrix jacchus*) to cooperate during routine husbandry procedures: ease of training and time investment. *Journal of Applied Animal Welfare Science* 6(3): 209–220.
- Meder A. (1989) Effects of hand-rearing on the behavioral development of infant and juvenile gorillas (*Gorilla g. gorilla*). *Developmental Psychobiology* 22: 357–376.

- Mershon B., Gorsuch R.L. (1988) Number of factors in the personality sphere: Does increase in factors increase predictability of real-life criteria? *Journal of Personality and Social Psychology* 55(4): 675.
- Paunonen S.V. (1998) Hierarchical organization of personality and prediction of behavior. *Journal of Personality and Social Psychology* 74(2): 538.
- Paunonen S.V., Ashton M.C. (2001) Big five factors and facets and the prediction of behavior. *Journal of Personality and Social Psychology* 81(3): 524.
- Pederson A.K., King J.E., Landau V.I. (2005) Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality* 39(5): 534–549.
- Pervin L.A. (1980) *Personality: Theory, Assessment, and Research*. John Wiley & Sons Inc., New York.
- Pervin L.A. (1994) A critical analysis of current trait theory. *Psychological Inquiry* 5(2): 103–113.
- Porton I., Niebruegge K. (2006) The changing role of hand rearing in zoo-based primate breeding programs. In: Sackett G.P., Ruppenthal G., Elias K. (eds). *Nursery rearing of nonhuman primates in the 21st century*. Springer US, pp. 21–31.
- Olson F., Gold K.C. (1985) Behavioral differences in mother-reared and hand-reared infant lowland gorillas. In: AAZPA Annual Conference Proceedings. American Association of Zoological Parks and Aquariums. Wheeling, WV, pp. 143–152.
- Réale D., Reader S.M., Sol D., McDougall P.T., Dingemanse N.J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews* 82(2): 291–318.
- Robbins M.M., Bermejo M., Cipolletta F.M., Parnell R.J., Stokes E. (2004) Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology* 64: 145–159.
- SPSS Inc. (2008) *SPSS Statistics for Windows, Version 17.0*. Chicago: SPSS Inc.
- Stevenson-Hinde J., Zunz M. (1978) Subjective assessment of individual rhesus monkeys. *Primates* 19: 473–482.
- Stoinski T.S., Czekala N., Lukas K.E., Maple T.L. (2002) Urinary androgen and corticoid levels in captive, male western lowland gorillas (*Gorilla g. gorilla*): age- and social group-related differences. *American Journal of Primatology* 56: 73–87.
- Stoinski T.S., Kuhar C.W., Lukas K.E., Maple T.L. (2004a) Social dynamics of captive western lowland gorillas living in all-male groups. *Behaviour* 141: 169–195.
- Stoinski T.S., Lukas K.E., Kuhar C.W., Maple T.L. (2004b) Factors influencing the formation and maintenance of bachelor gorilla groups in captivity. *Zoo Biology* 23: 189–203.
- Stoinski T.S., Lukas K.E., Kuhar C.W. (2013) Effects of age and group type on social behaviour of male western gorillas (*Gorilla gorilla gorilla*) in North American zoos. *Applied Animal Behaviour Science* 147(3): 316–323.
- Svartberg K., Forkman B. (2002) Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science* 79: 133–155.
- Tobin R.M., Graziano W.G., Vanman E., Tassinari L. (2000) Personality, emotional experience, and efforts to control emotions. *Journal of Personality and Social Psychology* 79: 656–669. doi:10.1037/0022-3514.79.4.656
- Tutin C.E.G. (2003). An introductory perspective: Behavioral ecology of gorillas. In: Taylor A.B., Goldsmith M.L. (eds). *Gorilla biology: A multidisciplinary Perspective*. Cambridge, UK: Cambridge University Press.
- Uher J., Asendorpf J.B. (2008) Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality* 42(4): 821–838.
- Watts D.P. (2003) Gorilla social relationships: A comparative overview. In: Taylor A.B., Goldsmith M.L. (eds). *Gorilla biology: A multidisciplinary Perspective*. Cambridge, UK: Cambridge University Press.
- Yamagiwa J., Basabose K., Kaleme K., Yumoto T. (2003) Within-group feeding competition and socioecological factors of gorillas in the Kahuzi-Biega National Park, Democratic Republic of Congo. In: Taylor A.B., Goldsmith M.L. (eds). *Gorilla biology: A multidisciplinary Perspective*. Cambridge, UK: Cambridge University Press.