Graphical Abstract

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Highlights

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- The sociality of vervet monkeys groups differs consistently across a nine years study despite similar genetic and ecological environments.
- Dispersing males adapt their sociality according to the group they integrate.
- In the most social group, grooming interactions were more reciprocal.

Social dynamics of vervet monkeys are dependent upon group identity

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Abstract

Traditions are widespread across the animal realm. Here, we investigated inter-group variability of social dynamics in wild vervet monkeys (*Chlorocebus pygerythrus*). We analysed 84 704 social behavioural interactions involving 247 individuals collected over nine years in three neighbouring groups of wild vervet monkeys. We found that, in one group - Ankhase - individuals had a higher propensity to be affiliative (i.e., sociality) and grooming interactions were more reciprocal. Despite yearly fluctuations in sociality, differences between groups remained stable over time. Moreover, our statistical model predictions confirmed that these findings were maintained for similar sex ratios, age distributions and group sizes. Strikingly, our results suggested that dispersing males adapted their sociality to the sociality of the group they integrated. As a whole, our study sheds light on the existence of stable social dynamics dependent upon group identity in wild vervet monkeys and suggests that at least part of this variability is socially mediated.

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1. INTRODUCTION

Across time and space, culture shapes us: from what we know, to how we behave and interact, it fuels the diversity of human behaviours. Over the last decades, the accumulation of evidence in wild and captive non-human animals (hereafter: animals) revealed the existence of cultures in a variety of mammals and birds, from tool use in chimpanzees to song dialects in birds[1]. These studies not only helped researchers to better understand the diversity of intra-species behavioural repertoires, but also to unravel the evolutionary roots and the selective pressures leading to the emergence of culture. A pioneer study reported the innovation and spread of sweet potato washing in a group of Japanese macaques (*Macaca fuscata*). Such behaviour was observed only in a few groups of Japanese macaques and spread to several individuals only in this specific group. Authors then described this behaviour as pre-cultural[2] (but see[3]). Besides observing intra-species behavioural variability between groups (i.e., a social unit of individuals) or between populations (i.e., several groups within a geographically defined area), a fundamental aspect of culture is that cultural behaviours should be transmitted through social learning, where social learning is defined as a learning process "facilitated by observation of, or interaction with, another individual (or its products)"[4]. Thus, culture encompasses "those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information"[5]. Each culture is then a specific set of cultural behaviours - traditions - which are defined as "a behavioral practice that is relatively enduring (i.e., is performed repeatedly over a period of time), that is shared among two or more group members, and that depends in part on socially aided learning for its generation in new practitioners"[6].

A classical method used to investigate the cultural origin of a behaviour is to exclude both obvious ecological and genetic variations, leaving culture as the only probable cause of the observed behavioural diversity (i.e., method of exclusion)[7]. However, across the literature, most studies have investigated the behavioural variability of geographically distant populations[1]. Quantifying the influence of ecological and genetic variation in such a setting can easily be misleading in the case of subtle environmental variations[8]. Recently, several researchers argued that studying neighbouring groups of animals of the same species limit genetic and ecological biases because they live in relatively similar ecological and genetical environments[9,10]. Thus, what was before a neglected scale of behavioural diversity - the inter-group level - is

now resurgent in recent literature and offers significant advantages in the study of culture in wild animals[9,11,12,13].

Ecological and genetic environments are however not the only source of variability which should be controlled for: group size, sex ratio or age distribution - broadly defined as group demographic variables - are another stream of variability which could explain inter-group behavioural diversity[14]. In species with sex or age specific behaviours, slight differences in proportions of the sex ratio and/or the age distribution could lead to specific group behavioural patterns. For example, in vervet monkeys, females spend more time grooming conspecifics than males[15,16] and thus a group with a higher proportion of females may overall dedicate more time to grooming rather than a group with a balanced sex ratio. DeTroy et al.[17], recently highlighted the influence of group demographics on co-feeding tolerance in four groups of sanctuary-housed chimpanzees across eight years. They found that co-feeding tolerance increased with the number of juvenile females and decreased as the number of infants increased. This study stressed that long-term studies have the potential to quantify and take into account group demographic variation across time and can extend our understanding of animal culture, especially in animals with slow life histories such as primates[18,17,19].

Animal traditions can be classified in three different categories: material, food-related and social traditions (see[20] for a review of monkey cultures). For a long time, social traditions have been overlooked in comparison to material or food-related animals' traditions[21]. Some studies even suggested a relative higher importance (41%) of social traditions over other types of traditions in specific species such as spider monkeys (*Ateles geoffroyi*)[22]. Qualitative (presence/absence) and quantitative (frequency) differences in non-human primates' (hereafter: primates) social behaviour have been reported. In comparison to qualitative differences in behaviour, quantitative behavioural diversity in primate social behaviour has been little investigated so far. However, when investigating the variation in the frequency of wild spider monkey behaviours (e.g. foraging, greetings and resting), Santorelli et al.[23] found a significant amount of variation and identified them as "candidate traditions". Quantitative variations in inter-species interactions have also been reported in different species of monkeys[24,25,26]. For example, over a four-year period, Rose et al.[24] found that one group of white-faced capuchin monkeys was highly involved in grooming with spider monkeys compared to five other neighbouring groups. De Waal & Johanowicz[27] reported that juvenile rhesus macaques dramatically increased their reconciliation rates after

being translocated to a group of a more conciliatory species, the stumptail macaques. In 2004, Sapolsky et al.[11,28] described the emergence and persistence of what they called a "pacific culture" in a group of wild olive baboons (*Papio anubis*). In the mid-1980s, half of the males from their study group died from tuberculosis. Two decades later, all surviving males died, and no adult males were native to the group anymore. Researchers observed a significantly higher inter-sexual grooming rate, and reduced spatial proximity as well as a "relaxed" hierarchy between males, where low-rankers had a higher probability of accessing contested resources. Incoming males first showed more usual aggressive patterns before conforming to the group social specificity. In the above-cited studies, such global changes in social behaviours were described as "social style", "social norms", "social climates", or "social dynamics"[29]. Here, we use the term "social dynamics" to align with research on great ape social traditions[30]. Overall, even if quantitative variability in social behaviours has been identified, strong evidence that social dynamics are dependent upon social learning in monkeys are still lacking.

Primate social behaviours are classified either as affiliative (friendly) or agonistic (aggressive and submissive). No broad agreement exists on how to measure group sociality. It can be assessed via social tolerance metrics (co-feeding and spatial proximity networks) or pro-social indices (food sharing indices)[18,17,31], but a variety of other metrics have been used in the literature[32,33]. Based on the definition of sociality in chimpanzees as "interaction tendencies"[30], we will use the term "sociality" to refer to the propensity to be affiliative (i.e., the relative amount of affiliative interactions compared to agonistic ones) either at the individual level or at the group level. Among affiliative behaviours, grooming is the most widespread and common in primates[34]. It has a crucial role in primate sociality: it maintains social bonds between individuals and decreases stress[34]. The definition of reciprocity in grooming behaviours (i.e., after A groomed B, the probability of B to groom A increases) lacks a consensus concerning the time-lapse in which reciprocity occurs. Here we align with the recent definition of O'Hearn et. al.,[35] of a global long-term reciprocity (hereafter: reciprocity) which stands for grooming behaviours that can be exchanged over timescales ranging from hours to years.

In the present study, we aim to describe the differences in social dynamics between three neighbouring groups of wild vervet monkeys (*Chlorocebus pygerythrus*) over nine years and to understand if these differences could be interpreted as different social traditions between groups.

Vervet monkeys are a well-suited species to investigate social traditions because they live in multi-male, multi-female groups, providing individuals with many opportunities to socially learn from different individuals. A body of studies has shown that vervet monkeys socially learn how to manipulate artificial fruits[36,37,9,38,39] and to process novel food[40], but their potential to socially learn social behaviours remains unknown. Here, we focused on two main aspects of primate social life. First, sociality (i.e., propensity to be affiliative) and second, grooming reciprocity (i.e., how reciprocal are grooming exchanges). We asked three main questions: (I) Is sociality influenced by group identity across years? If yes, do dispersing males adapt their sociality when they integrate a new group? (II) Is sociality similarly distributed between individuals in each group according to their socio-demographic category and kinship? (III) Are differences in grooming reciprocity between groups coherent with differences in sociality?

Here, we extend previous studies by gathering three grounding aspects of research on animal culture: the study of several neighbouring groups with overlapping home-ranges and migration flux; the quantification of the influence of group demographics, and the use of a continuous long term database. We used nine years of observational data from three neighbouring groups of wild vervet monkeys: Ankhase (AK), Baie Dankie (BD) and Noha (NH). Borgeaud et al.,[41] suggested in 2016 that the stability and structure of vervet monkeys' grooming networks differed over a two-year period using a social network-based analysis. Previous studies also found inter-group differences in co-feeding tolerance between adult females of AK, BD, and NH[42]. However, these studies did not investigate the long-term stability of these differences nor the influence of group's demographical conditions. In the later study[42], one of our study groups, AK, displayed a higher level of co-feeding tolerance. Based on these previous findings and regarding questions I, we predict AK to have an overall higher propensity to be affiliative than NH and BD. Additionally, van de Waal et al.[37] showed that dispersing males seem to conform to local norms in their food choice abandoning their natal preference. Thus, regarding question I, we predict that dispersing males might also conform to the local sociality. Concerning question II, we expect that individuals from all socio-demographic categories in AK are more social than individuals in the respective socio-demographic categories in BD and NH and the effect of kinship to be similar across groups. Previous analysis also suggested that females of distant ranks more regularly groom each other in AK[41]. Thus, regarding question III, we predict grooming reciprocity to be also higher in

AK. If such differences are stable over years and independent from group demography, it will favor an effect of group identity on social dynamics.

RESULTS

Question I: Groups' sociality differs congruently across years

Model 1.0 revealed that sociality was significantly different between the three groups of vervet monkeys (Figure 1A, Table 1). Indeed, *Group* had a significant effect on sociality ($LRT_{Group} = 729.47$, $p < 0.001$). In particular, AK had a significantly higher sociality than BD ($AME_{AK-BD} = 0.06$, $p < 0.001$) and NH ($AME_{AK-NH} = 0.10$, $p < 0.001$), and BD had a significantly higher sociality than NH ($AME_{NH-BD} = -0.03$, $p < 0.001$).
The magnitude of the effect of group identity was constant across time. Indeed, when we included the interaction *Year*Group* in the Model 1.1, it was not significant ($p = 0.47$). In other words, the differences in sociality between each group were statistically similar from one year to another. Furthermore, according to Model 1.1, within all groups, sociality significantly increased over time ($\beta_{Years} = 0.14, p < 0.001$). These statistical results are illustrated by the quasi-constant superiority of AK sociality and the relatively parallel and positive evolution of groups' sociality over years (Figure 1A).

Question I: AK has a higher sociality than other groups in similar demographic environments

Model 1.2 predicted that for similar age ratios, sex ratios and group sizes, group identity still had a significant effect on sociality ($LRT_{Group} = 563.01$, $p < 0.001$) (Figure 1B, Table 1). In such a setting, AK sociality was predicted to be 11% higher than BD sociality and 12% higher than NH sociality ($AME_{AK-BD} = 0.11$, $p < 0.001$; $AME_{AK-NH} = 0.12$, $p < 0.001$). However, in contrast to Model 1.0, we found no significant difference between the sociality of BD and of NH ($p = 1.00$). Regarding the global effect of demography on groups' sociality, we found that sociality decreased as the relative number of males or adults increased in the group ($AME_{Age-ratio} = -0.008$, $p = 0.001$; $AME_{Sex-ratio} = -0.01$, $p < 0.001$).

Question I: When all groups contain more females, differences in sociality are stronger

At a finer scale, we found evidence that the effect of group identity on sociality was stronger when all groups included more females than males (i.e.,

Response variable	Model	Type	Predictor variable	Control variable	Interaction	Random	Distribution	N Obs.	N Indiv.	Statistics (full vs. null model)			Analysis level
										Goodness-of-fit	DF	p-value	
1.Sociality	1.0	GLMM	Group	-	-	Year	Binomial	84704	275	$\chi 2 = 729.47$	2	< 0.001	Group
	1.1	GLM	Group Year	-	Group*Year	-	Quasibinomial	84704	275	Dev. = 1716.2	5	< 0.001	
	1.2	GLMM	Group Sex-ratio Age-ratio	Group size Time observation	-	Year	Binomial	84704	275	$\chi 2 = 564.62$	4	< 0.001	
	1.3	GLMM	Group Sex-ratio Age-ratio	Group size Time observation	Group*Sex-ratio	Year	Binomial	84704	275	$\chi 2 = 653.47$	6	< 0.001	
	1.4	GLMM	Group	Mean sociality groups		Individual	Binomial	1529	6	$\chi 2 = 29.29$	2	< 0.001	Individual
	1.5	GLMM	Group Sex Age Hierarchical rank	Mean sociality groups	-	Individual	Binomial	157 562	247	$\chi 2 = 303.74$	5	< 0.001	
	1.6	GLMM	Group Sex Age Hierarchical rank	Mean sociality groups	Group*Sex*Hierarchical rank Group*Hierarchical rank Group*Sex Sex*Hierarchical rank	Individual	Binomial	157 562	247	$\chi 2 = 341.14$	12	< 0.001	
2.Matri-love	2.0	LMM	Group Hierarchical rank	Sex Age Mean sociality groups	-	Individual	Gaussian	110687	205	$\chi 2 = 27.25$	3	< 0.001	
	2.1	LMM	Group Hierarchical rank	Sex Age Mean sociality groups	Group*Hierarchical rank	Individual	Gaussian	110687	205	$\chi 2 = 33.54$	5	< 0.001	
3.Grooming reciprocity	3.0	GLMM	Group	-	-	Year	Binomial	63510	247	$\chi 2 = 258.06$	2	< 0.001	Group
	3.1	GLM	Group Year	-	Group*Year	-	Binomial	63510	247	Dev. = 388.81	5	< 0.001	
	3.2	GLMM	Group Sex-ratio Age-ratio	Group size Time observation	-	Year	Binomial	63510	247	$\chi 2 = 442.26$	6	< 0.001	

Table 1. Statistical models summary: P-values correspond to the full vs. null model comparisons for each model. Dev.: Deviance, Df: Degree of freedom, GLM: Generalized Linear Model, GLMM: Generalized Linear Mixed-Model, Indiv : Individual, LMM: Linear Mixed Model, Obs.: Observation.

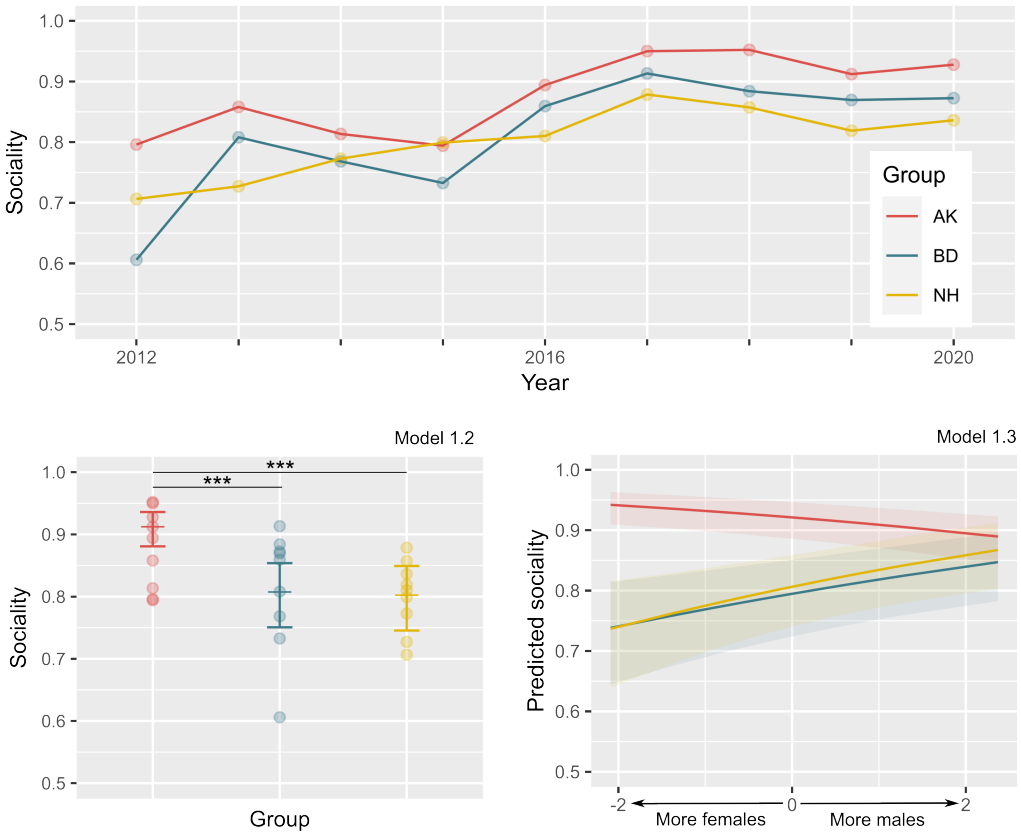


Figure 1. Groups' sociality depends on group identity A) Dynamics of the sociality of AK, BD and NH across years. Dots represent the sociality of each group for every year of the study as computed from raw data. B) Predicted sociality of AK, BD and NH in similar demographic environments. The small horizontal bars denote the predicted mean of sociality within each group and the error bars denote the standard error of the mean (SEM) as predicted by Model 1.2. Dots represent the sociality of each group for every year of the study as computed from raw data. (***) denotes the significant differences at the $\alpha < 0.001$ level. C) The effect of group identity in function of different values of the sex ratio within the groups. The x-axis represents the variation in the scaled value of the sex ratio, negative values represent a female skewed group and positive values represent a male skewed group compared to the mean observed sex ratio. 95% confidence interval (CI). Graphics representations are based on estimates from Model 1.3. AK: Ankhase, BD: Baie Dankie, NH: Noha.

low sex ratio) (Figure 1C). Indeed, we found that the sex ratio significantly

modified the influence of group identity on sociality ($LRT_{Group*Sex-ratio} = 88.85$, $p < 0.001$). The results of Model 1.3 (Table 1) revealed that in AK, a relative increase of females induced a significant increase of sociality ($\beta_{Sex-ratio} = -0.16$, $p < 0.001$) while the opposite effect was observed in BD ($\beta_{Sex-ratio} = 0.15$, $p = 0.001$) and NH ($\beta_{Sex-ratio} = 0.19$, $p = 0.002$). As a consequence, when all groups included relatively more females (*Sex ratio*: -2.09), Model 1.3 predicted that the sociality of the different groups diverged, AK being significantly more social than the two other groups ($AK > BD \sim NH$: $\beta_{BD-AK} = -1.75$, $p < 0.001$; $\beta_{NH-AK} = -1.76$, $p < 0.001$; $BD - NH$: $p = 1.00$). In contrast, when relatively more males were present in the group (*Sex ratio*: 2.3658) differences faded away. In such a setting, our model predicted that only AK and BD sociality were significantly different one from another ($AK > BD$: $\beta_{BD-AK} = -0.37$, $p = 0.004$) but neither AK nor BD was different from NH ($AK - NH$: $p = 1.00$, $NH - BD$: $p = 1.00$). Furthermore, within every group a mild interaction between *Sex ratio*Age-ratio* was detected ($LRT_{Sex-ratio*Age-ratio} = 42.29$, $p < 0.001$; see Figure S1).

Question I: Adult males become less social when they disperse to BD and NH compared to AK.

Comparing the sociality of dispersing males before and after they dispersed (during their first year of dispersal) between our study groups revealed that their sociality was on average higher of $+0.13 \pm 0.12$ ($N = 5$, Figure 2 and Figure 3) when they integrated into AK rather than when they dispersed to BD or NH. Six adult males dispersed within our three study groups during our study (Figure 2). Four males dispersed between AK and NH (WOL, TWE, YAN, KEK), one male dispersed from AK to BD (HAM), and one male dispersed from NH to BD (CHE). Only two of those males stayed a second year in both of their dispersing groups (CHE, HAM).

Model 1.4 (Table 1) highlighted, once again, an effect of group identity ($LRT_{Group} = 29.29$, $p < 0.001$), with AK being the group where males were significantly more social prior or after their dispersal ($AK > BD \sim NH$: $AME_{AK-BD} = 0.18$, $p < 0.001$; $AME_{AK-NH} = 0.15$, $p < 0.001$; $BD - NH$: $p = 1.00$). According to Model 1.4 - for a specific year of our study - the sociality of one dispersing male arriving in AK would be 18% higher than if he had dispersed to BD, and 15% higher than if he had dispersed to NH (Figure 3A).

Regarding males who stayed a second year within each group and in agree-

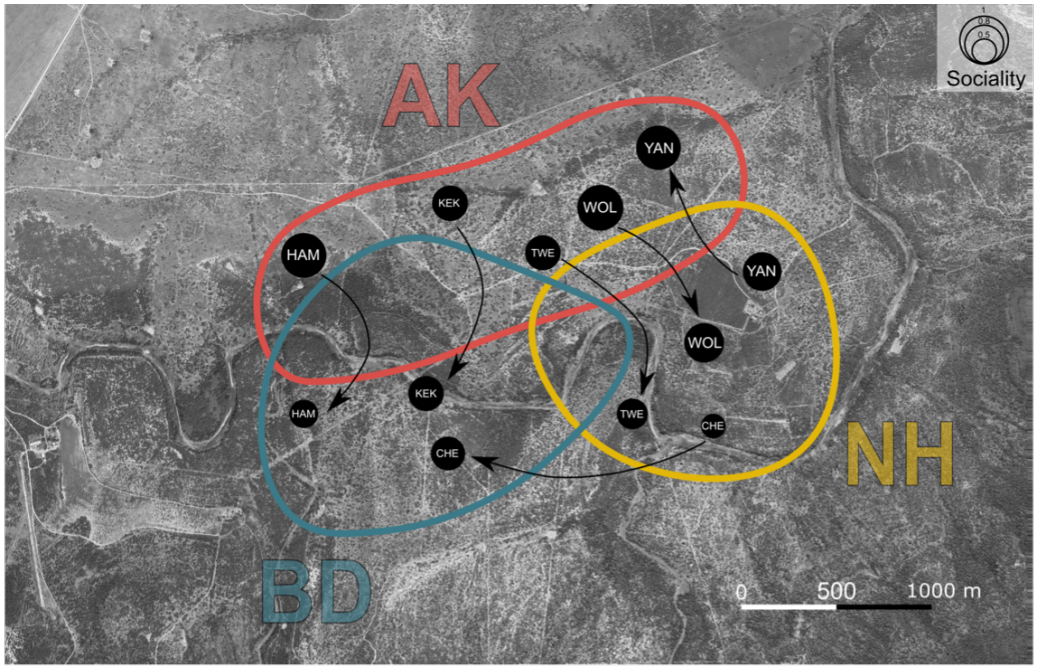


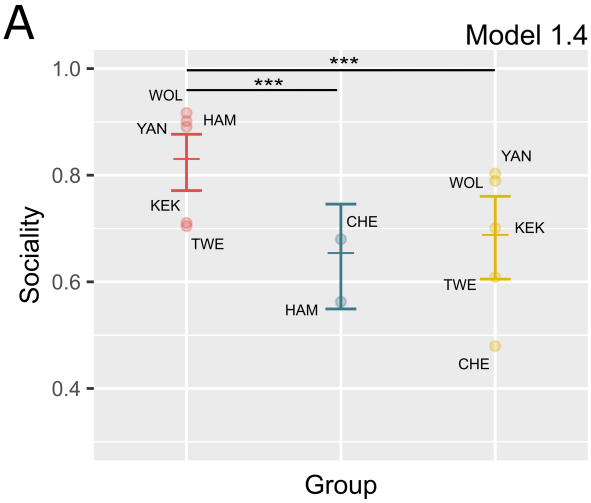
Figure 2. Dispersing map of males between groups
Map depicting the sociality of dispersing males between AK (red), BD (blue) and NH (yellow). Arrows represent the direction of dispersal. Each dot represents a male in a specific group. Bigger is a dot, the more social the individual was. Sociality is here computed from raw data. AK: Ankhase, BD: Baie Dankie, NH: Noha.

ment with our preceding results, we observed that HAM had a sociality 1.65 times higher in AK than in BD, while CHE had a similar sociality in BD and in NH (Figure 3C).

Question II: The effect of group identity is confirmed within all socio-demographic categories

Overall, Model 1.5 (Table 1) predicted that sex, age and hierarchical rank had a significant effect on individual sociality. Most importantly, these effects were similar within each group. Indeed, males' sociality was significantly lower than females' sociality ($AME_{M-F} = -0.09$, $p < 0.001$), juveniles' sociality was higher than adults' sociality ($AME_{Juv-Ad} = 0.02$, $p < 0.001$) and sociality significantly decreased as the hierarchical rank increased ($AME_{hierarchical-rank} = -0.07$, $p < 0.001$) (Figure 4A, Figure 4B).

A



B

Individual	Group	Year	Sociality	Dominance	Number of interactions
WOL	AK	2015	0.92	-	13
	NH	2018	0.79	0.52	210
HAM	AK	2013	0.90	0.33	101
	BD	2014	0.56	0.37	143
TWE	NH	2014	0.61	0.35	27
	AK	2020	0.70	0.46	170
CHE	NH	2012	0.48	0.38	103
	BD	2014	0.68	0.40	115
YAN	NH	2018	0.80	0.35	133
	AK	2020	0.89	0.47	405
KEK	AK	2019	0.71	0.42	43
	NH	2020	0.70	0.46	66

C

Individual	Group	Year	Sociality	Dominance	Number of interactions
CHE	NH	2013	0.63	0.52	208
	BD	2015	0.65	0.57	92
HAM	AK	2014	0.86	0.37	80
	BD	2015	0.52	0.73	48

Figure 3. Adult males become less social when they disperse to BD and NH compared to AK

A) Mean sociality of dispersing males that dispersed to AK, BD and/or NH. Each dot represents individual sociality during its first year of arrival in the group, computed from raw data. The small horizontal bars denote the predicted mean of male's sociality within their first year present in a group as predicted by Model 1.4. Error bars denote the standard error of the mean (SEM). (***) denotes the significant effects at the $\alpha < 0.001$ level. B) Table displaying sociality indices of dispersing males during their first year of presence in each group. C) Table displaying sociality indices of dispersing males during their second year of presence in each group. Dominance was computed from Elo-rating method. AK: Ankhase, BD: Baie Dankie, NH: Noha

The influence of *Sex* on sociality was about six times stronger than the one of *Age* and two times stronger than the effect of *Hierarchical rank*. These global effects were similar within each group as we found no significant effect of the interactions between *Group* and *Sex*, *Age* or *Hierarchical rank* (*Group*Sex*: $p = 0.25$; *Group*Age*; $p = 0.55$; *Group*hierarchical rank*: $p = 0.62$). Going in greater details revealed a significant interaction of *Group*Sex*hierarchical rank* ($LRT = 21.71$, $p < 0.001$). The results of Model 1.6 (Table 1) showed that the way the hierarchical rank influenced the effect of sex on sociality was different in NH compared to AK and BD (*NH-AK*Female*hierarchical-rank*: $p = 0.002$; *NH-BD*Female*hierarchical-rank*: $p < 0.001$; *BD-AK*Female*hierarchical-rank*: $p = 1.00$). In Figure 4C, this result is illustrated by the parallel evolution of sociality according to hierarchical rank in both males and females in BD and AK. However, the curve was greatly modified in NH males. Indeed, in NH, an increase in males hierarchical rank induced a strong decrease of their sociality ($\beta_{hierarchical-rank} = -1.37$, $p < 0.001$). We note that this interaction only influenced the relational order between BD and NH individuals' sociality, but not the relationship between AK and NH, such that, NH sociality curve never crossed AK curve on Figure 4C. It is still worth mentioning that this interaction influenced the magnitude of the difference between NH and AK individuals' sociality, so that sociality for males of low dominance (close to 0), the difference between AK and NH was not significant ($p = 1.00$) and similarly for the highest rank females, no differences between NH and other groups could be detected ($AK - NH$: $p = 0.60$; $BD - NH = 1.00$). We additionally found a significant interaction between *Age*, *Sex* and *Hierarchical rank* (see Figure S2).

Question II: The propensity to be affiliative is less directed towards related individuals in AK and BD.

In Model 2.0 (Table 1), we found a significant effect of group identity on the matri-love index ($p < 0.001$) (Figure 5A). NH individuals had a significantly higher matri-love index compared to individuals in AK and BD ($\beta_{AK-NH} = -0.07$, $p < 0.001$; $\beta_{BD-NH} = -0.04, p = 0.013$; $AK - BD$: $p = 0.19$). Model 2.1 (Table 1), revealed that the influence of hierarchical rank on matri-love was different across groups at a significance level of 0.05, however post-hoc analysis failed to identify which group(s) differed from others ($Group * hierarchical - rank$: $p = 0.043$; $NH - AK * hierarchical - rank$: $p = 0.86$; $NH - BD * hierarchical - rank$: $p = 0.157$; $AK - BD * hierarchical - rank$: $p = 1.00$). Figure 4B illustrates the effect of hierarchical rank on in-

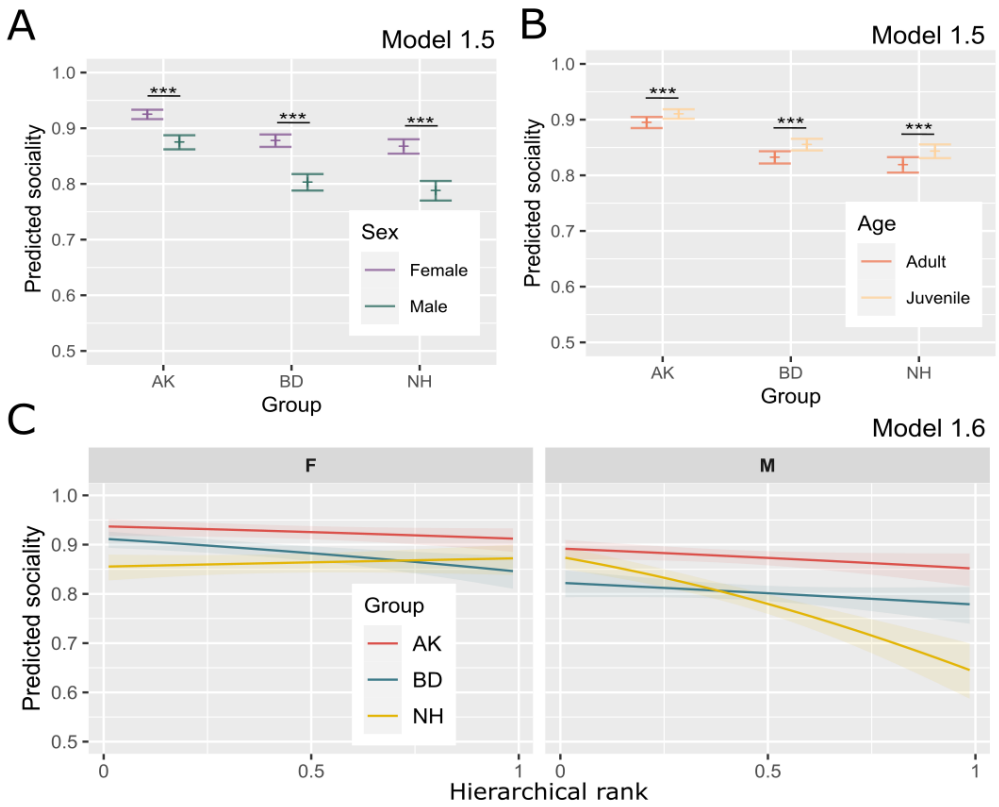


Figure 4. The effect of group identity is confirmed within all socio-demographic categories

A) Predicted sociality of individuals according to their sex in each group. The small horizontal bars denote the predicted mean sociality of males and females within each group according to Model 1.5. Error bars denote the standard error of the mean (SEM). (***) denotes the significant effects at the $\alpha < 0.001$ level. B) Predicted sociality of individuals according to their age in each group. The small horizontal bars denote the predicted mean sociality of adults and juveniles within each group according to Model 1.5. Error bars denote the standard error of the mean (SEM). (***) denotes the significant effects at the $\alpha < 0.001$ level. C) Differential effect of hierarchical rank in females' (F, on the left) and in males' (M, on the right) sociality within each group. Graphic representations are based on Model 1.6. Shaded areas denote 95% confidence interval (CI). AK: Ankhase, BD: Baie Dankie, NH: Noha.

dividual matri-love within each group and suggests that the interaction may emerge from a stronger effect of hierarchical rank on NH individuals matri-love.

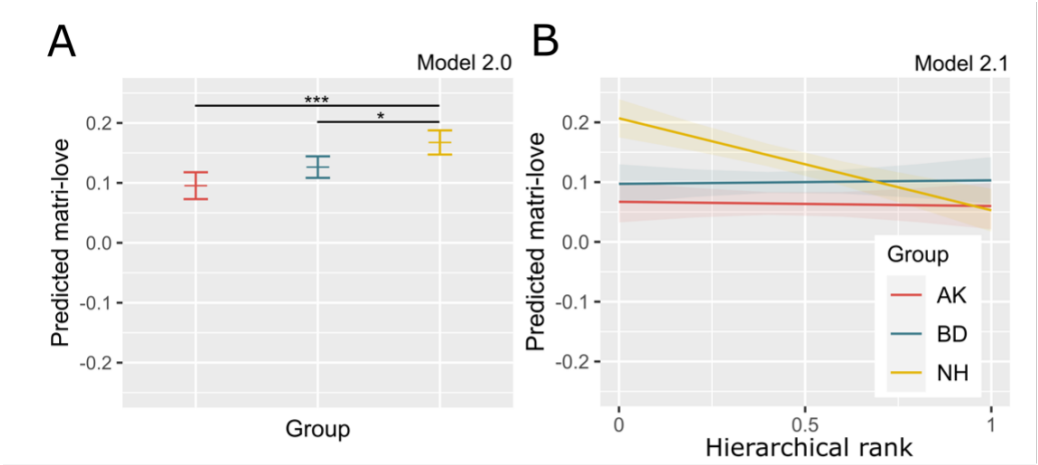


Figure 5. The propensity to be affiliative is less directed towards related individuals in AK and BD
A) Predicted matri-love per group. The small horizontal bars denote the predicted mean of matri-love as computed from Model 2.0. Error bars denote the standard error of the mean (SEM). (***) denotes the significant effects at the $\alpha < 0.001$ level. (*) denotes the significant effects at the $\alpha < 0.05$ level. B) Differential effect of hierarchical rank on matri-love within each group. Graphic representations are based on Model 2.1. Shaded areas denote 95% confidence interval (CI). AK: Ankhase, BD: Baie Dankie, NH: Noha

Question III: Grooming is more evenly distributed among individuals in AK.

In agreement with results of Model 1.0 regarding sociality index, we found in Model 3.0 (Table 1) that the degree of grooming reciprocity significantly differed across groups. Over the nine years of our analysis, according to a simple analysis (Model 3.0), grooming was more evenly distributed between individuals in AK rather than in BD and NH ($AME_{NH-AK} = -0.06$, $p < 0.001$; $AME_{BD-AK} = -0.07$, $p < 0.001$). Grooming was also significantly more reciprocal between NH rather than BD individuals ($AME_{BD-NH} = -0.01$, $p < 0.001$). Despite yearly fluctuations, the differences in grooming reciprocity between AK and BD individuals were similar across years (Year*AK-BD: $p = 0.36$), but this was not the case

when comparing NH to other groups (Year*AK-NH: $p < 0.001$; Year*BD-NH: $p < 0.001$) (Figure 6A). Similarly to our observations for sociality, the results of Model 3.2 (Table 1) indicated that, in similar demographic environments, groups of vervets still significantly differed from each other ($LRT = 150.459$, $p < 0.001$) with the same results as in Model 3.0 ($AK > NH > BD$: $AME_{NH-AK} = -0.05$, $p < 0.001$; $AME_{BD-AK} = -0.07$, $p < 0.001$; $AME_{BD-NH} = -0.02$, $p < 0.001$). Overall, as the relative number of males or adults increased in the group, the grooming reciprocity decreased ($AME_{Sex-ratio} = -0.03$, $p < 0.001$; $AME_{Age-ratio} = -0.03$, $p < 0.001$). At a more precise level, we found that the interaction between Sex-ratio*Age-ratio varied across groups with an opposite pattern between AK and the two other groups ($LRT_{Group*Sex-ratio*Age-ratio} = 13.874$, $p < 0.001$; see Figure S3 for details).

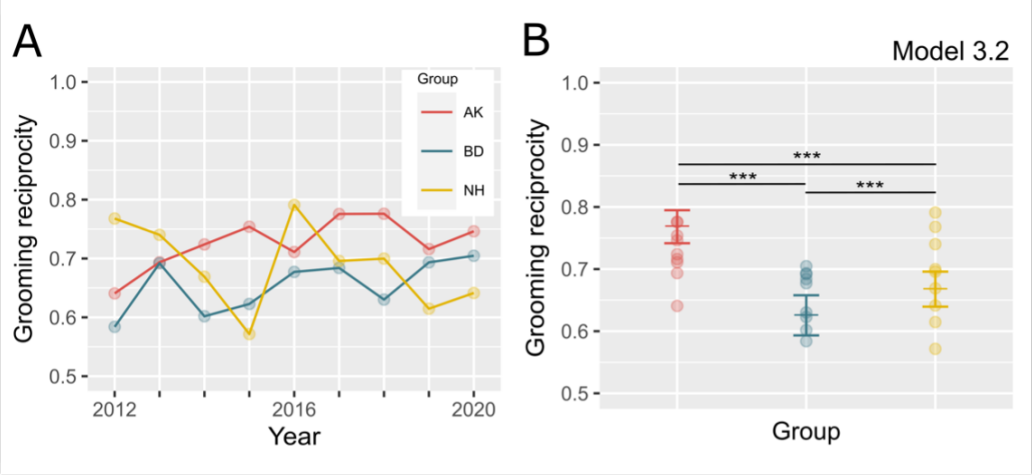


Figure 6. Grooming is more evenly distributed among individuals in AK. A) Dynamics of the level of grooming reciprocity in AK, BD and NH across years. Dots represent the grooming reciprocity of each group for each year of the study as computed from raw data. B) Predicted grooming reciprocity in AK, BD and NH for similar demographic environments. The small horizontal bars denote the predicted mean of grooming reciprocity within each group as predicted by the Model 3.2. Error bars denote standard error of the mean (SEM). Dots represent the grooming reciprocity of each group for every year of the study as computed from raw data. (***) denotes significant effects at the $\alpha < 0.001$ level. AK: Ankhase, BD: Baie Dankie, NH: Noha

DISCUSSION

Despite the large body of research on primate culture[7,5,43], there is still a lack of evidence regarding the existence and stability of social traditions, especially in the wild[44,22,28]. Our research contributed to fill this gap by investigating inter-group differences in sociality and their stability over nine years of data collected on three neighbouring groups of wild vervet monkeys. We found that individuals from one group – AK – were globally more affiliative than individuals in the two other groups, BD and NH. Taken together, our results show that these stable group differences in social dynamics are independent from demographic variables and are unlikely to be explained by genetic and ecological differences alone. Moreover, we report that males who dispersed between our study groups adjusted their sociality, becoming more social when they integrated into AK compared to the other groups and conversely becoming less social when they joined BD or NH, suggesting social conformity (as defined in[45]). Combined, these results suggest that these lasting group differences in basic social behaviours can be considered as social traditions in wild vervet monkeys.

Question I: sociality is predicted by group identity

AK individuals are more social

In agreement with our first hypothesis (I), we reported that individuals in one group - AK - had a higher propensity to be affiliative than individuals in the two other groups and that this effect was constant over the nine years of study despite the yearly fluctuations of each group's sociality. These differences were not due to trivial differences in demography, as group differences were maintained for similar group size, age, and sex ratios in our modelling. As an example, a change in one standard deviation value of sex or age ratio impacted group sociality ten times less than group identity did.

Origins of groups sociality differences: demographics, ecology and genetics sources of behavioural variability

The list of demographic variables influencing animal social behaviours is non-exhaustive[46] and we do not pretend to have captured the influence of the wide scope of potential demographic factors. For example, due to our data structure, we were unable to control for the number of births and deaths, which are known to influence social behaviour in vervet monkeys[47]. Even if we cannot completely exclude that one part of group's variability in sociality

might be due to variations in demography, the temporal scope of our study combined to the variability in each group demography enable us to exclude demography as the main and only sources of the observed differences in sociality.

Similarly, as already argued before[48], it is impossible to completely dismiss the potential effect of local ecological variability on sociality. Thus, even if ecological variability is unlikely to be the main driver of sociality differences as our study groups shared a similar global habitat, we can not exclude that groups' territories may be heterogeneous in resource availability and quality[49]. Variability in the ecological structure of each territory combined with the presence of specific predators may also have formed a heterogeneous "landscape of fear" (LOF)[50,51] where "prey perceive and respond to predation risk across both space and time simultaneously"[52] differently in each territory. Vervets are able to specifically recognize different predators[53] and their perception of predation risk (mainly from baboons and leopards) has been shown to influence their use of space[54]. We can then hypothesize that local differences in the LOF may have partially influenced the observed group differences in social behaviours.

Behavioural variability in primates can also be linked, to some extent, to genetic variability itself[55]. For example, Langergraber et al.[56] highlighted how behavioural dissimilarities reported by Whiten et al.[7] between wild groups or populations of chimpanzees were, for the majority (52%), significantly correlated with genetic dissimilarity between these groups. For the only social type of tradition reported in this paper, namely hand-clasp grooming, a genetic origin could not be explicitly excluded. At the neurobiological level, neurogenetics studies have highlighted how polymorphisms of coding or regulatory regions can lead to inter-individual variability in aggressive behaviours in primates, for example through the dopamine D4 receptor and the serotonin transporter[57]. However, in another study on wild orangutans[58], the proportion of geographic variations in cultural behaviours explained by genetic or environmental differences among populations was very low. A specific quantification of genetic dissimilarities between our groups of vervets could thus help future IVP-based studies to potentially exclude the hypothesis that genetic variability is partially linked to the observed behavioural variability. However, as highlighted by Schuppli et al.[48], "in practice, genetic components do not rule out the presence of social learning", so that even if we are unable to completely disregard the potential influence of genetics in our study it does not exclude the eventuality that social learning has a significant

role in the observed sociality differences between our group of vervets.

Transmission through social learning to dispersing males: a case of social conformity?

We reported that dispersing males were always more social in AK rather than in BD or NH. This effect was independent of the year of dispersal and of individual hierarchical ranks. These results were obtained from a limited set of individuals for which we had observation for a sufficient amount of time in the different groups. Nonetheless, these findings suggest that the previously mentioned differences in sociality between groups might be socially triggered. Conformity can be defined as "how individuals alter their behaviour to be similar to that of others"[59] and is central in recent reflection on animal behavioural variability[59] and more specifically animal[60,61] and human cultures[62]. Our result is consistent with the previously suggested conformity effect in dispersing males in wild vervet monkeys[37]. In the van de Waal et al. study[37], dispersing males adapted their foraging behaviour to the local norm rather than following their natal preference. This type of conformity relates to "Aschian conformity"[63] adopted through "overriding of personal knowledge or behavioural dispositions by countervailing options observed in others"[64]. Later, such conformity was also described in the food preference of female vervet monkeys[45] and was reported by authors as a potential "social conformity" where "individuals act like others not to achieve an informational function, but instead to achieve a social function that derives from simply "being like others"" as previously suggested by de Waal Bonding and Identification-based Observational Learning theory[65]. Such social conformity could be a potential vector of intra-group integration[45]. In the perspective of our study, social conformity could then play a similar role in the observed changes of adult males' sociality. Indeed, intra-group integration is a major challenge to dispersing males, who must join another group to mate and survive. Further experiments should be designed to assess if and how social dynamics can be socially transmitted and if it could assist in the intra-group integration of dispersing males.

Overall, our results add to previously published studies that argue for the existence of social traditions in bonobos[66], chimpanzees[67,68,69], capuchins[44,70], spider monkeys[23,22] and baboons[11,28].

A female-driven effect?

Interestingly, our results suggested that group differences in sociality may be driven by females. Indeed, differences in sociality between groups were stronger when groups contained a female-biased sex ratio. Regarding the literature, two main hypotheses (i; ii) on the origins of behavioural differences which could corroborate such result emerge. The first hypothesis (i) suggests that AK females might be more genetically linked to each other than females in BD and NH. According to Hamilton's theories on the selfish gene[71], increasing the number of females in a group, by highly increasing the overall genetic link between individuals, would therefore favour high levels of inter-individual affiliative behaviours. This genetic hypothesis is however contradictory with the decrease of sociality in BD and NH sociality when the groups had female-skewed sex ratios, and is thus insufficient to entirely explain our results. The second hypothesis (ii) proposes that increasing the relative number of females in a group might strengthen behavioural group differences, with females acting as "models" for social learning. Adult females (here the philopatric sex) form the social core of the groups[72] and may act as preferential "models" for social learning in wild vervet monkeys[36,38] (but, see[39,40]). Moreover, previous studies highlighted their role in the spread of social traditions to incoming adult males[28] and it has been shown that maternal affiliative relationships may be socially transmitted to offspring, similarly to the determination of offspring rank by maternal rank, in macaques and in hyenas[73,74]. This hypothesis is coherent with our results on dispersing males.

Effect of habituation on sociality

We observed a constant increase in sociality across the nine years of the study within each group. This result could be due to the gradual habituation of vervets to human presence, where habituation is defined as "the process by which repeated exposure to humans results in a gradual reduction in animals' fearful response, until animals no longer perceive humans as a direct threat"[75]. At the start of our study in 2012, the three groups were less habituated to observers and data collection was more difficult compared to nine years later where monkeys were highly habituated to human presence. Another potential explanation would be the existence of two stable states of the overall sociality: one before 2015 and one after 2015. Interestingly, 2015 was a year of unusual drought (see Newcastle station[76]), and such environmental perturbation may have elicited changes in groups social dynamics[77].

Question II: Group differences in sociality are not explained by simple effects of individuals socio-demographhy or kinship

An even increase of sociality across all socio-demographic classes in AK

Our results indicated that AK high sociality was not due to a specific socio-demographic category but rather emerged from a global increase of sociality within every socio-demographic category. Indeed, sex, age and hierarchical rank had similar effects on sociality in the three groups.

The effect of sex, age, and hierarchical rank on sociality

Our analysis confirmed the robustness of previous findings regarding socio-demographic influences on sociality and reported novel unexpected effects. First, we found that females were more social than males. This result corroborates previous studies showing that females tend to be more involved than males in grooming and play interactions and less involved in agonistic interactions[16,78,15]. More surprisingly, we found that juveniles were generally more social than adults. This could be due to the fact that juveniles are more often involved in play interactions than adults, but equally involved as adults regarding grooming interactions or agonistic interactions[16]. However, the effect of age on sociality was rather weak and may thus have a limited role in intra-group variation. Nevertheless, we found a negative effect of hierarchical rank on sociality. This result suggests that, even if high-rankers have been shown to be more involved in both grooming and agonistic interactions (acting more as aggressor and receiving more grooming than low-rankers)[16], the relative increase in aggression might be greater than the relative increase in grooming interactions. In particular, we found that this effect was even stronger in NH males compared to the other groups.

AK individuals are not more affiliative toward related ones

Our study also suggested that AK high sociality did not emerge from biased social interactions towards related individuals. However, in contrast with our hypothesis, we found that NH individuals had a higher tendency to be affiliative towards related conspecifics rather than unrelated ones, compared to AK. This group difference may derive from the behaviours of low-rankers in NH. However, as our knowledge of matriline cannot extend prior to 2010, we cannot exclude the fact that what we defined as "unrelated" conspecific which are relatively more related in our group than in another. Combined with the effect of the hierarchical rank on NH males' sociality, this

result suggests that the hierarchy had a greater impact on social behaviours in NH compared to AK and BD.

Influence of "keystone" individuals?

In the present study, some individuals were present from the start to the end of the study within a single group. It is possible that one or a few of these individuals had a significant impact, not by itself, but via a substantial influence on other members of the group ("keystone" individual[79]). We argue that the field would greatly benefit from the precise dissection of the influence of individuals' personalities on group-specific primate social behaviours. Indeed, several studies detected the presence of "key" individuals to have a significant impact on group-specific "collective behaviours"[79,80,81,82,83]. Their impact has been especially studied in the enhancement of cooperative behaviours[83].

Question III: Grooming is more evenly exchanged among AK individuals

Interestingly, our results on grooming reciprocity corroborated the ones on sociality, both highlighted the specificity of AK global social dynamics. We found that grooming was exchanged more evenly between AK individuals rather than between BD or NH individuals. This difference between groups was however less stable over time than the difference we found in sociality. Within the Biological Market Theory[42,84,85,86,87,88,89], this result could be interpreted as a less tense state of the biological market in AK than in BD and NH, where high-rankers have a lower power over low-rankers (i.e. less dominance-based disproportion in resource access)[84]. Our measure of grooming reciprocity is however unconventional, as we were unable to obtain consistent data on the more conventional direct reciprocity - number of grooming bouts within a single, time-condensed, grooming interaction. Further study using direct reciprocity and considering the time span of each grooming bout[90,91,87] should be considered to confirm these results.

In conclusion, our study reports the existence and stability of different degrees of sociality and grooming reciprocity in three groups of wild vervet monkeys. Such differences in social dynamics could not be explained by differences in group demographics, and they impacted every socio-demographic class. These differences in sociality across neighbouring groups of wild vervet monkeys cannot be explained by genetic and environmental differences alone. Thus, part of this variability may emerge from social learning, emphasized by

the fact that dispersing males conformed to the local sociality of the group they joined. Thus, these results provide new insights on the existence of social traditions in wild monkeys. In accordance with Schuppli & van Schaik[48], we believe that researchers have only discovered the tip of the primate culture iceberg so far, mainly composed of complex technical behaviours, while we miss information about the base of this iceberg. With this study, we contribute to filling this gap, suggesting that this base is composed of basic skills from the social realm.

Limit of the study

However, our work presents some limitations. First, we used data collected *ad libitum*, a method for which it is difficult to assess accurately the sampling effort (but see Canteloup et al.[92] for high correlation of social networks assessed via *ad libitum* and focal animal sampling). One limitation of *ad libitum* sampling is that shier individuals might be sampled less often than others, and appear thus less social than they are, which could lead to a potential bias in social networks. Second, although our study groups share the same environment with genetic flux between groups, we do not have precise data on ecological and genetic variability. A study of ecological and genetic variation of our study groups would bring some elements regarding potential fine-grained differences (e.g. "landscape of fear") in our study groups territories. Third, the influence of keystone' individuals on group social dynamics is still poorly known and more work on animal personalities are needed to disentangle between those effects.

Resources availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Elena Kerjean (elena.kerjean@gmail.com).

Data and code availability

Reproducible model code and data can be found here: zenodo.7997943

ACKNOWLEDGMENTS

We thank the onsite managers, Albert Driescher and Arend van Blerk and all the field assistants, Master students, PhD students and postdocs who collected the data over the study period. We are grateful to the van der Walt

family for giving us the permission to conduct the study on their land. We thank Pooja Dongre for her advice on the Elo-rating calculation and Rachel Harrison and Frédéric Schütz for their statistical advice. This project was funded by the Swiss National Science Foundation ($P300P3_151187$, $31003A_159587$, $PP00P3_170624$ and $PP00P3_198913$) along with Branco Weiss Fellowship–Society in Science (granted to EvdW) and to a Fyssen grant (granted to CC).

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DECLARATION OF INTERESTS

The authors declare no competing interests

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METHODS

Study site and subjects

Data were collected over nine years (2012-2020) within the Inkawu Vervet Project (IVP), at Mawana game reserve (28°00.327S, 031°12.348E) in KwaZulu Natal, South Africa. We used the data collected in three neighbouring groups of wild vervet monkeys: AK, BD, and NH. These groups have been studied as part of IVP since 2010 and have been habituated to human presence since that time. We only included individuals that stayed in their group for at least six months during a given year in data analysis to ensure we had sufficient data per individual to analyse. Unless mentioned, we included individuals of both sexes and all ages in our analysis. Data collection was approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa.

Behavioural sampling and coding

We used data collected by trained research assistants and researchers using *ad libitum* sampling[93,94]. In such a case, no constraints are placed on the individuals for which data are recorded nor the period when the data are recorded. An interaction is defined here as one or more behaviours performed between two individuals (hereafter, dyad). On the basis of established ethograms of social behaviours (Table S1, Table S2, Table S3), we defined affiliative interactions as interactions including only affiliative and neutral behaviours and agonistic interactions as interactions including only agonistic and neutral behaviours. Our dataset included a total of 68 443 affiliative interactions and 16 259 agonistic interactions. In 2017, three months (June, July, August) of missing time of observation and/or affiliative interactions were excluded from our analysis. Observers recorded behaviours as point events. To assess sampling effort, we took the total amount of time spent in the field during field days as a proxy for the effort of *ad libitum* sampling in

each group. We assessed this effort by computing the duration of observation of each group per day which we multiplied by an attenuating factor of the number of observers for each field session according to a binary logarithmic function, so that the weight of each observer decreased as the number of total observers increased (AK mean ± SD: 2706 ± 803, BD mean ± SD: 3360 ± 614, NH mean ± SD: 3439 ± 974). Before data collection, each observer passed an inter-observer reliability test (80 % agreement required between two observers).

Group demographic and individual socio-demographic variables

Group size was computed as the number of individuals included in our analysis for each group in each year (AK mean: 27 individuals ± 8.5, range: [18-41]; BD mean: 50 individuals ± 6, range: [43-62]; NH mean: 39 individuals ± 7, range: [31-50]). The sex ratio was computed as the number of males divided by the number of females in each group for each year, so that, the more the sex ratio increased, the greater the relative number of males was in the group. The age ratio was defined as the number of adults divided by the number of juveniles in the group, similarly, the more the age ratio increased, the greater the relative number of adults was in the group (Table S5). We classified individuals according to four age classes: newborn (from their birthday to the end of their birth year), infant (from the start of birthyear +1 until first birthday), juvenile (male: 1-5 years old; female: 1-4 years old) and adult. Regardless of their age, as soon as they gave birth (for females) or dispersed from their birth group (for males), individuals were considered adults. After the end point of juvenile period (five years old for males, four years old for females) even if they had not met these criteria of adulthood, individuals were considered as adults. Hereafter, when individual level analyses were performed, newborns and infants were excluded due to the lack of a hierarchical rank for these individuals. We computed the hierarchical rank of all individuals using the elo-rating method[95]. To do so, we based our analysis on the Elorating 0.46.11 package of R[96]. The specificity of this method lies in the fact that it updates individual hierarchical rank after each conflict: winners increase their rating while losers decrease their rating. The magnitude by which the rating changes depends on the expected outcome of the conflict (i.e., the difference between the previous ratings of the two opponents). We specified the relationship between the rating difference and the winning probability as a sigmoidal curve, following[97]. The k parameter of the maximal amplitude of change after an interaction has

been set to 50. The initial rating for all individuals was 1000. We computed hierarchical rank distance between individuals as the absolute value of the difference between the elo-rating of the two individuals from a dyad.

Social indices

Sociality indices: propensity of being affiliative

The sociality indices are here defined as the proportion of affiliative interactions (i.e., the number of affiliative interactions divided by the sum of the number of agonistic and affiliative interactions). We computed two sociality indices: a group sociality index and an individual sociality index. The group sociality index was computed as the proportion of affiliative interactions in a specific group during a year, regardless of the individuals involved in each interaction. The individual sociality index was computed as the proportion of affiliative interactions per individual. Both sociality indices ranged from 0 to 1. A sociality index close to 0 means that individuals were more agonistic than affiliative, and conversely, when close to 1, individuals were more affiliative than agonistic. Affiliative behaviours mainly included grooming events (80% of all affiliative behaviours), so each interaction was treated as qualitatively equivalent. To take into account the level of aggression of each agonistic interaction, we attenuated the weight of mild agonistic interactions (without direct contact) by a factor of 0.5. Sever agonistic interactions were classified as: attack, bite, chase, fight, grab or hit (Table S2).

Matri-love index

We computed a matri-love index at the individual level. The matri-love index quantified the directionality of individual sociality: either toward individuals from the same matriline or not. To do so we computed two sociality scores for each individual: the first one included only the interactions involving individuals from the same matriline while the second one included only the interactions between individuals from a different matriline. We defined the difference between these two measures as the matri-love index. The matri-love index is lower than 0 when sociality is higher with individuals from a different matriline and higher than 0 when sociality is higher with individuals from the same matriline.

Grooming reciprocity index

We computed one grooming reciprocity index at the group level. In total, we included 63 325 grooming behaviours in our analysis. To compute the grooming reciprocity index, we built a matrix of reciprocity (M) between individuals of a single group during a specific year. The reciprocity index (R) was then calculated with the following formula:

$$R = 1 - \frac{S_M}{\|M\|} = 1 - \frac{\frac{\|M - M^t\|}{2}}{\|M\|} \tag{1}$$

where $\|M\| \neq 0$ and with S_M the distance of the matrix M to the sub-vectorial space of symmetrical matrices and M^t denotes the transposed matrix of M with $\|\|$, being the euclidean norm. R is thus a measure of the similarity between the upper triangular part of the matrix M and its lower triangular part.

Statistical analysis

Statistical models (Table 1) were assigned a number in the form x.y, where x defines the dependant variable used in the model - either sociality (1), matri-love (2) or grooming reciprocity (3) - and y defined the sequential order of analysis. All models, unless mentioned, used a binomial distribution of the error terms with a logit link function. This structure defines our dependant variables by a logistic function (i.e., inverse of logit function). To help model convergence and to make interpretation of estimates easier, continuous covariates were Z-transformed to a mean of 0 and a standard deviation of 1 prior to model selection[98]. One exception was made for the variable describing the Elo-rating as it is bounded between 0 and 1. All final models were compared to a null model, containing control covariates and random effects. This method assessed whether the inclusion of predictors improved our model or not (we used the function *anova* with the test parameter set to "Chisq"). We chose random effects with at least five levels[99].

Model construction

We based our model selection on a forward selection strategy using the lowest Akaike information criterion (AIC) as a selection criterion[100]. We first interpreted the value of estimates of the main effects before including significant interactions in the models. We interpreted only significant interactions which included the fixed effect Group, as our interest was focused on the

effect of group identity. To assess the significance level of each of the predictors, we compared the full model to a model with one omitted predictor via a likelihood ratio test (we used the function *drop1* with the argument test set to "Chisq"). Post-hoc analysis on categorical variables was then performed using the Bonferroni p-value adjustment[101]. After a first interpretation, we tested interactions using *drop1* function and performed post-hoc analysis on these interactions. In models including significant interactions, we re-evaluated the effects of the main effects that were not included in the interactions, and only mentioned changes if the estimate changed from more than 2% or if the significance level changed. Then, we interpreted the main effects of the predictors part of the interaction as marginal effects conditional on the value of the second predictor being equal to its intercept value.

Model evaluation

For each final model selected, we performed a two-stage evaluation. First, we verified multi-collinearity, using the function *vif* from the package *car* 3.0.12, measuring the variance inflation factor (VIF) of each fixed effect in our model. We made sure that generalized VIF (GVIF) values of each of the continuous variables and the square of $GVIF^{1/2df}$ for each categorical variable were lower than 5[102]. Secondly, we visually checked the distribution of the residual deviance according to the predicted values of our dependant variable[103]. We made sure this distribution did not show any specific pattern.

Effect of predictors in GLMs and GLMMs

In the specific case of non-linear regression, GLMs and GLMMs (generalized linear mixed models), we obtained varying effect of predictors across the range of these predictors. The direction of the effect of the predictor was induced from the log-odds. To measure for the intensity of each effect we discussed the average marginal effects (AMEs) of each predictor and/or the estimated marginal means (EMMs) of the response variable for different values of each predictor. AMEs were obtained from the function *margins* from the package *margins* 0.3.26[104], while EMMs were obtained with the function *ggemmeans* from the package *ggeffects* 1.1.2[105]. When results from statistical analysis are mentioned for categorical variables, in such a way: A-B, the second category (i.e., B) refers to the category defined as intercept in our analysis. We ran all analyses in R Studio version 1.3.1093 using R version 4.1.2[106].

Question I: Is sociality predicted by group identity and do dispersing males adapt to their local group?

In order to have a global understanding of the overall differences in sociality between groups, we first computed a trivial model which isolated *Group* as the only main predictor of group sociality (Model 1.0). We used *Year* as a random effect and not as a fixed effect, because including it as a fixed effect induced a slight abnormal pattern in residuals. In order to inspect the stability of group differences across years we included *Year* as a fixed effect in a second model (Model 1.1) to evaluate the interaction *Group*Year*.
Next, we constructed a more complex model to control for the group demographic (sex ratio, age ratio and group size) and experimental (time of observation) variables, using *Year* as a random effect (Model 1.2). Due to a high collinearity of *Group Size* ($20 > VIF > 10$), and as the correlation between the group size and other variables in our model was low to mild ($Group : 0.45$, $Sex\ ratio : 0.15$, $Adult\ ratio : 0.42$), we kept this variable as a control in our models. To have a more precise understanding of the socio-demographic conditions under which group differences in sociality was modified we then included significant interactions (Model 1.3).
Because some males dispersed between our study groups over the course of the nine years study, we could investigate whether their sociality changed between the group they quit and the group they integrated. We included in the analysis (Model 1.4) behavioural data collected of six males who dispersed in between our three study groups and for which we had sufficient data. We calculated the mean group sociality as the mean of the sociality of the three group during a year. As the mean group sociality during the arrival year of the males could be globally influenced by yearly ecological changes, we included it as a control variable in the model. As this analysis was performed at the individual level, individual identity was included as a random intercept. We removed individual hierarchical rank from the model as its effect on individual sociality was not significant (Log-Odds $= -3.87$, Confidence Interval : $[-8.37, 0.63]$, $p = 0.46$).

Question II: Is sociality similarly distributed between individuals in each group?

We aimed to study the dynamic of sociality at the individual level. First, we analysed the overall effect of sex, age and hierarchical rank on sociality (Model 1.5) and inspected their interaction with *Group*. In a following model (Model 1.6) we included the significant three-way interaction

*Group*Sex*Hierarchical rank* but excluded the interaction of *Sex*Age*Hierarchical rank*. We did so in order to reduce the complexity of interpretation and to focus on the different relations between groups rather than the effect of socio-demographic categories on individuals sociality.

To deal with the potential effect of genetic link between individuals, we calculated the matri-love of each individual classified as adult females or juveniles (males and females) according to the group they stayed in (Model 2.0). We excluded adult males as they originated from a different natal group. In this model, we kept *Age* and *Sex* as control variables. We included group and hierarchical rank as covariates and individual's identity as a random intercept. In a following model (Model 2.1), we added the significant interaction *Group*Hierarchical rank* to test for the differential effect of hierarchical rank across groups.

Question III: Are group differences in grooming reciprocity coherent with group differences in sociality?

Similarly, to our analysis of sociality at the group level, in Model 3.0 the dependent variable was the group grooming reciprocity, the fixed effect was the *Group*, and the *Year* was the random intercept. In model 3.1, *Year* was considered as a fixed effect along with the interaction *Year*Group*. Finally, in Model 3.2, *Group*, *Sex ratio*, *Age ratio*, *Group size* and the *Time of observation* were used as fixed effects and the *Year* set as a random intercept.

SUPPLEMENTAL INFORMATION

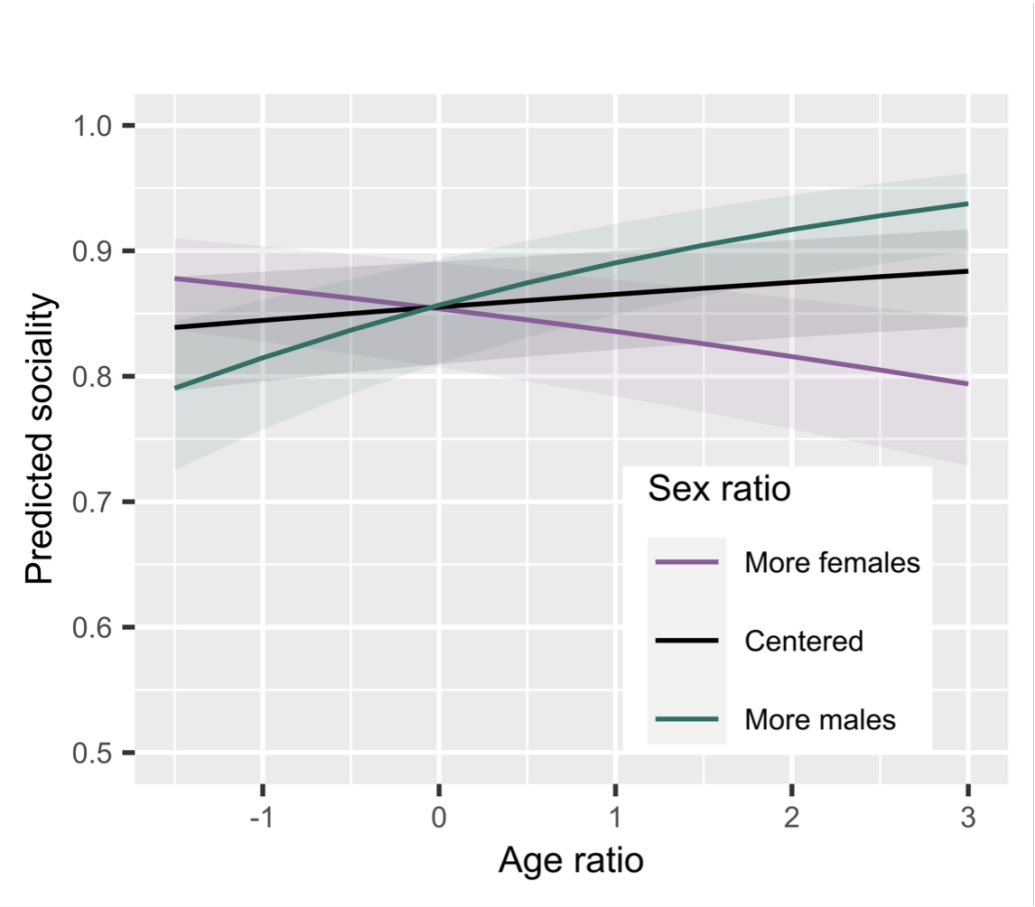

Figure S1. The influence of sex ratio on the effect of age ratio on sociality.
The x-axis represents the variation in the scaled value of the age ratio, negative values represent a juvenile skewed group and positive values represent an adult skewed group compared to the mean observed age ratio. Shaded areas denote 95% confidence interval (CI).

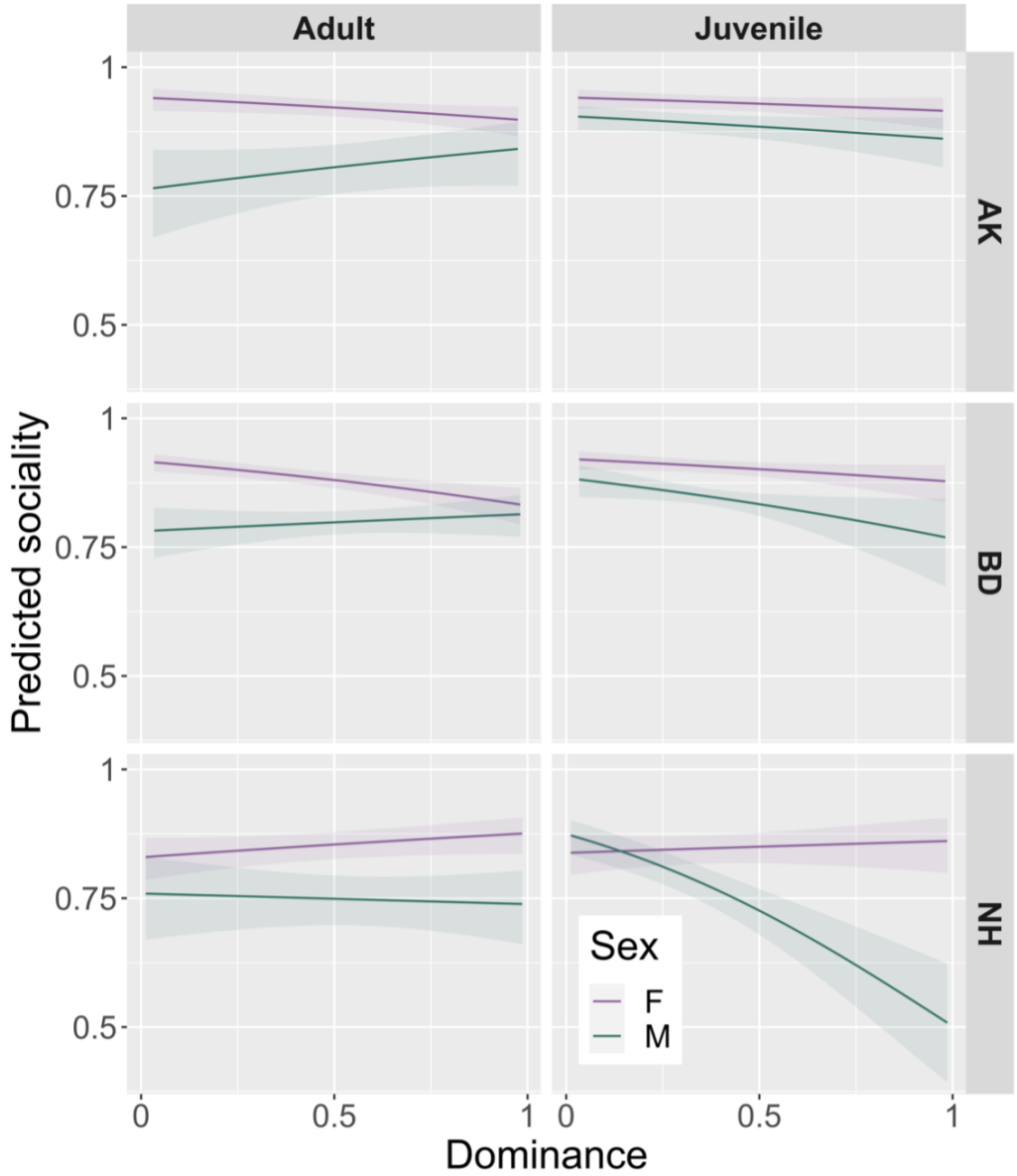

Figure S2. The interaction of sex, age and hierarchical rank on individual sociality within each group.
Predicted sociality is computed from models predicting the sociality of individuals according to the interaction *Sex*Age*Hierarchical rank* in each group. Shaded areas denote 95% confidence interval (CI). AK: Ankhase, BD: Baie Dankie, NH: Noha.

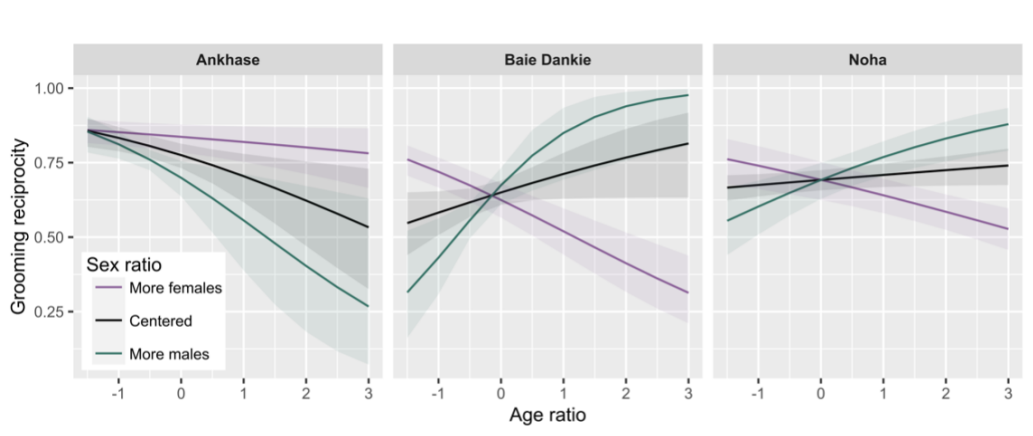

Figure S3. Differences of interaction between age ratio and sex ratio on grooming reciprocity within each group.

Behaviour	Code	Type of interaction	Description
Embrace	EM/HU	Affiliative	Individual is taking another one in its arm in an affiliative way.
Grooming	GR	Affiliative	Individual groom a partner.
Infant handling	IH	Affiliative	Individual is manipulating the infant of another individual.
Lip smacking	LS	Affiliative	Making noise by clapping lips together, or clicking teeth together.
Mouth contact	MM/MC	Affiliative	Individual touches its mouth to/near its partner's (as if giving a kiss).
Nursing	NU	Affiliative	Infant is suckling on its mother.
Play	PL	Affiliative	Individual play with another.
Present	PR	Affiliative	Presenting a part of body to be groomed.
Sit in contact	SG	Affiliative	Individuals sitting in contact, one next to another.
Sleep with	SW	Affiliative	Individual is sleeping in contact with another individual.
Touch	TO	Affiliative	Individual touching a partner in a gentle way.

Table S1. Ethogram of behaviours included in affiliative interactions.

Behaviour	Code	Type of interaction	Description
Attack	AT	Agonistic (direct)	Forward motion of the body.
Bark	BA	Agonistic	Individual produce a specific alarm call type (bark).
Bite	BI	Agonistic (direct)	Biting another individual.
Chase	CH	Agonistic (direct)	Running after another individual who is fleeing.
Crawl	CR	Agonisitc	Bow down to an aggressor while looking at them.
Fight	FI	Agonistic (direct)	When two or more individuals engage in an aggressive interaction.
Flee	FL	Agonistic	Run away from an aggressor as they chase.
Grab	GB	Agonistic (direct)	Grabbing another individual.
Hit	HI	Agonistic (direct)	Hitting another individual.
Jump Aside	JA	Agonistic	Jump aside to avoid something or someone.
Kidnapping Baby	KB/SB	Agonistic	Stealing a baby and refusing to hand it back to its mother.
Look for support	LO	Agonistic	Looking around for support while they are being threatened by an aggressor.
Scream	SC	Agonistic	Distress/scream to an aggressor.
Stare	ST	Agonistic	Popping up the eyelids so white above eyes is visible. Often combined with attack.
Steal Food	SF	Agonistic	Take another individual's food.
Stand Up	SU	Agonistic	Stand up during a conflict with another individual, often following a crawl.
Take Place	TP	Agonistic	Individual displaces another and takes their place, usually combined with approach.

Table S2. Ethogram of behaviours included in agonistic interactions only.

Behaviour	Code	Type of interaction	Description
Approach	AP	All	Approaching another individual.
Auto-groom	AG	All	Individual groom itself.
Avoid	AV	All	Head or body movement away from an aggressor, or stopping previous behaviour.
Carry infant	CA	All	Individual carries another's infant whilst moving.
Feed from mouth	FM	All	Individual takes food from another individual's cheek pouches.
Follow	FO	All	Individual clearly walks behing another one.
Frustration hop	FH	All	Individual jumps up and down , usually while screaming and potentially looking intensely at another individual.
Grunt	GU	All	Individual produces low-frequency guttural calls (grunts).
Ignore	IG	All	Carry on with previous behaviour.
Leave	LE	All	Walk away.
Retrieve baby	RB	All	Mother retrieves her infant from a partner or from the ground if the infant was independent.
Retreat	RT	All	Quickly leave the proximity of another individual.
Refuse	RF	All	Individual refuses attempts to interact.
Smell	SM	All	Individual smells or sniffs its own or another individual
Scream	SC	All	Individual produces a distress call/scream usually during agonistic interactions but also produced during frustrating situations.
Teeth-chattering	TC	All	jaw movements that are noisy, usually between males of different ranks to initiate close proximity/grooming.
Walk by	WB	All	Individual walks parallel (approaches indirectly) to another one.
Vocalization	VO	All	Individual produces any call that is not an alarm call or a scream.

Table S3. Ethogram of behaviours included in all types of interactions.

Year	Group	Sex ratio	Age ratio	Group size
2012	Ankhase	1.31	0.58	30
2012	Baie Dankie	0.76	0.76	44
2012	Noha	1.24	0.81	38
2013	Ankhase	1.57	0.50	36
2013	Baie Dankie	0.96	0.44	49
2013	Noha	1.10	0.56	42
2014	Ankhase	1.33	0.67	35
2014	Baie Dankie	1.27	0.52	50
2014	Noha	1.14	0.47	47
2015	Ankhase	1.33	0.45	42
2015	Baie Dankie	1.12	0.56	53
2015	Noha	1.08	0.52	50
2016	Ankhase	1.20	0.47	22
2016	Baie Dankie	0.79	0.59	43
2016	Noha	1.07	0.38	29
2017	Ankhase	0.64	0.64	18
2017	Baie Dankie	0.92	0.92	46
2017	Noha	0.82	0.35	31
2018	Ankhase	0.46	0.36	19
2018	Baie Dankie	0.81	1.45	49
2018	Noha	0.88	0.60	32
2019	Ankhase	0.86	0.53	26
2019	Baie Dankie	0.82	0.94	62
2019	Noha	0.83	0.91	42
2020	Ankhase	0.82	0.82	20
2020	Baie Dankie	0.81	1.24	56
2020	Noha	0.82	1.11	40

Table S4. Demography within each group across year.

Year	Group	Adult Females	Adult Males	Juvenile Females	Juvenile Males	Total
2012	Ankhase	5	4	5	7	21
2012	Baie Dankie	14	4	8	4	30
2012	Noha	11	5	4	7	27
2013	Ankhase	6	4	5	9	24
2013	Baie Dankie	11	4	8	12	35
2013	Noha	11	3	6	13	33
2014	Ankhase	8	4	4	14	30
2014	Baie Dankie	10	5	10	20	45
2014	Noha	12	3	7	15	37
2015	Ankhase	8	2	5	13	28
2015	Baie Dankie	12	7	8	15	42
2015	Noha	12	3	8	16	39
2016	Ankhase	3	3	6	8	20
2016	Baie Dankie	12	4	10	13	39
2016	Noha	6	2	7	10	25
2017	Ankhase	5	2	4	4	15
2017	Baie Dankie	15	7	6	15	43
2017	Noha	7	1	7	11	26
2018	Ankhase	4	1	6	4	15
2018	Baie Dankie	17	12	7	6	42
2018	Noha	10	2	6	5	23
2019	Ankhase	7	2	5	5	19
2019	Baie Dankie	20	9	7	7	43
2019	Noha	13	6	4	7	30
2020	Ankhase	7	2	4	5	18
2020	Baie Dankie	20	10	10	12	52
2020	Noha	13	5	8	6	32

Table S5. Number of individuals in each socio-demographic category within each group across years.