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 with.
- 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 with. 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. Culture encompasses "those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information" [1] and includes several 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" [2]. The accumulation of evidence in wild and captive non-human animals (hereafter: animals) revealed the existence of traditions in a variety of mammals and birds, from tool use in chimpanzees to song dialects in birds[3]. Although traditions appear to be widespread in non-human animals, the use of the term "culture" for non-humans is still debated. While, some researchers consider that culture relies on complex cognitive processes involving symbols and that cumulative culture is a hallmark of human beings[4,5], depending on know-how copying processes[6], others adopt a broader definition of culture defined as socially transmitted knowledge which is not based on genetic inheritance[7,8]. It has been proposed that the difference between human and animal culture might rely on the fact that, contrary to other animals, humans are able to generate knowledge that accumulate over generations[9,5].

Over the last decades, animal tradition 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*) on Koshima Islet, Japan[10]. Such behaviour was observed only in a few groups of Japanese macaques[4], authors then described this behaviour as pre-cultural[10]. However, 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)" [11]. In this example, Koshima group was the only one where the sweet potato washing behaviour progressively spread : by 1956, eleven monkeys of the same group acquired this behaviour (80 % of adults). What remains

controversial in this example is the mechanism implied in the spread of the behaviour; imitation being unlikely to explain the adoption of the habit that could be due to simpler mechanisms (e.g. enhancement; social facilitation)[4]. A classical method used to investigate the social origin of a behaviour is to exclude both obvious ecological and genetic variations, leaving social transmission as the only probable cause of the observed behavioural diversity (i.e., method of exclusion)[12]. However, across the literature, most studies have investigated the behavioural variability of geographically distant populations[3]. Quantifying the influence of ecological and genetic variation in such a setting can easily be misleading in the case of subtle environmental variations[13]. Recently, several researchers argued that studying neighbouring groups of animals of the same species limits genetic and ecological biases because they live in relatively similar ecological and genetical environments[14,15]. 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 traditions in wild animals[14,16,17,18,19,20].

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[21]. 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[22,23] 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.[24], 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 traditions, especially in animals with slow life histories such as primates[25,24?] .

Animal traditions can be classified in three different categories: material, food-related and social traditions (see[26] for a review of monkey traditions). Even though, several social behaviours are known to be transmitted socially[27,28,29], strong evidence for social traditions is still lacking in comparison to material or food-related animal traditions[30]. 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*)[31]. 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 less 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.[32] 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 (*Cebus capucinus*, *Macaca fascicularis*)[33,34,35]. For example, over a four-year period, Rose et al.[33] found that one group of white-faced capuchin monkeys (*Cebus capucinus*) was highly involved in grooming with spider monkeys compared to five other neighbouring groups. De Waal & Johanowicz[36] reported that juvenile rhesus macaques (*Macaca mulatta*) dramatically increased their reconciliation rates after being translocated to a group of a more conciliatory species, the stumptail macaques (*Macaca arctoides*). In 2004, Sapolsky et al.[16,37] 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 males from the original study died and were replaced by immigrants, 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"[38]. Here, we use the term "social dynamics" to align with research on great ape social traditions[39]. Overall, even if quantitative variability in social behaviours have been identified, more evidence that these differences in social dynamics are mainly dependent upon social learning in monkeys is 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)[25,24,40], but a variety of other metrics have been used in the literature[41,42]. Based on the definition of sociality in chimpanzees as "interaction tendencies"[39], 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[43]. It has a crucial role in primate sociality: it maintains social bonds between individuals and decreases stress[43]. 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.,[44] 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 discover 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[45]. A body of studies has shown that vervet monkeys socially learn how to manipulate artificial fruits[46,47,14,48,49] and to process novel food[50], but their potential to socially learn global social dynamics remains poorly known. 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 into 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 consistent with differences in sociality?

Here, we extend previous studies by combining three grounding aspects of research on animal traditions: 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 from the Inkawu Vervet Project (IVP) : Ankhase (AK),

Baie Dankie (BD) and Noha (NH). Borgeaud et al.,[51] suggested in 2016 that the stability and structure of vervet monkey 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[52]. However, these studies did not investigate the long-term stability of these differences nor the influence of group demographical conditions. In the later study[52], one of our study groups, AK, displayed a higher level of co-feeding tolerance. Based on these previous findings and regarding question I, we predict AK to have an overall higher propensity to be affiliative than NH and BD. Additionally, van de Waal et al.[47] 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 predict 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[51]. 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 and that this difference was stable across time (Figure 1A, Table 1). Indeed, *Group* had a significant effect on sociality (Likelihood ratio-test $LRT_{Group} = 729.47$, $p < 0.001$) whatever the year. In particular, AK had a significantly higher sociality than BD (Average marginal effect $AME_{AK-BD} = 0.06$, $p < 0.001$) and NH ($AME_{AK-NH} = 0.1$, $p < 0.001$), and BD had a significantly higher sociality than NH ($AME_{NH-BD} = 0.03$, $p < 0.001$). Furthermore, according to Model 1.1 the sociality of each group increased with time. AK and BD followed a similar trend (Conditional mode $CM_{Years|AK} = 0.17$; $CM_{Years|BD} = 0.16$) while NH trend was slightly slower ($CM_{Years|BD} = 0.09$). 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 in each group (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., 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 from each other ($AK > BD$: $\beta_{BD-AK} = -0.37$, $p = 0.004$) 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 by $+0.13 \pm 0.12$ ($N = 5$, 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 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 agreement 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, Table S5) 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). 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*: $p = 0.62$). More detailed analysis 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 - for males of low dominance (close to 0), the difference in sociality between AK and NH was not significant ($p = 1.00$). 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 S1).

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). Matri-love index indicates the directionality of the sociality of an individual, directed either towards individuals from the same matriline (related individuals) or other individuals: the higher the value, the higher the propensity to be affiliative toward related individuals. 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 5B illustrates the effect of hierarchical rank on

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

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

In agreement with the 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 ($AME_{BD-NH} = -0.01$, $p < 0.001$) (Figure 6A). Similarly to our observations for sociality, the results of Model 3.1 (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 ($AK > NH > BD$: $AME_{NH-AK} = -0.05$, $p < 0.001$; $AME_{BD-AK} = -0.07$, $p < 0.001$; $AME_{BD-NH} = -0.02$, $p < 0.001$) (Figure 6B). 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 S2 for details).

DISCUSSION

Despite the large body of research on primate culture[12,1,53], there is still a lack of evidence regarding the existence and stability of social traditions, especially in the wild[54,31,37]. Our research contributes filling 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[55]). 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 find 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 stable 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.

Origin of group sociality differences: demographics, ecology and genetics sources of behavioural variability

The list of demographic variables influencing animal social behaviours is non-exhaustive[56] and we do no 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[57] and in gorillas[58]. Even if we cannot completely exclude that one part of group variability in sociality might be due to variations in demography, the temporal scope of our study combined with the variability in each group demography enable us to exclude demography as the main and only source of the observed differences in sociality.

Similarly, as argued before[59], 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 cannot exclude that groups' territories may be heterogeneous in resource availability and quality[60]. 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)[61,62] where "prey perceive and respond to predation risk across both space and time simultaneously"[63] differently in each territory. Vervets are able to specifically recognize different predators[64] and their perception of predation risk (mainly from baboons and leopards) has been shown to influence their use of space[65]. 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[66]. For example, Langergraber et al.[67] highlighted how behavioural dissimilarities reported by Whiten et al.[12] between wild groups or populations of chimpanzees were, for the majority (52%), significantly correlated with genetic dissimilarity between these groups although no causality was here advanced. 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[68]. However, in another study on wild orangutans[69], the proportion of geographic variations in traditions 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.[59], "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 groups 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 maintained.

Conformity can be defined as "how individuals alter their behaviour to be similar to that of others"[70] and is central in recent reflection on animal behavioural variability[70] and more specifically animal[71,72] and human traditions[73]. Our result is consistent with the previously suggested conformity effect in dispersing males in wild vervet monkeys[47]. In the van de Waal et al. study[47], dispersing males adapted their foraging behaviour to the local norm rather than following their natal preference. This type of conformity relates to "Aschian conformity"[74] adopted through "overriding of personal knowledge or behavioural dispositions by countervailing options observed in others"[75]. Later, such conformity was also described in the food preference of female vervet monkeys[55] and was reported 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's Bonding and Identification-based Observational Learning theory[76]. We can hypothesize that a "chameleon effect"[77] might be at stake with males mimicking others in their social behaviour. This behavioural mimicry would act as a social glue and allow males to get better integrated in their new group. Such social conformity could be a potential vector of intra-group integration[55]. 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. Even after dispersal, males may inherit the social bonds of certain conspecifics serving as role models[78]. 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. Interestingly, cases where dispersing males bring their individual knowledge to their new group after dispersal have also been reported, however, such observation often concerns food-related and material traditions[79,80,81,82,83] and have rarely been reported in social traditions[54,84,83].

Overall, our results add to previously published studies which offer evidence for the existence of social traditions in bonobos[85], chimpanzees[86,87,88], capuchins[54,89], spider monkeys[32,31] and baboons[16,37].

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) 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"[90], 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 contradicted by 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[45] and may act as preferential "models" for social learning in wild vervet monkeys[46,48] (but see[49,50]). Moreover, previous studies highlighted the females' role in the spread of social traditions to incoming adult males[37] 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[91,92]. More precisely, longitudinal observational studies and cross-fostering experiments reported similarities in behaviour such as rate of infant rejection and social contacts between mothers and daughters in vervet monkeys[27] and rhesus macaques,[28,29] suggesting that these similarities may be the result of daughters' early experience. Regarding the maintenance of group differences in sociality, Ilany & Akçay[93] proposed a model of social inheritance from parents. According to their model, juveniles are likely to form social bonds with their parent's conspecifics with whom they had positively interacted before. This model has been validated in elephants[94] but not yet in vervet monkeys[95].

Effect of habituation on sociality

We observed a constant increase in sociality across the nine years of the study for 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"[96]. At the start of our study in 2012, the three groups were less habituated to observers so human presence might have stressed monkeys, impacted their behaviour and generated more conflicts. Data collection was also more difficult compared to nine years later where monkeys were highly habituated to human presence. It is thus possible that loud conflicts were easier to spot than silent grooming at that period, and especially if the monkeys were hiding from researchers when doing it. Another hypothesis would be that growing interactions with humans resulted in enhanced sociality in monkeys as enculturation in great apes improves their socio-physical cognitive skills[97,98?] . 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[99]), and such environmental perturbation may have elicited changes in groups social dynamics[100].

Question II: Group differences in sociality are not explained by simple effects of individuals' socio-demography 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 report 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[23,101,22]. Additionally, 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[23]. 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)[23], 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 towards 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" conspecifics may be relatively more related in our group than in another. For example, two adult females identified as unrelated in 2010 could actually be sisters so that we underestimate how closely related individuals from these matrilines are. 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, among them one individual in each group (GUGU for AK, OULI for NH, UPSS for BD) had a mean elo-rating higher than 0.8 over the whole study. It is possible that these individuals had a significant impact on the sociality of the group, via a substantial influence on other members of the group ("keystone" individual[102]). 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"[102,103,104,105,106]. Their impact has been especially studied in the enhancement of cooperative behaviours[106].

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. Grooming has been postulated as an exchange currency according to the Biological Market Theory (BMT) (Baboons[107], Chimpanzees[108] , Rhesus macaques[109], Bonobos[110], Tibetan macaques[111], Vervet monkeys[52]). According to this theory, grooming (i.e. good) is exchanged with another commodity (i.e. service) based on the law of supply and demand and predicts differences in rank and high overall competition to influence negatively reciprocity of grooming[112]. Within the BMT, 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)[107]. 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 studies using direct reciprocity and considering the time span of each grooming bout[113,114,110] 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[59], we believe that researchers have only discovered the tip of the primate tradition iceberg so far, mainly composed of complex technical behaviours, while missing 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.

Limitations of the study

In our study, we used data collected *ad libitum*, a method for which it is difficult to accurately assess the sampling effort (but see Canteloup et al.[115] for high correlation of social networks assessed via *ad libitum* and

focal animal sampling). One limitation of *ad libitum* sampling is that shier individuals may be sampled less often than others, and thus appear less social than they are, which could lead to a potential bias in social networks. Additionally, although our study groups share the same environment with genetic flux between groups, we do not have precise data on ecological and genetic variability. Future work on the 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. Finally, the influence of keystone individuals on group social dynamics is still poorly known and more work on animal personalities are needed to disentangle between such effects.

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CONTRIBUTION

Conceptualisation: Elena Kerjean, Erica van de Waal, Charlotte Canteloup
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Validation: Charlotte Canteloup
Visualization: Elena Kerjean
Writing – Original draft preparation: Elena Kerjean, Charlotte Canteloup
Writing – review & Editing: Elena Kerjean, Charlotte Canteloup, Erica van de Waal

DECLARATION OF INTERESTS

The authors declare no competing interests

Tables

Response variable	Model	Type	Predictors	Controls	Interactions	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	χ2 = 729.47	2	< 0.001	Group
	1.1	GLMM	Group	-	-	Year	Binomial	84704	275	AIC diff. = 1016.5	-	-	
	1.2	GLMM	Group Sex-ratio Age-ratio	Group size Time observation	-	Year	Binomial	84704	275	χ2 = 564.62	4	< 0.001	
	1.3	GLMM	Group Sex-ratio Age-ratio	Group size Time observation	Group*Sex-ratio	Year	Binomial	84704	275	χ2 = 653.47	6	< 0.001	
	1.4	GLMM	Group	Mean sociality groups	-	Individual	Binomial	1529	6	χ2 = 29.29	2	< 0.001	
	1.5	GLMM	Group Sex Age Hierarchical rank	Mean sociality groups	-	Individual	Binomial	157 562	247	χ2 = 303.74	5	< 0.001	Individual
	1.6	GLMM	Group Sex Age Hierarchical rank	Mean sociality groups	Group*Sex*Hierarchical rank	Individual	Binomial	157 562	247	χ2 = 341.14	12	< 0.001	
2. Matri-love	2.0	LMM	Group Hierarchical rank	Sex Age Mean sociality groups	-	Individual	Gaussian	110687	205	χ2 = 27.25	3	< 0.001	
	2.1	LMM	Group Hierarchical rank	Sex Age Mean sociality groups	Group*Hierarchical rank	Individual	Gaussian	110687	205	χ2 = 33.54	5	< 0.001	
3. Grooming reciprocity	3.0	GLMM	Group	-	-	Year	Binomial	63510	247	χ2 = 258.06	2	< 0.001	Group
	3.1	GLMM	Group Sex-ratio Age-ratio	Group size Time observation	-	Year	Binomial	63510	247	χ2 = 442.26	6	< 0.001	

Table 1. Statistical models summary.: P-values correspond to the full vs. null model comparisons for each model. Variables in *italic* in the random column correspond to random slopes while the one not in italic correspond to random intercepts. Dev.: Deviance, Df: Degree of freedom, diff. : difference, GLM: Generalized Linear Model, GLMM: Generalized Linear Mixed-Model, Indiv : Individual, LMM: Linear Mixed Model, Obs.: Observation.

Figures

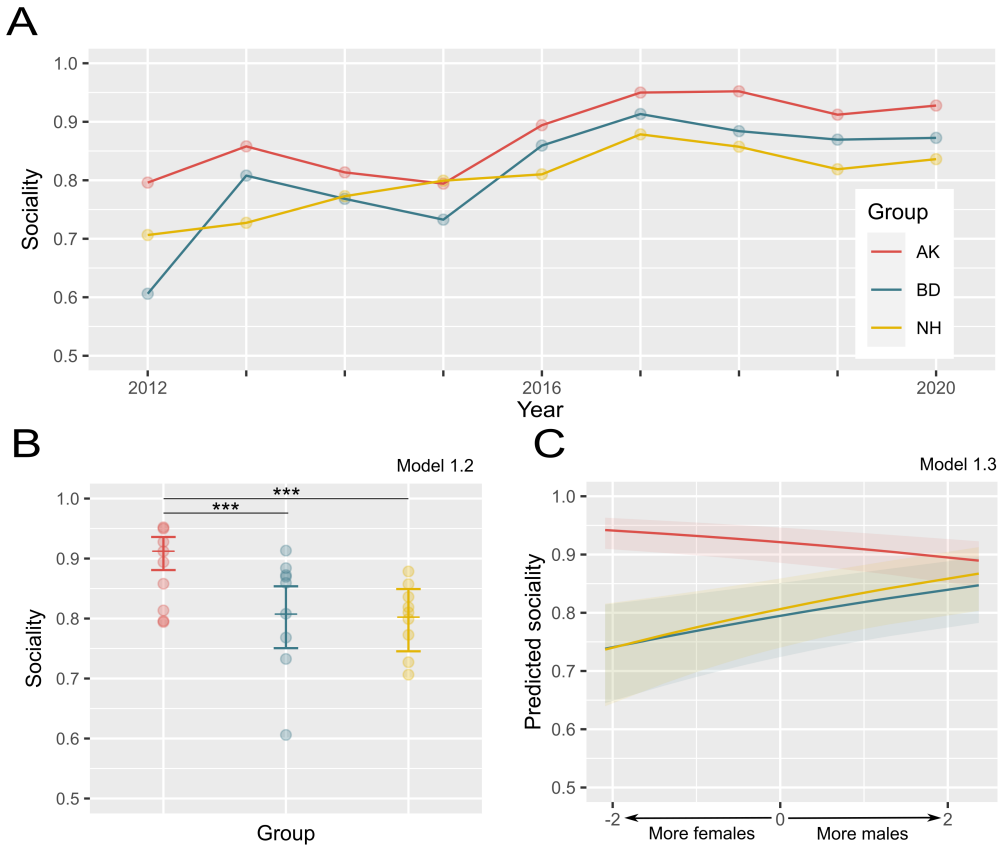


Figure 1. Groups' sociality depends on group identity A) Dynamics of the sociality of AK, BD and NH across years. Dots represent the sociality of each group for every year of the study as computed from raw data. B) Predicted sociality of AK, BD and NH in similar demographic environments. The small horizontal 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 as a function of the different values of 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). Graphical representations are based on estimates from Model 1.3. AK: Ankhase, BD: Baie Dankie, NH: Noha.

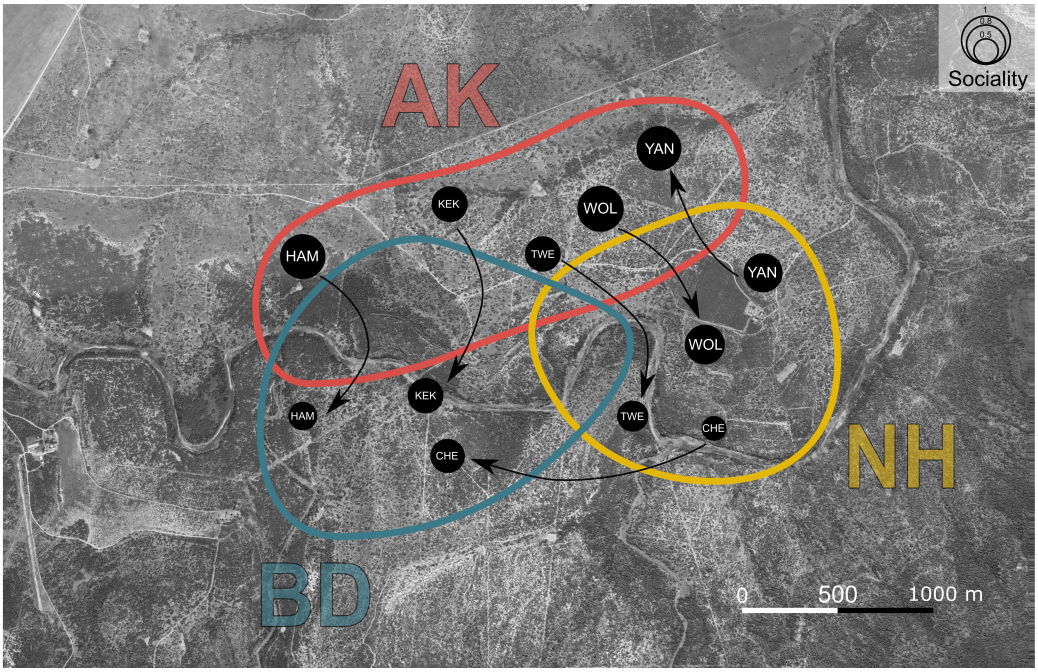
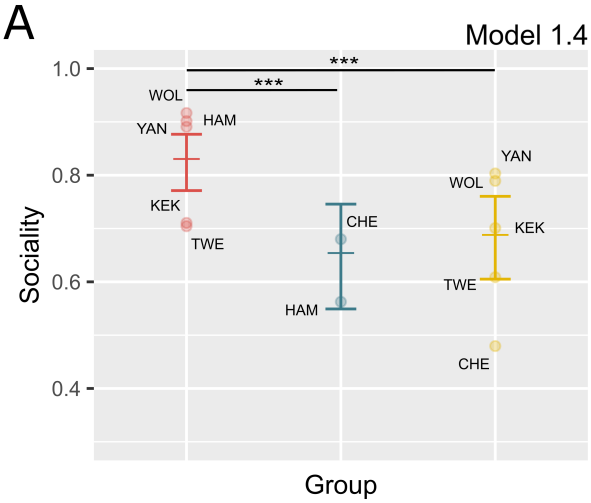


Figure 2. Dispersing map of males between groups
Map depicting the sociality of dispersing males between AK (red), BD (blue) and NH (yellow). Arrows represent the direction of dispersal. Each dot represents a male in a specific group. The bigger the dot, the more social the individual was. Sociality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

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 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

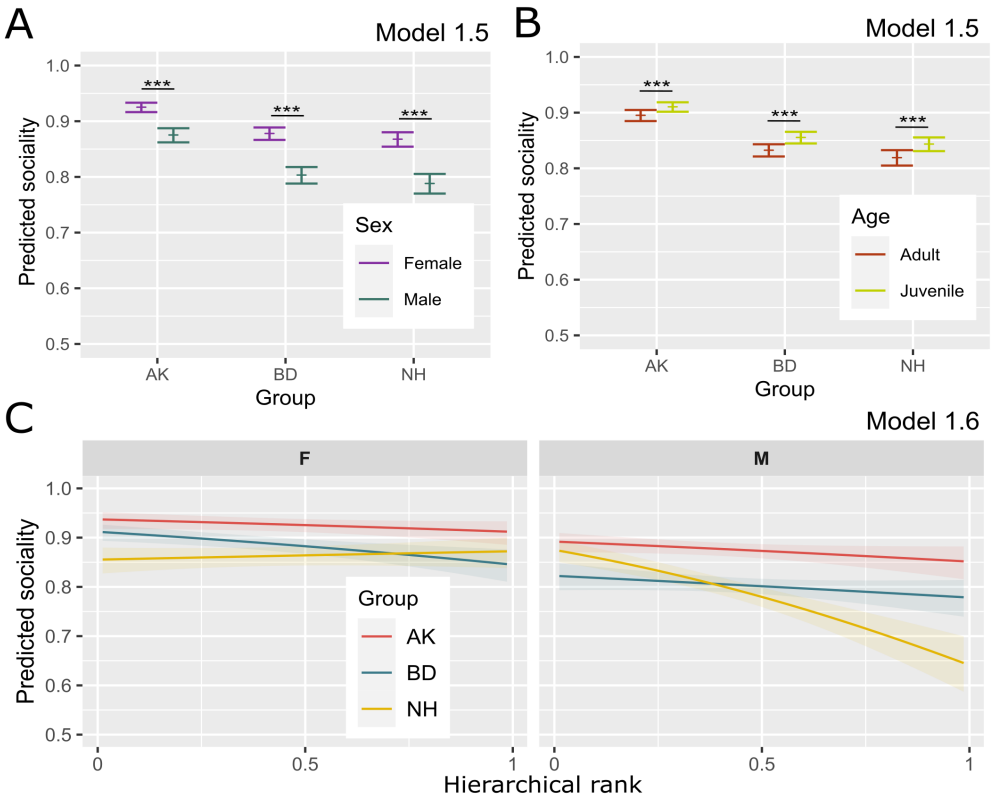


Figure 4. The effect of group identity is confirmed within all socio-demographic categories

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. Graphical representations are based on Model 1.6. Shaded areas denote 95% confidence interval (CI). AK: Ankhase, BD: Baie Dankie, NH: Noha.

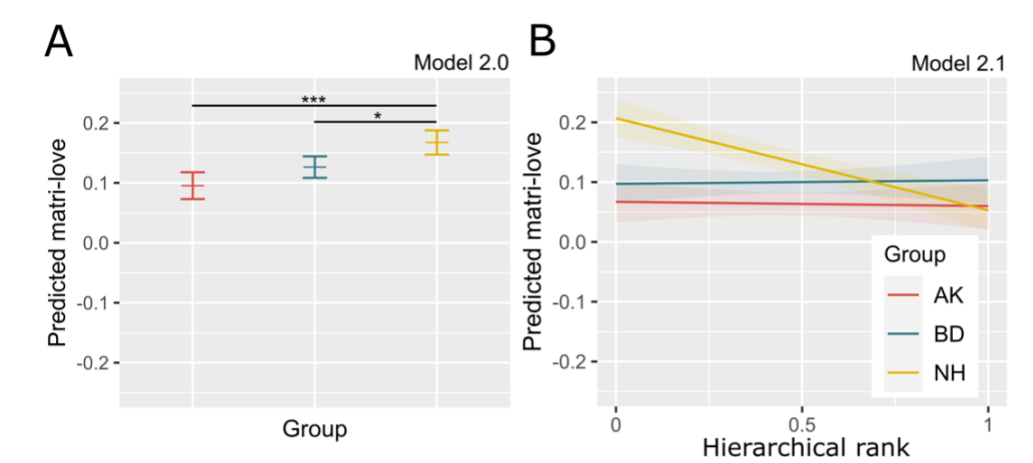


Figure 5. The propensity to be affiliative is less directed towards related individuals in AK and BD

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. Graphical representations are based on Model 2.1. Shaded areas denote 95% confidence interval (CI). AK: Ankhase, BD: Baie Dankie, NH: Noha

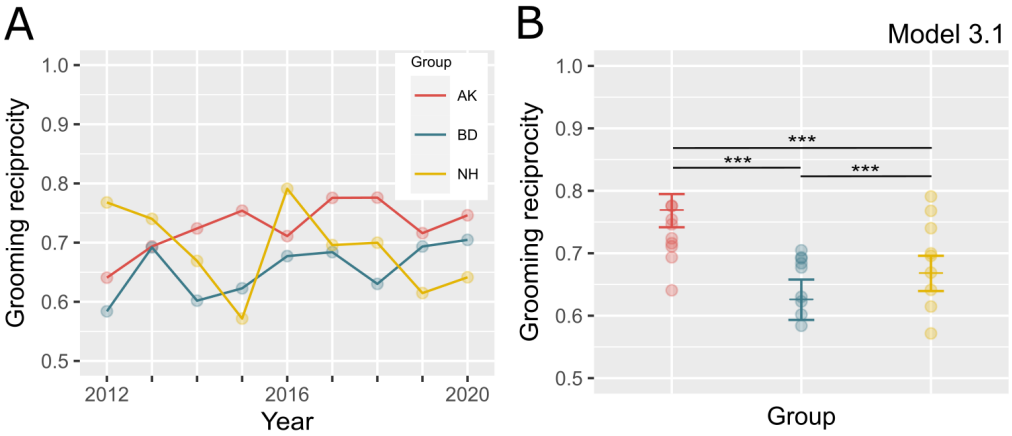


Figure 6. Grooming is more evenly distributed among individuals in AK. A) Dynamics of the level of grooming reciprocity in AK, BD and NH across years. Dots represent the grooming reciprocity of each group for each year of the study as computed from raw data. B) Predicted grooming reciprocity in AK, BD 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 3.1. 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

METHODS

RESOURCE 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).

Materials availability

This study did not generate newly generated materials.

Data and code availability

Behavioural data and all codes use for statistical analysis have been deposited at zenodo.7997943 and are publicly available as of the date of publication. Accession numbers are listed in the key resources table. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Data were collected over nine years (2012-2020) within the 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.

METHOD DETAILS

Behavioural sampling and coding

We used data collected by trained research assistants and researchers using *ad libitum* sampling[116,117]. 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).

Demographics and socio-demographics

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 S4). 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 the 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[118]. To do so, we

based our analysis on the Elorating 0.46.11 package of R[119]. 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[120]. 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.

Social indices

Sociality indices

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. A matriline, includes mothers and their offsprings. All siblings are from the same matriline. Each matriline starts from one of the adult females present at the starts of IVP.

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.

QUANTIFICATION AND 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[121]. One exception was made for the variable describing the Elo-rating as it is bounded between 0 and 1. Final models were compared to a corresponding null model. To assess whether the inclusion of predictors improved our model or not we built null models including only controls and random effects. We used the function *anova* with the test parameter set to "LRT" to compare two GLMMs (generalized linear mixed models). To assess the relevance of random effects we used the lowest Akaike information criterion (AIC) to we compare GLM and GLMMs (with a difference higher than 2[122]). We used the function *ranef* to assess the effect of random slopes. We chose random effects with at least five levels[123].

Model construction

We based our model selection on a forward selection strategy using the AIC as a selection criterion[124]. 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[125]. 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[126]. Secondly, we visually checked the distribution of the residual deviance according to the predicted values of our dependant variable[127]. 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, 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[128], while

EMMs were obtained with the function *ggemmeans* from the package *ggeffects* 1.1.2[129]. 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[130]. Statistical parameters for each models are reported in Table 1.

Question I

In order to have a global understanding of the differences in sociality between groups across years, we first computed a simple model which isolated *Group* as as the only main predictor of group sociality (Model 1.0). In this model, we used *Year* as a random intercept to take into account latent variables we did not collected such as temperature or food availability at each specific year and to assess the stability of group differences. In order to assess the effect of time in each group, and because we cannot expect *Year* to have a linear effect, we then constructed a model using *Year* as a random slope, keeping *Group* as a fixed effect (Model 1.1) and compared it to a model without *Year* as a random slope.

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 groups 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

We aimed to study the dynamic of sociality at the individual level. First, we analysed the overall effects 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

In model 3.0, similarly to our analysis of sociality at the group level, the dependent variable was the group grooming reciprocity and the fixed effect was the *Group* with *Year* as random intercept. Finally, in Model 3.1, *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.

KEY RESOURCES TABLE

SUPPLEMENTAL INFORMATION

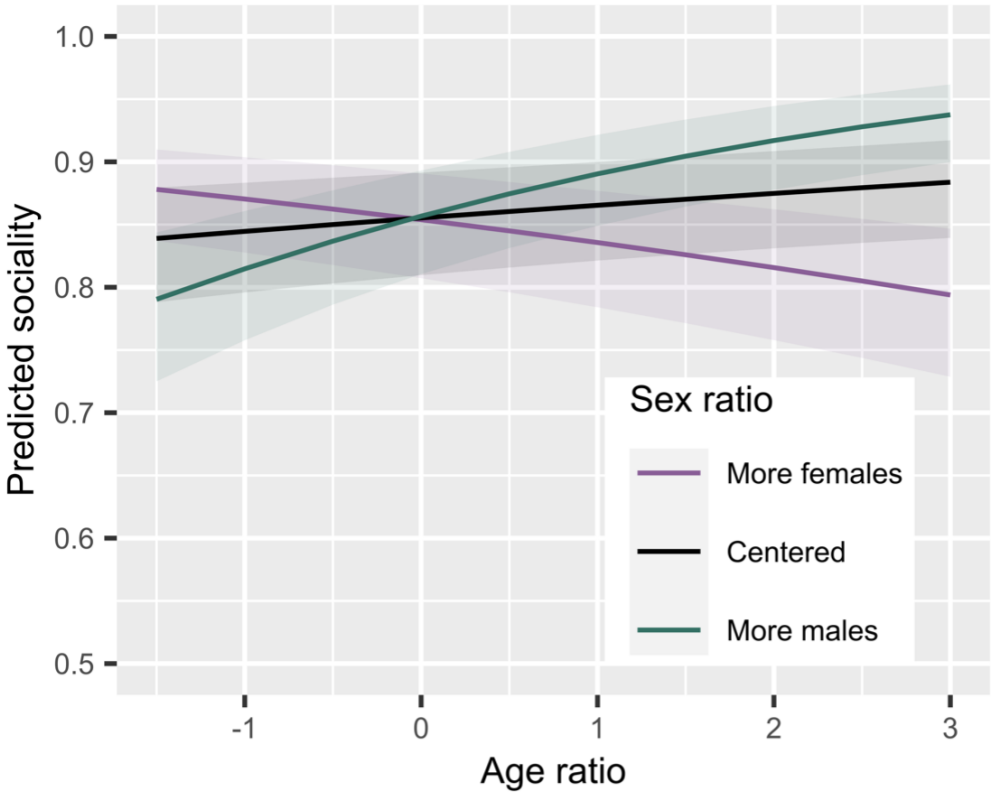


Figure S1. The influence of sex ratio on the effect of age ratio on sociality. *Related to Figure 1.*
The x-axis represents the variation in the scaled value of the age ratio, negative values represent a juvenile skewed group and positive values represent an adult skewed group compared to the mean observed age ratio. Shaded areas denote 95% confidence interval (CI).

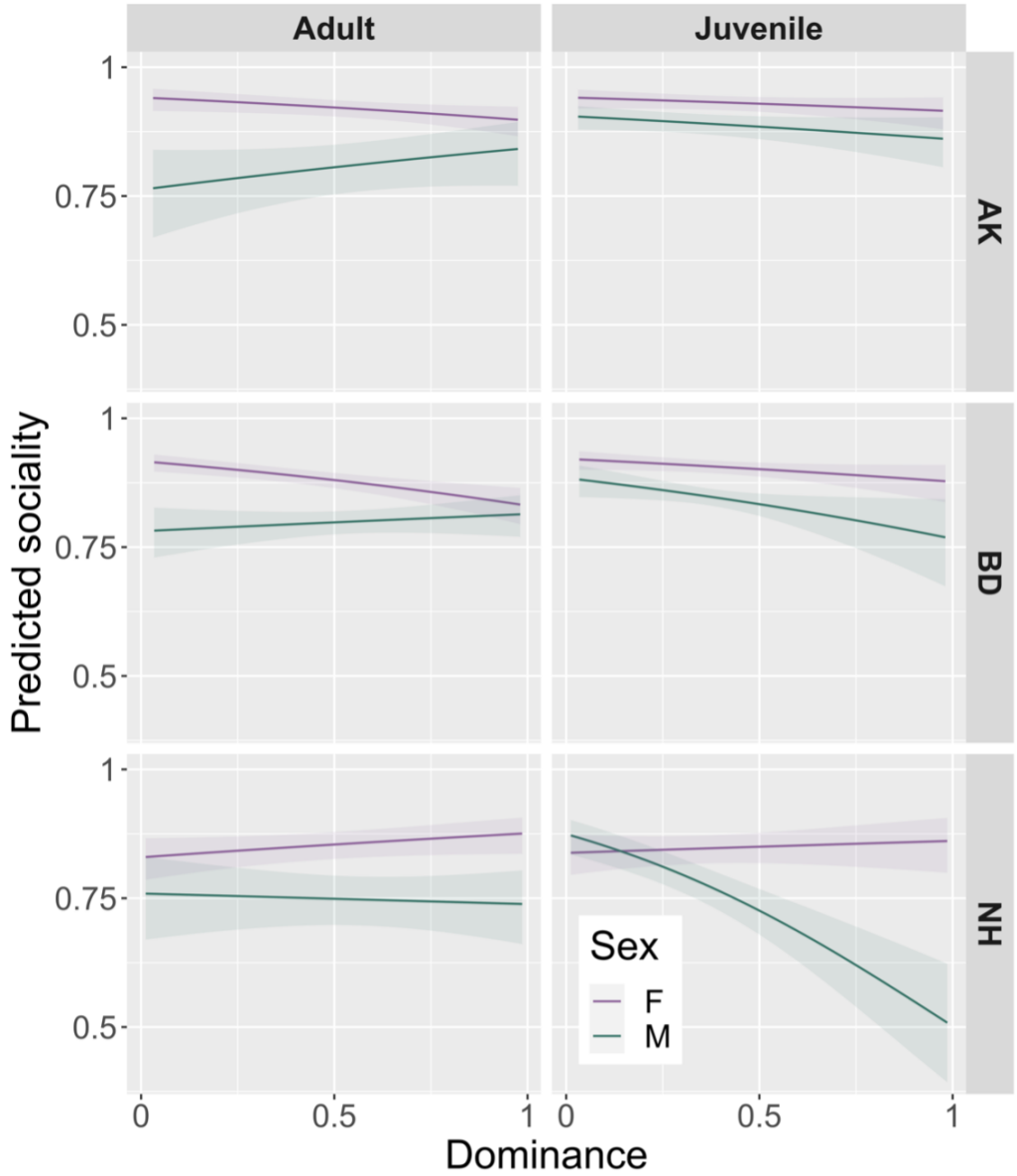


Figure S2. The interaction of sex, age and hierarchical rank on individual sociality within each group. ***Related to Figure 4.*** Predicted sociality is computed from models predicting the sociality of individuals according to the interaction *Sex*Age*Hierarchical rank* in each group. Shaded areas denote 95% confidence interval (CI). AK: Ankhase, BD: Baie Dankie, NH: Noha.

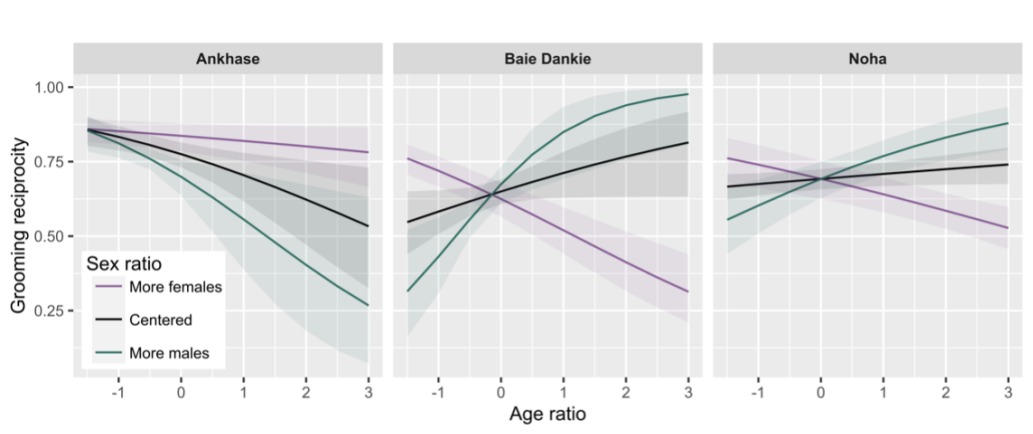


Figure S3. Differences of interaction between age ratio and sex ratio on grooming reciprocity within each group. ***Related to Figure 6.*** Predicted grooming reciprocity is computed from model predicting the grooming reciprocity according to the interaction *Age-ratio*Sex-ratio* in each group. Shaded areas denote 95% confidence interval (CI).

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. ***Related to Methods.***

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. ***Related to Methods.***

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. ***Related to Methods.***

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. ***Related to Figure 1 and Figure 6.***

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. ***Related to Figure 4.***

References

1. K. N. Laland, W. Hoppitt, Do animals have culture?, Evolutionary Anthropology 12 (2003) 150–159.

2. D. M. Fragaszy, S. Perry, The biology of traditions, Cambridge: University Press Cambridge, 2003.

3. A. Whiten, The burgeoning reach of animal culture, Science 372 (2021).

4. B. G. Galef, The question of animal culture, Human nature 3 (1992) 157–178.

5. M. Tomasello, The question of chimpanzee culture, in: Chimpanzee cultures, Harvard University Press, 1994.

6. C. Tennie, L. M. Hopper, C. P. van Schaik, On the origin of cumulative culture: consideration of the role of copying in culture-dependent traits and a reappraisal of the zone of latent solutions hypothesis, in: Chimpanzees in context: A comparative perspective on chimpanzee behavior, cognition, conservation, and welfare, The University of Chicago Press, 2020, p. 428–453.

7. C. Boesch, Wild cultures: a comparison between chimpanzee and human cultures, Cambridge University Press, 2012.

8. W. C. McGrew, Culture in nonhuman primates?, Annual review of anthropology 27 (1998) 301–328.

9. J. Henrich, R. McElreath, The evolution of cultural evolution, Evolutionary Anthropology 12 (2003) 123–135.

10. M. Kawai, Newly-acquired pre-cultural behavior of the natural troop of japanese monkeys on koshima islet, Primates 6 (1965) 1–30.

11. C. M. Heyes, Imitation, culture and cognition, Animal Behaviour 46 (1993) 999–1010.

12. A. Whiten, J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. Tutin, R. W. Wrangham, C. Boesch, Cultures in chimpanzees, Nature 399 (1999) 682–685.

13. T. Humle, T. Matsuzawa, Ant-dipping among the chimpanzees of bossou, guinea, and some comparisons with other sites, American Journal of Primatology: Official Journal of the American Society of Primatologists 58 (2002) 133–148.

14. E. van de Waal, On the neglected behavioural variation among neighbouring primate groups, Ethology 124 (2018) 845–854.

15. S. P. Kaufhold, E. J. van Leeuwen, Why intergroup variation matters for understanding behaviour, Biology letters 15 (2019) 20190695.

16. R. M. Sapolsky, L. J. Share, A pacific culture among wild baboons: its emergence and transmission, PLoS biology 2 (2004) e106.

17. A. Pascual-Garrido, Cultural variation between neighbouring communities of chimpanzees at gombe, tanzania, Scientific Reports 9 (2019) 8260.

18. L. V. Luncz, C. Boesch, Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females, American Journal of Primatology 76 (2014) 649–657.

19. E. J. van Leeuwen, Temporal stability of chimpanzee social culture, Biology Letters 17 (2021) 20210031.

20. L. Samuni, F. Wegdell, M. Surbeck, Behavioural diversity of bonobo prey preference as a potential cultural trait, Elife 9 (2020) e59191.

21. J. C. Mitani, Demographic influences on the behavior of chimpanzees, Primates 47 (2006) 6–13.

22. C. Canteloup, C. Borgeaud, M. Wubs, E. van de Waal, The effect of social and ecological factors on the time budget of wild vervet monkeys, Ethology 125 (2019) 902–913.

23. C. Canteloup, I. Puga-Gonzalez, C. Sueur, E. van de Waal, The consistency of individual centrality across time and networks in wild vervet monkeys, American Journal of Primatology 83 (2021) e23232.

24. S. E. DeTroy, C. T. Ross, K. A. Cronin, E. J. van Leeuwen, D. B. Haun, Cofeeding tolerance in chimpanzees depends on group composition: a longitudinal study across four communities, iScience 24 (2021) 102175.

25. E. J. van Leeuwen, K. A. Cronin, D. B. Haun, Population-specific social dynamics in chimpanzees, Proceedings of the National Academy of Sciences 115 (2018) 11393–11400.

26. E. van de Waal, C. Canteloup, Social learning and culture in monkeys, in: Cultural Evolution Handbook, Oxford University Press, In press.

27. L. A. Fairbanks, Early experience and cross-generational continuity of mother-infant contact in vervet monkeys, Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology 22 (1989) 669–681.

28. C. M. Berman, Intergenerational transmission of maternal rejection rates among free-ranging rhesus monkeys, Animal Behaviour 39 (1990) 329–337.

29. D. Maestripieri, S. G. Lindell, J. D. Higley, Intergenerational transmission of maternal behavior in rhesus macaques and its underlying mechanisms, Developmental psychobiology 49 (2007) 165–171.

30. A. Whiten, Primate culture and social learning, Cognitive Science 24 (2000) 477–508.

31. C. J. Santorelli, C. M. Schaffner, C. J. Campbell, H. Notman, M. S. Pavelka, J. A. Weghorst, F. Aureli, Traditions in spider monkeys are biased towards the social domain, PLoS One 6 (2011) e16863.

32. C. J. Santorelli, C. M. Schaffner, F. Aureli, Universal behaviors as candidate traditions in wild spider monkeys, PLoS One 6 (2011) e24400.

33. L. M. Rose, S. Perry, M. A. Panger, K. Jack, J. H. Manson, J. Gros-Louis, K. C. Mackinnon, E. Vogel, Interspecific interactions between cebus capucinus and other species: data from three costa rican sites, International Journal of Primatology 24 (2003) 759–796.

34. F. Brotcorne, G. Giraud, N. Gunst, A. Fuentes, I. N. Wandia, R. C. Beudels-Jamar, P. Poncin, M.-C. Huynen, J.-B. Leca, Intergroup variation in robbing and bartering by long-tailed macaques at uluwatu temple (bali, indonesia), Primates 58 (2017) 505–516.

35. J.-B. Leca, N. Gunst, M. Gardiner, I. N. Wandia, Acquisition of object-robbing and object/food-bartering behaviours: a culturally maintained token economy in free-ranging long-tailed macaques, Philosophical Transactions of the Royal Society B 376 (2021) 20190677.

36. F. B. de Waal, D. L. Johanowicz, Modification of reconciliation behavior through social experience: an experiment with two macaque species, Child development 64 (1993) 897–908.

37. R. Sapolsky, Social cultures among nonhuman primates, Current Anthropology 47 (2006) 641–656.

38. S. DeTroy, Apes on a plane: Capturing and comprehending variation in social dynamics among chimpanzees, Ph.D. thesis, Universität Leipzig, Leipzig, 2021.

39. E. J. van Leeuwen, S. E. DeTroy, S. P. Kaufhold, C. Dubois, S. Schütte, J. Call, D. B. Haun, Chimpanzees behave prosocially in a group-specific manner, Science Advances 7 (2021).

40. K. A. Cronin, E. J. van Leeuwen, V. Vreeman, D. B. Haun, Population-level variability in the social climates of four chimpanzee societies, Evolution and Human Behavior 35 (2014) 389–396.

41. J. Duboscq, J. Micheletta, M. Agil, K. Hodges, B. Thierry, A. Engelhardt, Social tolerance in wild female crested macaques (macaca nigra) in tangkoko-batuangus nature reserve, sulawesi, indonesia, American Journal of Primatology 75 (2013) 361–375.

42. J. Duboscq, M. Agil, A. Engelhardt, B. Thierry, The function of postconflict interactions: new prospects from the study of a tolerant species of primate, Animal Behaviour 87 (2014) 107–120.

43. S. P. Henzi, L. Barrett, The value of grooming to female primates, Primates 40 (1999) 47–59.

44. W. J. O'Hearn, A. Ruiz-Lambides, M. L. Platt, L. J. Brent, No evidence that grooming is exchanged for coalitionary support in the short- or long-term via direct or generalized reciprocity in unrelated rhesus macaques, Behavioral Ecology and Sociobiology 76 (2022) 1–14.

45. D. L. Cheney, R. M. Seyfarth, How monkeys see the world: inside the mind of another species, University of Chicago Press, 1990.

46. E. van de Waal, N. Renevey, C. M. Favre, R. Bshary, Selective attention to philopatric models causes directed social learning in wild vervet monkeys, Proceedings of the Royal Society B: Biological Sciences 277 (2010) 2105–2111.

47. E. van de Waal, C. Borgeaud, A. Whiten, Potent social learning and conformity shape a wild primate's foraging decisions, Science 340 (2013) 483–485.

48. A. E. Bono, A. Whiten, C. van Schaik, M. Krützen, F. Eichenberger, A. Schnider, E. van de Waal, Payoff-and sex-biased social learning interact in a wild primate population, Current Biology 28 (2018) 2800–2805.

49. C. Canteloup, W. Hoppitt, E. van de Waal, Wild primates copy higher-ranked individuals in a social transmission experiment, Nature communications 11 (2020) 1–10.

50. C. Canteloup, M. B. Cera, B. J. Barrett, E. van de Waal, Processing of novel food reveals payoff and rank-biased social learning in a wild primate, Scientific Reports 11 (2021) 1–13.

51. C. Borgeaud, S. Sosa, R. Bshary, C. Sueur, E. van de Waal, Intergroup variation of social relationships in wild vervet monkeys: a dynamic network approach, Frontiers in psychology 7 (2016) 915.

52. C. Borgeaud, R. Bshary, Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts, Current Biology 25 (2015) 3011–3016.

53. C. P. van Schaik, M. Ancrenaz, G. Borgen, B. Galdikas, C. D. Knott, I. Singleton, A. Suzuki, S. S. Utami, M. Merrill, Orangutan cultures and the evolution of material culture, Science 299 (2003) 102–105.

54. S. Perry, M. Baker, L. Fedigan, J. GrosLouis, K. Jack, K. MacKinnon, J. Manson, M. Panger, K. Pyle, L. Rose, Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a neotropical primate, Current Anthropology 44 (2003) 241–268.

55. E. van de Waal, C. P. van Schaik, A. Whiten, Resilience of experimentally seeded dietary traditions in wild vervets: evidence from group fissions, American journal of primatology 79 (2017) e22687.

56. D. Shizuka, A. E. Johnson, How demographic processes shape animal social networks, Behavioral Ecology 31 (2020) 1–11.

57. C. Borgeaud, S. Sosa, C. Sueur, R. Bshary, The influence of demographic variation on social network stability in wild vervet monkeys, Animal Behaviour 134 (2017) 155–165.

58. R. E. Morrison, W. Eckardt, F. Colchero, V. Vecellio, T. S. Stoinski, Social groups buffer maternal loss in mountain gorillas, Elife 10 (2021) e62939.

59. C. Schuppli, C. P. van Schaik, Animal cultures: how we've only seen the tip of the iceberg, Evolutionary Human Sciences 1 (2019) e2.

60. L. Brun, J. Schneider, E. M. Carrió, P. Dongre, P. Taberlet, v. d. Waal, L. Fumagalli, Focal vs. fecal: seasonal variation in the diet of wild vervet monkeys from observational and dna metabarcoding data, Ecology and Evolution 12 (2022) e9358.

61. J. S. Brown, J. W. Laundré, M. Gurung, The ecology of fear: optimal foraging, game theory, and trophic interactions, Journal of mammalogy 80 (1999) 385–399.

62. J. W. Laundré, L. Hernández, K. B. Altendorf, Wolves, elk, and bison: reestablishing the "landscape of fear" in yellowstone national park, usa, Canadian Journal of Zoology 79 (2001) 1401–1409.

63. M. S. Palmer, K. M. Gaynor, J. A. Becker, J. O. Abraham, M. A. Mumma, R. M. Pringle, Dynamic landscapes of fear: understanding spatiotemporal risk, Trends in Ecology & Evolution (2022).

64. R. M. Seyfarth, D. L. Cheney, P. Marler, Monkey responses to three different alarm calls: evidence of predator classification and semantic communication, Science 210 (1980) 801–803.

65. E. P. Willems, R. A. Hill, Predator-specific landscapes of fear and resource distribution: effects on spatial range use, Ecology 90 (2009) 546–555.

66. G. E. Robinson, R. D. Fernald, D. F. Clayton, Genes and social behavior, science 322 (2008) 896–900.

67. K. E. Langergraber, C. Boesch, E. Inoue, M. Inoue-Murayama, J. C. Mitani, T. Nishida, A. Pusey, V. Reynolds, G. Schubert, R. W. Wrangham, et al., Genetic and 'cultural' similarity in wild chimpanzees, Proceedings of the Royal Society B: Biological Sciences 278 (2011) 408–416.

68. C. S. Barr, C. Driscoll, Neurogenetics of aggressive behavior: studies in primates, Neuroscience of aggression (2014) 45–71.

69. M. Krützen, E. P. Willems, C. P. van Schaik, Culture and geographic variation in orangutan behavior, Current Biology 21 (2011) 1808–1812.

70. C. C. Ioannou, K. L. Laskowski, Conformity and differentiation are two sides of the same coin, Trends in Ecology & Evolution (2023).

71. L. V. Luncz, C. Boesch, Tradition over trend: neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females, Am. J. Primatol. 76 (2014) 649–657.

72. A. Whiten, R. A. Harrison, N. McGuigan, G. L. Vale, S. K. Watson, Collective knowledge and the dynamics of culture in chimpanzees, Philosophical Transactions of the Royal Society B 377 (2022) 20200321.

73. A. Whiten, Conformity versus transmission in animal cultures, Behavioral and Brain Sciences 45 (2022) e273.

74. S. E. Asch, Studies of independence and conformity: I. a minority of one against a unanimous majority., Psychological monographs: General and applied 70 (1956) 1.

75. A. Whiten, Conformity and over-imitation: an integrative review of variant forms of hyper-reliance on social learning, in: Advances in the Study of Behavior, Advances in the study of behavior, Elsevier, 2019, pp. 31–75.

76. F. De Waal, The ape and the sushi master: cultural reflections of a primatologist, Basic Books, 2008.

77. T. L. Chartrand, J. A. Bargh, The chameleon effect: the perception–behavior link and social interaction., Journal of personality and social psychology 76 (1999) 893.

78. D. L. Cheney, R. M. Seyfarth, Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences, The American Naturalist 122 (1983) 392–412.

79. R. C. O'Malley, W. Wallauer, C. M. Murray, J. Goodall, The appearance and spread of ant fishing among the kasekela chimpanzees of gombe: a possible case of intercommunity cultural transmission, Current anthropology 53 (2012) 650–663.

80. D. Biro, N. Inoue-Nakamura, R. Tonooka, G. Yamakoshi, C. Sousa, T. Matsuzawa, Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments, Animal cognition 6 (2003) 213–223.

81. B. J. Barrett, R. L. McElreath, S. E. Perry, Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate, Proceedings of the Royal Society B: Biological Sciences 284 (2017) 20170358.

82. H. Péter, K. Zuberbühler, C. Hobaiter, Well-digging in a community of forest-living wild east african chimpanzees (pan troglodytes schweinfurthii), Primates 63 (2022) 355–364.

83. P. Dongre, G. Lanté, , M. Cantat, C. Canteloup, , E. van de Waal, Role of immigrant males and muzzle contacts in the uptake of a novel food by wild vervet monkeys, bioRxiv (2022) 2021–12.

84. L. Samuni, R. Mundry, J. Terkel, K. Zuberbühler, C. Hobaiter, Socially learned habituation to human observers in wild chimpanzees, Animal Cognition 17 (2014) 997–1005.

85. E. J. van Leeuwen, N. Staes, J. Verspeek, W. J. Hoppitt, J. M. Stevens, Social culture in bonobos, Current Biology 30 (2020) R261–R262.

86. W. C. McGrew, C. E. Tutin, Evidence for a social custom in wild chimpanzees?, Man (1978) 234–251.

87. E. J. van Leeuwen, S. van Donink, M. Eens, J. M. Stevens, Group-level variation in co-feeding tolerance between two sanctuary-housed communities of chimpanzees (pan troglodytes), Ethology 127 (2021) 517–526.

88. G. Badihi, K. E. Graham, B. Fallon, A. Safryghin, A. Soldati, K. Zuberbühler, C. Hobaiter, Dialects in leaf-clipping and other leaf-modifying gestures between neighbouring communities of east african chimpanzees, Scientific Reports 13 (2023) 147.

89. T. Falótico, E. B. Ottoni, Stone throwing as a sexual display in wild female bearded capuchin monkeys, sapajus libidinosus, PLoS One 8 (2013) e79535.

90. W. D. Hamilton, The genetical evolution of social behaviour. ii, Journal of theoretical biology 7 (1964) 17–52.

91. F. de Waal, Macaque social culture: development and perpetuation of affiliative networks., Journal of Comparative Psychology 110 (1996) 147.

92. A. Ilany, K. E. Holekamp, E. Akçay, Rank-dependent social inheritance determines social network structure in spotted hyenas, Science 373 (2021) 348–352.

93. A. Ilany, E. Akcay, Social inheritance can explain the structure of animal social networks, Nature communications 7 (2016) 12084.

94. N. Goldberg, Writing down the bones: freeing the writer within, Shambhala Publications, 2016.

95. J. D. Jarrett, T. R. Bonnell, C. Young, L. Barrett, S. P. Henzi, Network integration and culture in monkeys to social inheritance in vervet monkeys, Proceedings of the Royal Society B: Biological Sciences 285 (2018) 20172668.

96. C. Hernández Tienda, B. Majolo, T. Romero, R. Illa Maulany, P. Oka Ngakan, V. Beltrán Francés, E. Gregorio Hernández, J. Gómez-Melara, M. Llorente, F. Amici, The habituation process in two groups of wild moor macaques (macaca maura), International Journal of Primatology (2022) 1–26.

97. J. M. Bering, A critical review of the "enculturation hypothesis": the effects of human rearing on great ape social cognition, Animal cognition 7 (2004) 201–212.

98. M. Tomasello, J. Call, The role of humans in the cognitive development of apes revisited, Animal Cognition 7 (2004) 213–215.

99. M. Ndlovu, A. D. Clulow, M. J. Savage, L. Nhamo, J. Magidi, T. Mabhaudhi, An assessment of the impacts of climate variability and change in kwazulu-natal province, south africa, Atmosphere 12 (2021) 427.

100. U. Kalbitzer, C. A. Chapman, Primate responses to changing environments in the anthropocene, Primate life histories, sex roles, and adaptability: essays in honour of Linda M. Fedigan (2018) 283–310.

101. C. Borgeaud, S. Sosa, C. Sueur, R. Bshary, The influence of demographic variation on social network stability in wild vervet monkeys, Animal Behaviour 134 (2017) 155–165.

102. A. P. Modlmeier, C. N. Keiser, J. V. Watters, A. Sih, J. N. Pruitt, The keystone individual concept: an ecological and evolutionary overview, Animal Behaviour 89 (2014) 53–62.

103. S. K. Robson, J. F. Traniello, Key individuals and the organisation of labor in ants, in: Information processing in social insects, Springer, 1999, pp. 239–259.

104. J. E. Smith, S. Gavrilets, M. B. Mulder, P. L. Hooper, C. El Mouden, D. Nettle, C. Hauert, K. Hill, S. Perry, A. E. Pusey, et al., Leadership in mammalian societies: emergence, distribution, power, and payoff, Trends in ecology & evolution 31 (2016) 54–66.

105. L. Glowacki, R. McDermott, Key individuals catalyse intergroup violence, Philosophical Transactions of the Royal Society B 377 (2022) 20210141.

106. K. McAuliffe, R. Wrangham, L. Glowacki, A. F. Russell, When cooperation begets cooperation: the role of key individuals in galvanizing support, Philosophical Transactions of the Royal Society B: Biological Sciences 370 (2015) 20150012.

107. L. Barrett, S. P. Henzi, T. Weingrill, J. E. Lycett, R. A. Hill, Market forces predict grooming reciprocity in female baboons, Proceedings of the Royal Society of London. Series B: Biological Sciences 266 (1999) 665–670.

108. N. E. Newton-Fisher, P. C. Lee, Grooming reciprocity in wild male chimpanzees, Animal Behaviour 81 (2011) 439–446.

109. K. Balasubramaniam, C. Berman, Grooming interchange for resource tolerance: biological markets principles within a group of free-ranging rhesus macaques, Behaviour 154 (2017) 1145–1176.

110. S. Anzà, E. Demuru, E. Palagi, Sex and grooming as exchange commodities in female bonobos' daily biological market, Scientific reports 11 (2021) 1–10.

111. D. Xia, J. Li, P. A. Garber, L. Sun, Y. Zhu, B. Sun, Grooming reciprocity in female tibetan macaques macaca thibetana, American journal of Primatology 74 (2012) 569–579.

112. R. Noë, P. Hammerstein, Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating, Behavioral ecology and sociobiology 35 (1994) 1–11.

113. T. G. O'Brien, Asymmetries in grooming interactions between juvenile and adult female wedge-capped capuchin monkeys, Animal behaviour 46 (1993) 929–938.

114. M. G. García, D. Lemieux, R. Bshary, Factors affecting tolerance persistence after grooming interactions in wild female vervet monkeys, chlorocebus pygerythrus, Animal Behaviour 177 (2021) 135–145.

115. C. Canteloup, I. Puga-Gonzalez, C. Sueur, E. van de Waal, The effects of data collection and observation methods on uncertainty of social networks in wild primates, American journal of primatology 82 (2020) e23137.

116. P. Martin, P. P. G. Bateson, P. Bateson, Measuring behaviour: an introductory guide, Cambridge university press, 1993.

117. J. Altmann, Observational study of behavior: sampling methods, Behaviour 49 (1974) 227–266.

118. C. Neumann, J. Duboscq, C. Dubuc, A. Ginting, A. M. Irwan, M. Agil, A. Widdig, A. Engelhardt, Assessing dominance hierarchies: validation and advantages of progressive evaluation with elo-rating, Animal Behaviour 82 (2011) 911–921.

119. C. Neumann, L. Kulik, EloRating: animal Dominance Hierarchies by Elo Rating, 2020. R package version 0.46.11.

120. A. S. Goffe, J. Fischer, H. Sennhenn-Reulen, Bayesian inference and simulation approaches improve the assessment of elo-ratings in the analysis of social behaviour, Methods in Ecology and Evolution 9 (2018) 2131–2144.

121. H. Schielzeth, Simple means to improve the interpretability of regression coefficients, Methods in Ecology and Evolution 1 (2010) 103–113.

122. K. P. Burnham, D. R. Anderson, Multimodel inference: understanding aic and bic in model selection, Sociological methods & research 33 (2004) 261–304.

123. A. Gelman, J. Hill, Data analysis using regression and multilevel/hierarchical models, Cambridge university press, 2006.

124. M. Z. I. Chowdhury, T. C. Turin, Variable selection strategies and its importance in clinical prediction modelling, Family medicine and community health 8 (2020).

125. W. R. Rice, Analyzing tables of statistical tests, Evolution 43 (1989) 223–225.

126. J. Fox, G. Monette, Generalized collinearity diagnostics, Journal of the American Statistical Association 87 (1992) 178–183.

127. P. McCullagh, J. Nelder, Binary data, in: Generalized linear models, Springer, 1989, pp. 98–148.

128. T. J. Leeper, margins: Marginal Effects for Model Objects, 2021. R package version 0.3.26.

129. D. Lüdecke, ggeffects: Tidy data frames of marginal effects from regression models., Journal of Open Source Software 3 (2018) 772.

130. R Core Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2021.