On the neglected behavioural variation among neighbouring primate groups

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Abstract

Behavioural variation in primates has been well studied at the level of individuals by behavioural ecologists, and more recently at a population level by cultural biologists. Behavioural differences between groups of the same population, however, have rarely been considered. Here I review intergroup variation in universally occurring behaviours between up to six neighbouring groups of vervet monkeys. Group differences have been found in several domains including foraging, conflicts, grooming and proximity. An exclusively ecological explanation for the observed variation appears implausible, as these monkey groups have overlapping home ranges, and their ecology is therefore very similar. The presence of a genetic bias underlying the observed group differences is also implausible, as males disperse between groups at sexual maturity and multiple times within their lives creating a continuous gene flow between the six groups. This leaves socially learned group-level traditions as the most plausible explanation. I discuss ways in which this working conclusion can be tested. The likely presence of group-level traditions in close proximity, well known in humans, has rarely been considered for nonhuman primates, and adds an important dimension to research on conformity in nonhuman cultures.

Keywords: behavioural variation, neighbouring primate groups, universal behaviours, social learning, vervet monkeys, traditions

Introduction

Evolutionary biology focuses on the selective forces acting on variation. Microevolution investigates variation between individuals as well as variation between populations of the same species; whereas macroevolution investigates variation between species providing adaptations to their respective ecologies (Dobzhansky & Dobzhansky 1937, Endler 1986). In social species living in groups, the ‘group’ is an important intermediate level between individual and population.

When studying individual variation in animals, researchers investigate variation in characteristics such as morphology or behaviour and try to link them with elements such as an individual’s ontogeny, genetics or environment (Kappeler 2010). If individual variation is studied in group-living species, individuals described belong to the same social unit. These individuals are interdependent across gradients in various factors such as social structure, kinship, and group size. We know that group-living animals have opportunities to learn from each other, thus, groups members might express more behavioural similarities than individuals randomly selected within the population.

Studies of between-species variation often correlate variation in aspects such as diet, group size, body size or sexual dimorphism, with variation in factors such as social structure, mating system, or brain size across species (Mitani et al. 2012). Due to the scarcity of wild study groups in each population, these analyses often rely on small sample sizes for each species, with the risk that data are not particularly representative of the whole species. This can lead to increased unexplained variance in analyses. The question is then: how much of the variation observed is really explained by differences between populations rather than variation present within populations? This issue famously occurred in human studies using the ultimatum game, a two-player bargaining experiment extensively used across disciplines to measure fairness. One study revealed very high cross-cultural variation in fairness (and thus great excitement: Henrich et al. 2006), but Lamba & Mace (2013) found a similar amount of variation between local villages in an Indian sub-culture. Such findings warrant interest in whether a similar amount of variation can be found between neighbouring groups in other species.

In this review I will focus on variation between groups of the same population, asking similar questions to those often asked when comparing populations, but on a smaller scale. Studying variation among groups within a population is not the standard, particularly in wild primate studies, where many field researchers still study only one or two groups per field site. I think the time is ripe to explore behavioural variation in neighbouring primate groups and I predict that we will gain many insights from it.

Studies of variation between populations of a single species have had two main goals: first, linking diet or social organization with ecology, and second, detecting potential traditions. Biologists have defined culture as group-typical behavioural patterns, shared by members of a community, which rely on socially learned and transmitted information (Hoppitt & Laland 2013). Social learning is the mechanism underlying ‘cultural transmission’ (Whiten 2005). This cultural transmission is an important phenomenon to understand within the Life Sciences as a whole, because if innovations spread and persist across generations, the result is a ‘second inheritance system’ (Whiten 2005) that has evolved in addition to genetic inheritance and now forms a parallel evolutionary stream (Dawkins 1976; Mesoudi et al. 2006). Cultural and genetic evolution share fundamental characteristics, notably information transmission, mutation, selection and adaptation (Mesoudi et al. 2006). We now know much about genetic or ‘biological’ evolution, but still relatively little about cultural evolution.

Studies of behavioural variation within single primate species have often used the 'exclusion method'. Behavioural repertoires exhibiting variation across study populations without obvious ecological explanation are recorded and classified as habitual, customary or absent in each population (in chimpanzees, Whiten et al. 1999; in orang-utans, van Schaik et al. 2003; in capuchin monkeys, Perry et al. 2003; in spider monkeys, Santorelli et al. 2011a; and in gorillas, Robbins et al. 2016). Examples include nut-cracking, present in some chimpanzees populations and absent in others, or the use of tools to open fruits, present at some Sumatran orang-utan sites but absent in others. However, more recent studies showed that some tool use that appeared to be traditional was in fact predicted by the prey behaviour. Variation in the severity of biting behaviour of ants predicted both the length of tool and the technique used to strip the ants from the tools by some chimpanzees (Humle & Matsuzawa 2002). Therefore, one must be cautious about results from the 'exclusion method' studies, as what appeared to be a clear case of arbitrary tradition may have other more subtle ecological explanations. I therefore suggest that we focus on behavioural variation between neighbouring groups within a population, to limit potential ecological biases.

To identify potential culture in animals, some researchers have studied behavioural variation in multiple wild groups of the same populations. For example, Thornton et al. (2010) studied 15 meerkat groups simultaneously over 11 years, and found differences in emergence time, some groups having the apparent tradition to be 'late sleepers'. Other important studies of variation within populations have been conducted on cetaceans: one on the cultural diversity of sponge use in a single population of dolphins (Krützen et al. 2005); and another on the transmission of lobtail feeding in a population of humpback whales (Allen et al. 2013). Both of these studies were conducted over many years and on multiple groups of the same population.

Intergroup differences in neighbouring groups of primates were first reported when comparing the diet of three such groups of capuchin monkeys (Chapman & Fedigan 1990). This study found that dietary variation was not linked to food availability and thus the authors concluded that it was either due to food profitability or to local traditions. Later research on two neighbouring communities of chimpanzees in the Mahale moutains found variation in hand-clasp grooming, demonstrating the first such example concerning social customs (McGrew et al. 2001). A review by Perry & Mason (2013) highlighted that studies on monkey traditions were focussing essentially on foraging behaviour (food processing or choice) and rarely on social behaviours, with most research being conducted on one group, some on two, or a maximum of three groups.

In two populations of monkeys, more groups have been studied. Tan et al. (2015) found that five groups of Burmese long-tailed macaques on the Piak Nam Yai Island, Thailand, exhibit group-level differences in their use of stone-tools to crack open oysters, in both material and behavioural elements of tool use. Perry et al. (2003) studied traditions in a total of 13 capuchin groups, but across four different study sites. The largest number of groups within the same population was seven, of which six were neighbouring. Within this population, the capuchin groups varied in their use of handsniffing, a social convention, across different parameters: frequency, durability, and number spread across the social network. In some groups of the population this behaviour was absent, and the usage across sex classes also varied between groups. I agree with McGrew's (2003) comment on Perry et al. (2003): "One can imagine a study of a single population revealing fascinating customs".

Santorelli et al., (2011b) employed a novel approach which highlighted variation in the proportional use of 'universal' behaviours, in domains such as feeding, greeting and resting, in two neighbouring groups of spider monkeys, and a third group from another population. The authors concluded first, that repertoires of traditions could be larger than assumed previously from exclusion method studies, and second, that the relative use of behavioural variants could contribute to the recognition of group membership, if the variants are functionally equivalent.

Luncz and Boesch (2015) studied three neighbouring communities of chimpanzee in the Taï National Park, Côte d'Ivoire, and identified 27 putative cultural traits (in various domains such as foraging, social interaction, communication and tool use) despite frequent exchange of adult females among the groups (Luncz & Boesch 2014). The rich variation in behaviours between these neighbouring groups demonstrates great diversity within the population. Indeed, the authors commented: "we expect that these are not the only populations in which such variation occurs and therefore urge researchers working elsewhere to do similar studies to broaden our understanding of underlying transmission mechanisms and of cultural variation in wild primates"(Luncz & Boesch 2015).

Noting the studies reviewed above, I here present suggestions for future work focussing on intergroup variation in universal behaviours. I propose that the current focus on innovative behaviours, tool use and the exclusion method should shift towards behaviours that every individual of a population has in its behavioural repertoire, but uses, does not use or even uses differently, depending on its group membership. This approach might yield a more realistic understanding of the wide range of intergroup behavioural variation, and thus the size and scope of each potentially unique repertoire of traditions.

Since 2005, I have worked with wild vervet monkeys (*Chlorocebus pygerythrus*) in South Africa, mainly conducting social learning experiments but also collecting baseline data on natural behaviours. I first worked with six groups of the population living in the Loskop Dam nature reserve, Mpumalanga, for six years; then on six groups of the population at the Inkawu Vervet Project (IVP) in the Mawana private game reserve, KwaZulu Natal since 2010. Here, I review intergroup behavioural variation observed in neighbouring groups (with often overlapping home ranges) of wild vervet monkeys. First, I report intergroup dietary variation found through analyses of the amount of foraging on 14 preferred fruiting tree species, in association with the abundance of these trees in each home range (Tournier et al. 2014). Second, I report results on intergroup variation in the frequency of lip smacking (a facial expression) during grooming between dyads of adult females (van de Waal et al. 2013a). Third, I describe intergroup variation in social network structure and dynamics (Borgeaud et al. 2016). Finally, I present data on agonistic behaviours showing intergroup variation in three respects: 1) conflict frequency, 2) the number of conflicts followed by a response and 3) the number of aggressive and affiliative responses used.

The first aim of this review is to document the behavioural variation found between these neighbouring groups of vervet monkeys as summarized in table 1. The second aim is to explore the causes of this variation. A plausible hypothesis for the observed variation could be group level culture, but to confirm this, each plausible alternative explanation, such as ecological or genetic variation, group composition, identity of the alpha male or female or number of infants in the group, must be excluded. In addition, consistency over time must be demonstrated in order to call these behaviours cultural, whereby the between-year variation within groups remains smaller than variation between groups.

Field and other experiments with vervet monkeys revealed the ability of this species to learn socially. Wild vervet infants copied their mother selectively in both food choice (van de Waal et al. 2013b) and food manipulation (van de Waal et al. 2014) experiments. In two-action tasks, vervets paid more attention to female models than male models (van de Waal et al. 2010). Biased attention towards the philopatric females of this species could form the base for social learning of group level arbitrary traditions. Immigrant males conformed to experimentally induced food preferences in their new groups which conflicted with their own previously experimentally induced food preferences (van de Waal et al. 2013b). This demonstrates how group level traditions could be maintained even with frequent immigrations. Experiments on captive vervets showed detailed matching of participant’s actions to those of a model (body part to open a tube: van de Waal & Whiten 2012; way to open a door: van de Waal et al. 2013c).

All these examples illustrate the great potential of vervet monkeys for social learning. Now we need to understand how they use it in their daily life by comparing behavioural repertoires of neighbouring wild groups.

1. Variation in the diet of vervet monkeys

As this data set is already published (Tournier et al., 2014) I shall only summarize the methods. These researchers recorded information about diet through scans every 30 min. in six groups of wild vervet monkeys. Group composition is shown in Table 2. Each scan period lasted 10 min. during which the observers located as many monkeys as possible (Altmann 1974). If an individual was foraging whilst being scanned, the type of food eaten was noted. The most commonly eaten trees by the vervets in this population (Barrett 2010) were phenologically examined and mapped in each home range (up to 50 trees per home range – if more were present the species was considered as ‘abundant’ and counting stopped). Fourteen species of trees were studied: *Acacia caffra* (AcC), *Acacia karoo* (AcK), *Acacia nilotica* (AcN), *Berchemia zeyheri* (BeZ), *Celtis africana* (CeA), *Combretum zeyheri* (CoZ), *Ficus sp.* (FiSP), *Lannea sp.* (LaSP), *Mimusops zeyheri* (MiZ), *Olea europea* (OlE), *Rhus pyroides* (RhP), *Sclerocarya birrea* (ScB), *Ximenia caffra* (XiC) and *Ziziphus mucronata* (ZiM). The researchers then computed a correlation between the contribution in the diet of each tree species and its abundance in the home range.

Results

Tournier et al. (2014) analysed scan samples with diet data, and assessed the availability of the 14 most important tree species utilised by the monkeys during the study, using abundance measures and phenology. They calculated indices of diet overlap between groups, which were highly variable and could be remarkably low. They found significant intergroup differences in diet with respect to the relative utilisation of 13 of the 14 tree species. Ecology seemed an important factor for diet composition, as the researchers found a positive correlation between the proportion in the diet and local abundance for 13 tree species. However, when analysing pairs of groups in more detail, the authors discovered that these comparisons revealed a significant number of mismatches between the abundance of a tree species in a home range and the relative importance of it in the diet of the corresponding group (Fig. 1). The authors concluded that while their results are compatible with the possibility that traditions exist on a local group scale (rather than population scale) potential alternative explanations need to be ruled out. For example, these differences could reflect particular nutrient deficiencies in the total diets of the monkeys, whereby they prefer to eat a certain other food to compensate; or the results might be due to different group compositions. In order to establish whether the patterns observed are local traditions, I suggest observation of fissioned groups that are using a new home range and have a different group composition, to see if they maintain their feeding preference from their original home range. If this is found, then the most plausible explanation would be that these differences are due to socially learned feeding patterns, thus potentially, traditions in the diets of wild vervet monkeys.

<u>2. Variation in facial expression (lip smacking) during grooming</u>

This data set was already published by van de Waal and colleagues (2013a). To summarize their methods, lip smacking data were extracted from ad libitum video recordings of grooming bouts between adult females of two study groups. The Picnic group had three adult females and the Donga group six. The researchers analysed lip smack frequency (smacks per second) when the groomer groomed with the mouth. Whenever lip smacking occurred and the mouth of the subject was clearly visible, the frequency of mouth movements was calculated. Lip smacks per second were counted using slow motion video playback, and correlations between lip smacking frequency and the recipient's rank were computed. The female rank order was calculated using Matman (Matrix manipulation and analyses package in The Observer, Noldus). The term "rank" referred to the place of an individual in the dominance hierarchy of adult females with rank 1 being that of the highest ranking female. The goal was to study communicative signals (body presentations and lip smacking) produced during grooming between adult females of two groups of vervet monkeys (van de Waal et al. 2013a).

Results

The results showed that the frequency of lip smacking did not correlate in any obvious way with the rank of the groomee, as the sign of the correlation coefficients differed between the two groups (negative correlation in the Donga group; positive correlation in the Picnic group, Fig.2). Analyses revealed that individuals of the Picnic group produced significantly more lip smacks per second than individuals of the Donga group. The reason for intergroup variation in this signal, observed in the context of an adult female grooming another with her mouth, remains unclear. The authors explain lip smacking as a request for tolerance when directed to a higher-ranked individual, or as an appeasement signal when directed to a lower-ranked individual (van de Waal et al. 2013a), but this did not explain the variation found between the two study groups. Though the explanation remains unclear, I suggest deeper consideration of this group level variation. Since all the females in the Picnic group express a higher frequency of smacks than females in the Donga group, it could be a socially learned trait, akin to another lip smacking 'dialect' in each group. Should this possibility be confirmed, for example through more detailed study of more neighbouring groups or study of fissionned groups, vervets would show a social custom, as in the chimpanzee hand-clasp grooming custom that differs between neighbouring communities limiting a potential genetic base for the observed behavioural variation (McGrew et al. 2001).

3. Variation in the social network structure

These findings have already been published by Borgeaud et al. (2016). Grooming and 1m and 5m proximity data were collected through scan sampling (Altmann 1974) of three neighbouring groups (Ankhase: AK; Noha: NH; and Baie Dankie: BD) of wild vervets at the Inkawu Vervet Project (IVP). During this study, the group size of AK, excluding infants, ranged from 26 to 33 individuals (including 6 to 8 adult females, 4 to 7 adult males, and 12 to 19 juveniles); BD comprised 36 to 48 individuals (11 to 14 adult females, 4 to 5 adult males, and 19 to 33 juveniles), and NH varied from 25 to 41 individuals (11 to 12 adult females, 2 to 7 adult males, and 11 to 25 juveniles). In contrast to traditional social network analyses, which rely on temporally isolated snapshots, this study applied a novel approach to capture changes over time in both the structure and the dynamics of the relationships of the three groups using a stochastic actor-oriented model (SAOM; Borgeaud et al. 2016).

Results

A temporally sensitive stochastic actor-oriented model (SAOM) was used to test the group-level structure and dynamics of social relationships in three groups of wild vervet monkeys (AK, BD, NH; Borgeaud et al., 2016). Triadic closure (i.e. the friend of a friend is a friend) was significant in all three groups, whereas the degree popularity (i.e. the willingness to associate with individuals with high degree of connections) was significant in only two groups (AK, BD).

The dynamics and the structure of relationships differed significantly among the groups according to four factors: sex, age, matriline and hierarchy. In terms of dynamics, no similarities were found among groups, according to these four attributes, in how quickly relationships were modified. In two groups (AK, BD), females' relationships were more prone to variation than males'. In BD, relationships within high-ranking matrilines were less stable than in low-ranking ones; whilst in NH, juveniles' relationships were less stable than adults'. In terms of network structure, the likelihood of social bonds according to sex, age, matriline and hierarchy was investigated. Individuals were found to preferentially associate with individuals of the same sex in only two groups (AK, NH), and with individuals of the same matriline also in just two groups (BD, NH). Borgeaud and colleagues (2016) concluded: 'The intergroup variation indicates that establishing species-specific or even population specific characteristics of social networks for later between-species comparisons will be challenging'.

4. Variation in agonistic behaviours

As the results presented in this section have not been published before, the present method section is more detailed than those for the previous three published data sets.

Study area

The study was conducted from July 2007 until March 2008 at the ABEERU (Applied Behavioural Ecology and Ecosystem Research Unit) research site of UNISA (University of South Africa) in the Loskop Dam Nature Reserve, Mpumalanga Province, South Africa. This site was chosen for the presence of a tourist road passing through the territories of six groups of vervet monkeys (*Chlorocebus pygerythrus*) allowing observers to travel easily from one group to another. The six groups were subject to social learning experiments during the course of this study (van de Waal et al. 2010, 2012; van de Waal & Bshary 2011). All group compositions are detailed in Table 2.

Data Collection

The material used for data collection consisted of Swarowski EL Binocular 8X32, a chronometer, handheld computer (Palm Zire 22 or HP travel companion iPAQ rx5935) running PenDragon 5.1 data collection software, and a video-camera JVC Everio GZ-MG 130. Seven observers (Martina Spinelli, Erica van de Waal & Yaëlle Bouquet for the Picnic and the Donga groups; Virginia Tournier & Emilie Tournier for the Bay and the Fishing groups; Christèle Borgeaud & Amélie Piller for the Blesbokvlakte and the Nooitgedacht groups) recorded all aggressive interactions on an 'all occurrence' basis (Altmann 1974). After an initial joint training phase to reduce potential observer biases, data were collected for six to 10 hours daily. All six groups were habituated for a minimum of three months before data collection, and all individuals tolerated observers within 10m or less. All individuals were considered.

Behavioural interactions were recorded during (all occurrence sampling) and just after (focal sampling) a conflict. The context of the conflict (natural or around experiments) was also recorded. Presence or absence of a conflict management strategy was recorded, and if present, it was identified as aggressive (redirection of aggression) or affiliative (consolation or reconciliation). Post-conflict interactions were recorded through focal sampling of both the victim and the aggressor (if possible) for five minutes after a conflict (post conflict period; PC). Five minutes were considered sufficient to collect all post conflict behaviours, which occur mainly in the first minutes after a conflict (Kazem & Aureli 2005). According to the PC and matched control period (MC) method (de Waal & Yoshihara 1983), every PC observation requires a corresponding context-matched control observation. The MC was initiated, and a five minute focal sample collected, as soon as the victim or the aggressor was observed in the same behavioural context but without a prior aggression.

Data analyses

Conflict frequency in natural contexts: comparison of six groups

To investigate whether there were differences in conflict frequencies between groups, the natural context data (i.e not associated with experiments) were analysed in two steps. First, conflict frequency per hour for every day of observation for each group (n=165 days in total) was calculated. Conflict frequency for each group was then standardized per number of individuals in the group and analysed using a Kruskal-Wallis test. Second, to test whether differences in conflict frequency between groups were due to the presence of more aggressive individuals, conflict frequencies for each individual in the six groups was calculated and then analysed with a Kruskal-Wallis test.

Conflict management

a) Reaction after an aggression: Response or no response

The researchers calculated the percentage of conflicts to which individuals responded in a natural context. Using a Wilcoxon signed ranks test, they tested this observed percentage against the normal distribution (50:50) that would be expected by chance. They then tested if there was a difference in the likelihood of reaction after a conflict between the six groups with a χ^2 test.

b) Affiliative versus aggressive responses

To have a large enough sample size they included conflicts recorded during both natural observations and around experiments. They first compared the absolute frequencies of aggressive versus affiliative responses to conflicts using a χ^2 test. Using the PC (Post-conflict period)–MC (Matched control period) method they compared the timing of the first affiliative interaction between the former opponents during one PC with the corresponding MC. If this interaction occurred only in the PC or earlier in the PC than in the MC the PC-MC pair was considered to be “attracted”. Alternatively, if affiliative behaviours occurred sooner or only in the MC, the pair was considered to be “dispersed”. When no affiliative interactions took place in either the PC or the MC, or when the interaction occurred at the same time in both, the PC-MC pair was considered “neutral” (de Waal & Ren 1988).

The researchers investigated differences in reconciliation between the study groups in two steps. First, they made the number of attracted pairs independent from the baseline level of affiliative contact. Indeed, this baseline level may differ between different categories of individuals, for example there are generally more affiliative contacts between kin than non-kin. According to Veenema et al. (1994) the number of attracted pairs that are due to baseline levels of contact is reflected by the number of dispersed pairs. By subtracting the number of dispersed pairs from the number of attracted pairs, they obtained an estimate of the amount of attracted pairs that reflects the increase in affiliative interactions due to the preceding conflict. The second step was to compare the “real attracted pairs” with the total number of PC-MC pairs for each group with a χ^2 test.

Statistics

Statistical analyses were performed with SPSS (version 14.0 for Windows). All the tests used are non-parametric, two-tailed and with p set at 0.05. Infants (juveniles of less than 1 year old) were not considered in the data analyses.

Ethics Guidelines

The study consisted mainly of natural observations. Some conflict data were collected around experiments conducted for different projects that were all approved by the relevant local authority, Mpumalanga Parks Board and ABEERU of UNISA, South Africa; and as a consequence by the funder, Swiss National Science Foundation.

Results

a) Conflict frequency in natural context

The daily conflict frequency differed significantly across the six groups (Kruskal-Wallis test, n= 165, X^2 =54.74, df =5, p<0.001, Fig. 3). This intergroup difference persisted when the frequencies of aggressions per individual in each group were calculated, suggesting that these intergroup differences are due to differences in aggressiveness of all group members rather than one or few individuals (Kruskal-Wallis test, n=100, X^2 = 22.9, df=5, p<0.001, Fig. 4).

b) Conflict management

Reaction after an aggression: Response or no response

Some groups were more likely to respond to aggressions than other groups (χ^2 test, n=258, X^2=25.17, df=5, p<0.001, Fig. 5).

Affiliative versus aggressive responses

Two of the three groups were more likely to respond with affiliative behaviour (either through consolation of the victim from third parties, or through reconciliation between the aggressor and the victim). In contrast, the third group, reacted more often with an aggressive behaviour such as a coalition or redirection (χ^2 test, n=140, X^2=8.9, df=2, p=0.01, Fig. 6). In addition, groups also differed in their probability to reconcile after a conflict (χ^2 test, attracted pairs – dispersed pairs as one column, neutral pairs as the other column, n=159, X^2=9.1, df=2, p=0.007).

Discussion

Our findings of variation across four different behavioural domains highlight that local variation merits increased attention by primatologists. Indeed, intergroup variation was found everywhere we looked for it, from diet to facial expression, from social network dynamics to conflict management. Taken as an example, in the literature, descriptions of conflict management strategies in a given species of primate typically rely on data collected from one or few groups per study site, much like most behavioural studies of primates. On this topic, primatologists have shown much interest in variation between individuals and variation between populations (Whiten & Byrne 1988; Aureli & Schaffner 2007). They have nonetheless neglected intergroup variation, so that behaviour observed in one or few groups has been generalized across the whole species. An elegant experiment of social exposure between two species of macaques (de Waal & Johanowicz 1993) revealed that a modification in post-conflict behaviour, here reconciliation, can be socially learned in monkeys. As a consequence, when a deviation from this “species baseline” was found, the tradition hypothesis (stipulating that the variation in the observed behaviour was socially learned, thus a potential tradition) was used to explain such a difference (see for example on chimpanzees: Nakamura et al. 2000). Comparisons between several neighbouring groups may give new insights into how variation in individual conflict behaviour may translate into intergroup variation with respect to conflict management. Though the present data analyses at the group level were limited by the sample size of conflict occurrence, and by the time over which the data were collected (ideally the data would have been from multiple years of observation). Nonetheless, this work highlights the importance of studying particular behaviours at different levels.

The variation presented here in all four behavioural domains is extracted from a dataset of one to two years, thus limiting the potency of the findings. Ideally one would investigate the long term stability (over multiple generations) of the observed differences to check that they are not a result of the presence of particular individuals, such as the personality of a dominant individual or to the group structure at a particular period (Sapolsky & Share 2004). Social interactions of adult males in a troop of wild savannah baboons were studied for over 10 years, and the researchers described a ‘pacific culture’ persisting long after the death of the more aggressive males in a spate of disease (Sapolsky & Share 2004). This result is echoed in our findings that some groups were more likely to respond to a conflict with reconciliation or consolation, whereas others mainly escalated the conflict by responding with redirection or coalition. The finding of a ‘pacific culture’ in a baboon troop would have been more convincing if it multiple troops had been studied over a similar time period, and had different stable conflict management strategies emerging despite frequent turnover of males.

In vervet monkeys, males disperse between the groups at sexual maturity and multiple times within their lives, creating a continuous gene flow between the study groups, thus limiting the chances of a genetic cause of the observed group differences. Furthermore, as most of the neighbouring vervet monkey groups described above have overlapping territories, their ecology is very similar. Nonetheless, to exclude ecological explanations for the observed behavioural variation we must confirm that the variation remains just as pronounced in overlap zones as it is elsewhere in their home ranges. An even more promising way to test whether the observed intergroup variation is cultural would be through examination of the consequences of recent group fissions documented in our study population (van de Waal et al. 2017). Fissions provide an opportunity to compare the behaviour of a subgroup of individuals, retrospectively in their origin group, with the behaviour they exhibit once in their splinter group, with a different social structure and in a different environment (usually neighbouring their origin home range). Investigating this specific context offers a promising way to examine whether ecology and group structure or composition are the only factors contributing to the observed variation. If the splinter groups continue to exhibit the same behavioural variants to those observed in their origin group as it was the case in an experimental context (van de Waal et al. 2017), then a socially learned basis of the observed variation will be the most likely explanation. This would shed light upon whether intergroup behavioural variation is due to different local traditions or other socio-ecological factors.

Studies of multiple groups of wild primates within single populations have demonstrated social learning through field experiments (in four groups of lemurs, Schnoell & Fichtel 2012; in up to13 groups of marmosets, Gunhold et al. 2014a, 2014b; in up to six groups of vervet monkeys, van de Waal et al. 2010, 2012, 2013b, 2014, 2015; van de Waal & Bshary 2011). However, long-term observations of these populations, with the aim of revealing potential intergroup differences, are to my knowledge lacking, until this present review of behavioural variation in wild vervet monkeys.

In conclusion, this study of four different behavioural domains in up to six neighbouring groups of wild vervet monkeys contrasts with most studies, which have focussed on a specific behaviour and drawn a general picture of that behaviour in a particular species only on the basis of only one or two groups. Results warn scientists about the risks of generalization from data collected from only a few groups in a population and suggest that, in the future, studies of any behaviour should include several groups. These data reveal that we should take between-group differences within a single population seriously for any larger scale evolutionary comparisons (between populations and/or between species) as well as a potential source for studying animal culture. The intergroup variation found also indicates that establishing species-specific or even population specific behaviours for later between-species comparisons will be challenging. In their conclusions, Luncz and Boesch (2012) stated that “Our study shows that cultural differences in chimpanzees can be found over a very small spatial scale and between neighbouring communities”. The results presented here on vervet monkeys are consistent with this finding, and I urge other researchers to investigate behavioural variation between multiple groups within a single population.

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References:

Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. 2013: Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science **340**, 485-488.

Altmann, J. 1974: Observational study of behavior – sampling methods. Behaviour **49**, 227—267.

Aureli, F., & Schaffner, C. M. 2007: Aggression and conflict management at fusion in spider monkeys. Biol. Letters **3**, 147-149.

Barrett, A. S. 2010: Spatial and temporal patterns in resource dispersion and the structure of range use and co-existence in a social omnivore *Chlorocebus aethiops*. Ph.D. dissertation, Department of Environmental Sciences, Univ. of South Africa, Florida, South Africa.

Borgeaud, C., Sosa, S., Sueur, C., Bshary, R., & van de Waal, E. 2016: Intergroup variation of social relationships in wild vervet monkeys: a dynamic network approach. Front Psychol **7**, 915.

Chapman, C. A., & Fedigan, L. M. 1990: Dietary differences between neighboring *Cebus capucinus* groups: local traditions, food availability or responses to food profitability?. Folia Primatol. **54**, 177-186.

Clutton-Brock, T. H., & Harvey, P. H. 1977: Primate ecology and social organization. J. Zool. **183**, 1-39.

Dawkins, R. 1976: The selfish gene. Oxford: Oxford University Press.

Dobzhansky, T., & Dobzhansky, T. G. 1937: Genetics and the Origin of Species. Columbia, Columbia university press.

Endler, J. A. 1986: Natural selection in the wild (No. 21). Princeton, Princeton University Press.

Gunhold, T., Massen, J. J., Schiel, N., Souto, A., & Bugnyar, T. 2014a: Memory, transmission and persistence of alternative foraging techniques in wild common marmosets. Anim. Behav. **91**, 79-91.

Gunhold, T., Whiten, A., & Bugnyar, T. 2014: Video demonstrations seed alternative problem-solving techniques in wild common marmosets. Biol. Letters **10**, 20140439.

Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., Bolyanatz, Cardenas, J. C., Gurven, M., Gwako, E., Henrich, N., Lesorogol, C., Marlowe, F., Tracer, D., & Ziker J. 2006: Costly punishment across human societies. Science **312**, 1767-1770.

Hoppitt,W., & Laland, K. N. 2013: Social learning: An introduction to mechanisms, methods, and models. Princeton, NJ, Princeton University Press.

Humle, T., & Matsuzawa, T. 2002: Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. Am. J. Primatol. **58**, 133-148.

Kappeler, P. 2010: Animal behaviour: Evolution and mechanisms. Berlin Heidelberg, Springer.

Kazem, A. J. N., & Aureli, F. 2005: Redirection of aggression: multiparty signalling within a network? In: Animal Communication Network (McGregor, P. K, ed.). Cambridge, Cambridge University Press, pp. 191-218.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. 2005: Cultural transmission of tool use in bottlenose dolphins. Proc. Natl. Acad. Sci. USA **102**, 8939-8943.

Lamba, S., & Mace, R. 2013: The evolution of fairness: Explaining variation in bargaining behaviour. Proc. R. Soc. B. **280**, 20122028.

Luncz, L.V., Mundry, R., & Boesch, C. 2012: Evidence for cultural differences between neighboring chimpanzee communities. Curr. Biol. **22**, 922–926.

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

Luncz, L. V., & Boesch, C. 2015: The extent of cultural variation between adjacent chimpanzee (Pan troglodytes verus) communities; a microecological approach. Am. J. Phys. Anthropol. **156**, 67-75.

McGrew, W. C., Marchant, L. F., Scott, S. E., & Tutin, C. E. 2001: Intergroup Differences in a Social Custom of Wild Chimpanzees: The Grooming Hand-Clasp of the Mahale Mountains1. Curr. Anthropol. **42**, 148-153.

Mesoudi, A., Whiten, A., & Laland, K. N. 2006: Towards a unified science of cultural evolution. Behav. Brain Sci. **29**, 329-383.

Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.). 2012: The evolution of primate societies. Chicago, University of Chicago Press.

Nakamura, M., McGrew, W. C., Marchant, L. F., & Nishida, T. 2000: Social scratch: Another custom in wild chimpanzees? Primates **41**, 237-248.

Perry, S., Baker, M., Fedigan, L., Gros-Luis, J., Jack, K., Mackinnon, K. C., Manson, J., Panger, M., Pyle, K., & Rose, L. M. 2003: Social conventions in white-face capuchins monkeys: evidence for behavioral traditions in a neotropical primate. Curr. Anthropol. **44**, 241-268.

Perry, S., & Manson, J. H. 2003: Traditions in monkeys. Evol. Anthropol. **12**, 71-81.

Robbins, M. M., Ando, C., Fawcett, K. A., Grueter, C. C., Hedwig, D., Iwata, Y., Lodwick, J., L., Masi, S., Salmi, R., Stoinski, T. S., Todd, A, Vercellio, V., & Yamagiwa, J. 2016: Behavioral Variation in Gorillas: Evidence of Potential Cultural Traits. PloS ONE **11**, e0160483.

Santorelli, C. J., Schaffner, C. M., Campbell, C. J., Notman, H., Pavelka, M.S, Weghorst, J. A., & Aureli, F. 2011a: Traditions in Spider Monkeys Are Biased towards the Social Domain. PLoS ONE **6**, e16863.

Santorelli, C. J., Schaffner, C. M., & Aureli, F. 2011b: Universal behaviors as candidate traditions in wild spider monkeys. PloS ONE **6**, e24400.

Sapolsky, R. M., & Share, L. J. 2004: A pacific culture among wild baboons: its emergence and transmission. PLoS Biol. **2**, e106. (doi:10.1371/journal.pbio.0020106)

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

Schnoell, A. V., & Fichtel, C. 2012: Wild redfronted lemurs (*Eulemur rufifrons*) use social information to learn new foraging techniques. Anim. Cogn. **15**, 505-516.

Tan, A., Tan, S. H., Vyas, D., Malaivijitnond, S., & Gumert, M. D. 2015: There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. PloS ONE **10**, e0124733.

Thornton, A., Samson, J., & Clutton-Brock, T. 2010: Multi-generational persistence of traditions in neighbouring meerkat groups. Proc. R. Soc. B. **277**, 3623-3629.

Tournier, E., Tournier, V., van de Waal, E., Barrett, A., Brown, L. & Bshary, R. 2014: Differences in diet between six neighbouring groups of vervet monkeys. Ethology **120**, 1-12.

Veenema, H. C., Das, M., & Aureli, F. 1994: Methodological Improvements for the Study of Reconciliation. Behav. Process. **31**, 29-37.

de Waal, F. B., & Yoshihara, D. 1983: Reconciliation and redirected affection in rhesus monkeys. Behaviour **85**, 224-241.

de Waal, F. B. M., & Ren, R. 1988: Comparison of the reconciliation behavior of stumptailed and rhesus macaques. Ethology **78**, 129-142.

de Waal, F., & Johanowicz, D. L. 1993: Modification of reconciliation behavior through social experience: an experiment with two macaque species. Child Dev. **64**, 897-908.

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. 2010: Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proc. R. Soc. B. **277**, 2105-2111.

van de Waal, E., & Bshary, R. 2011: Social learning abilities of wild vervet monkeys in a two-step task artificial fruit experiment. Anim. Behav. **81**, 433-438.

van de Waal, E.,& Whiten, A. 2012: Spontaneous emergence, imitation and spread of alternative foraging techniques among groups of vervet monkeys. PLoS ONE **7**, e47008.

van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. 2012: Similarity in food cleaning techniques within matrilines in wild vervet monkeys. PLoS ONE **7**, e35694.

van de Waal, E., Spinelli, M., Bshary, R., & Noë, R. 2013a: Negotiations over grooming in wild vervet monkeys (*Chlorocebus pygerythrus*). Int. J. Primatol. **34**, 1153-1171.

van de Waal, E., Borgeaud, C., & Whiten, A. 2013b: Potent social Learning and conformity shape a wild primate’s foraging decisions. Science **340**, 483–485.

van de Waal, E., Claidière, N., & Whiten, A. 2013c: Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. Anim. Behav. **85**, 71-76.

van de Waal, E., Bshary, R., & Whiten, A. 2014: Field experiments show wild vervet monkey infants acquire maternal food-processing techniques. Anim. Behav. **90**, 41-45.

van de Waal, E., Claidière, N., & Whiten, A. 2015: Wild vervet monkeys discriminate and copy alternative methods for opening an artificial fruit. Anim. Cogn. **18**, 617-627.

van de Waal, E., van Schaik, C. P., & Whiten, A. 2017: Resilience of experimentally seeded dietary traditions in wild vervets: Evidence from group fissions. Am. J. Primatol. **79**(10).

Whiten, A., & Byrne, R. W. 1988: Tactical Deception in Primates. Behav. Brain Sci. **11**, 233-244.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. 1999: Cultures in chimpanzees. Nature **399**, 682-685.

Whiten, A. & van Schaik, C. P. 2007: The evolution of animal ‘cultures’ and social intelligence. Philos. T. Roy. Soc. B. **362**, 603-620.

Whiten, A. 2005: The second inheritance system of chimpanzees and humans. Nature **437**, 52-55.

Figures legends

Fig. 1. Cumulative histogram of the relative importance of 14 preselected tree species in five groups of vervet monkeys. Items (fruits, leaves, etc.) were not distinguished, and for each group, all items eaten of the 14 tree species add up to 100%. For abbreviations of tree species, see 1. *Variation in the diet of vervet monkeys* (Figure 2 in Tournier et al. 2014).

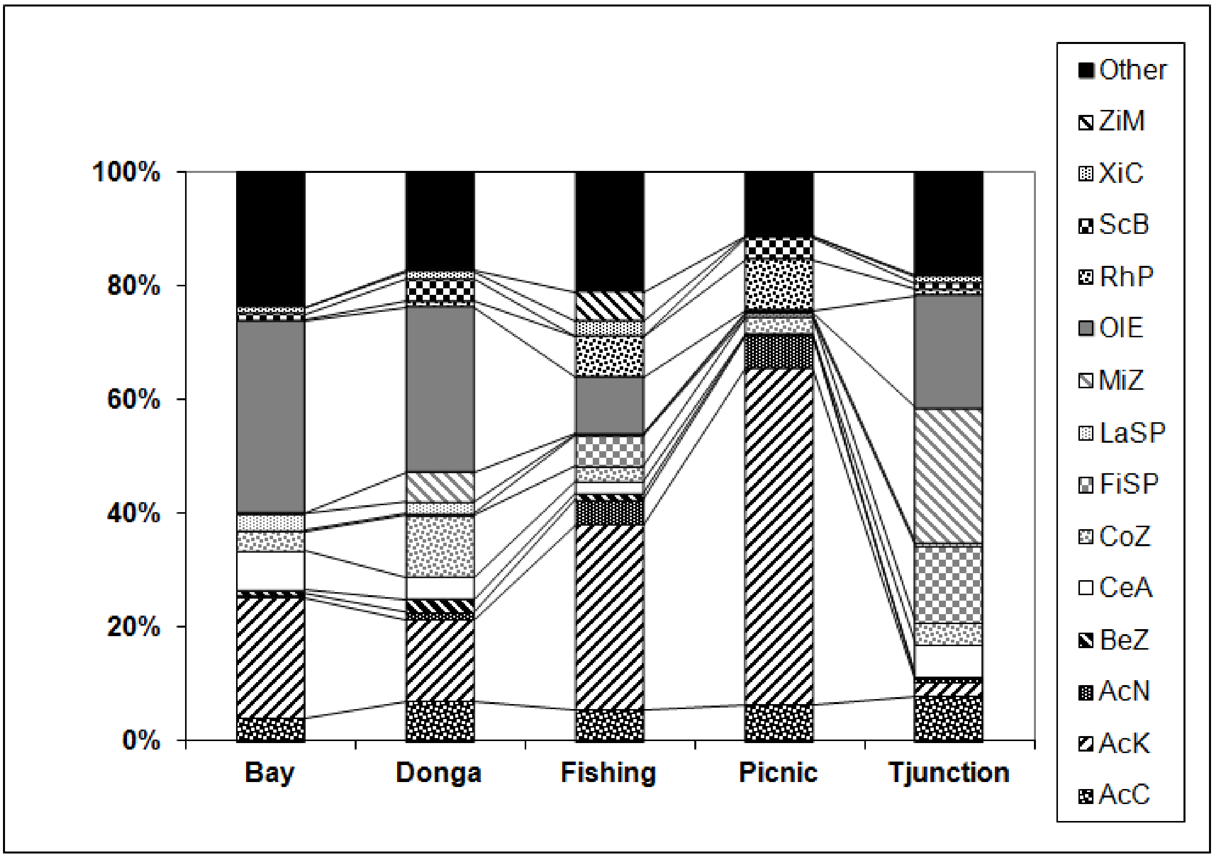


Fig. 2. Mean lip-smacks per second performed by groomers during grooming-with-mouth events in relation to the recipient’s rank. The dashed lines represent the linear trend lines (Figure 7 in van de Waal et al. 2013a).

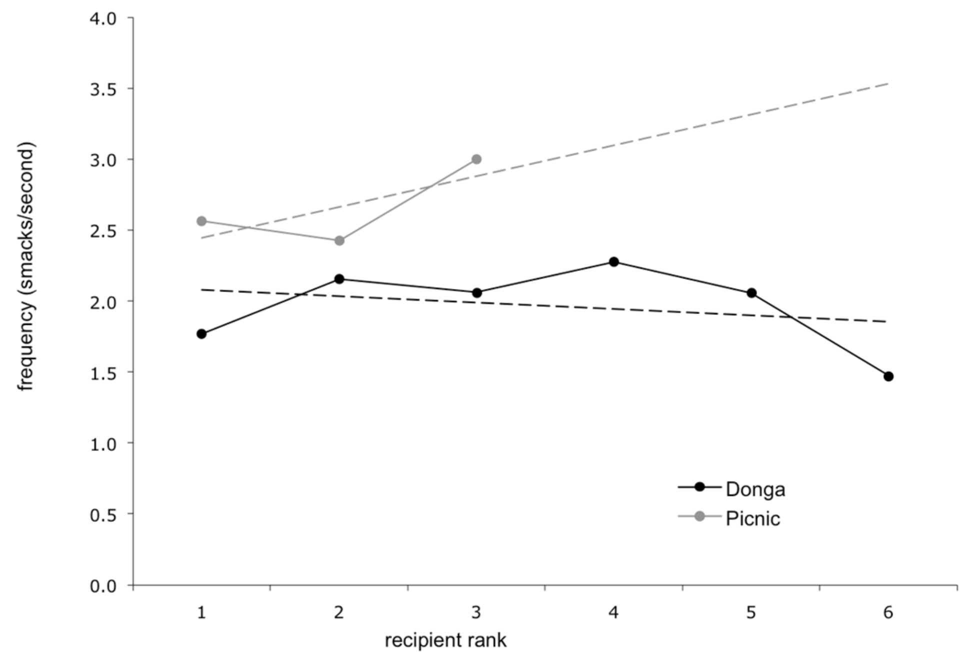


Fig. 3. Comparison in conflict frequency per day of observation and per the number of individuals between the six groups in a natural context.

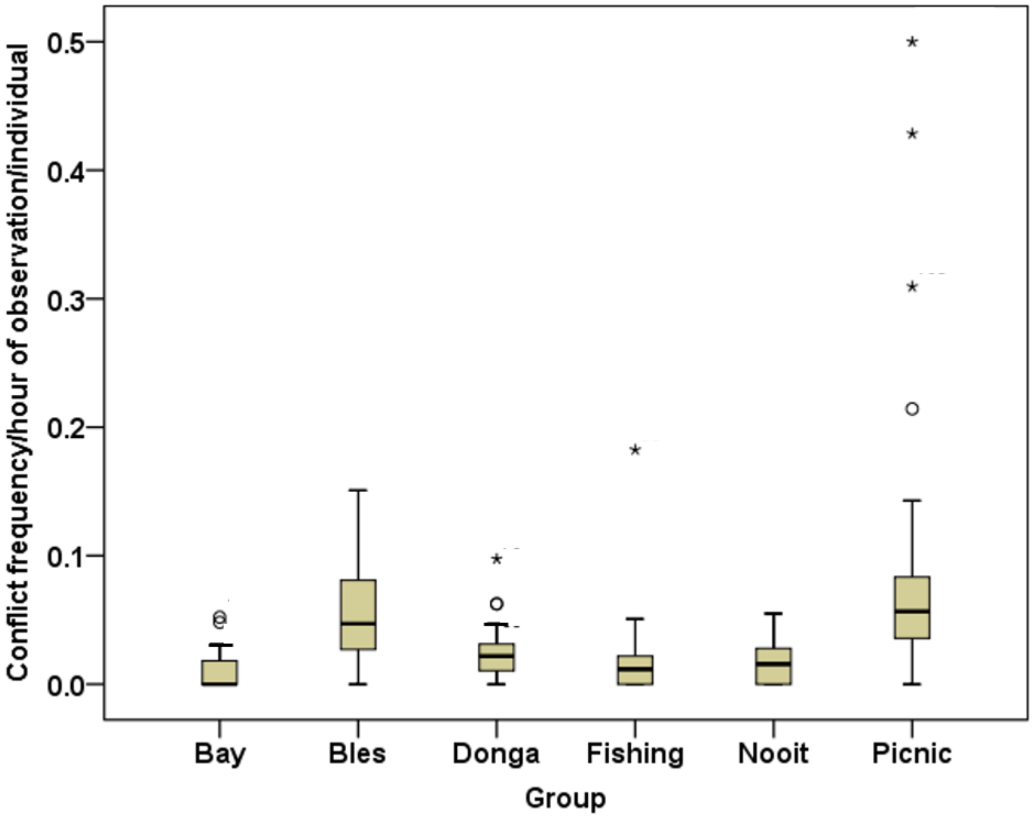


Fig. 4. Comparison of conflict frequency (Number of conflict per hour of observation) per individual (classified by their rank of aggressiveness within their group) between the six groups in natural context. The six groups are represented by different coloured lines and each symbol on a line is the score of a group member. Blesbokvlakte group is the smallest with only 14 individuals and the Fishing camp is the largest with 23 group members (Details of all group composition in Table 2).

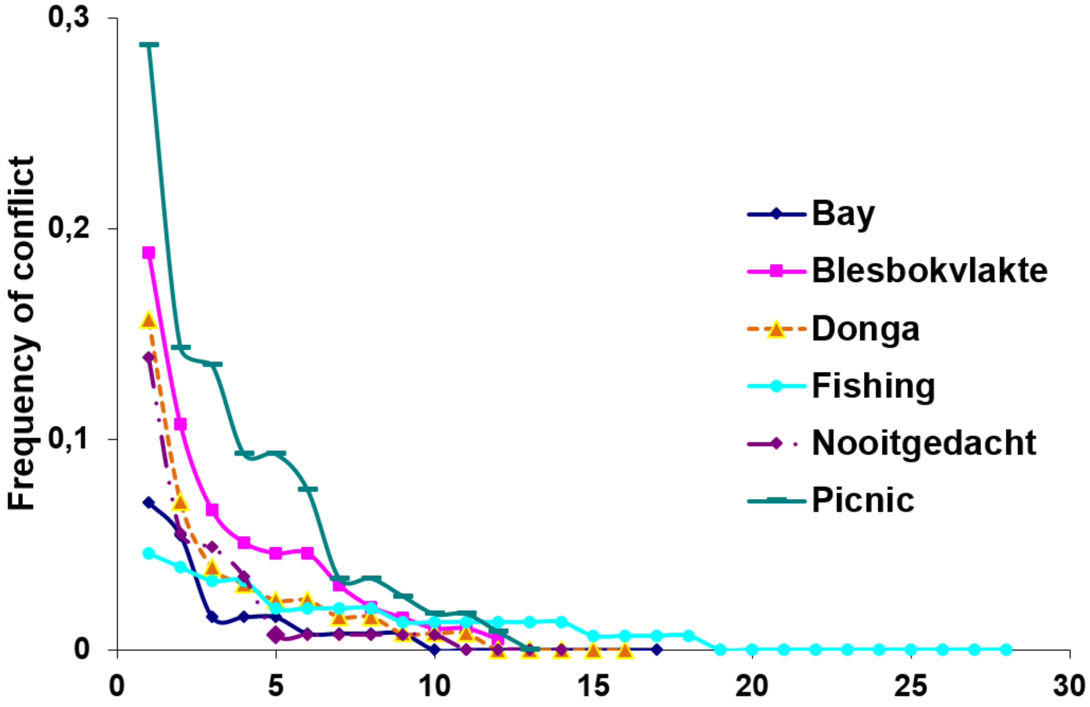


Fig. 5. Number of conflicts followed (white) or not (black) by a reaction from the victim for the six groups in natural context.

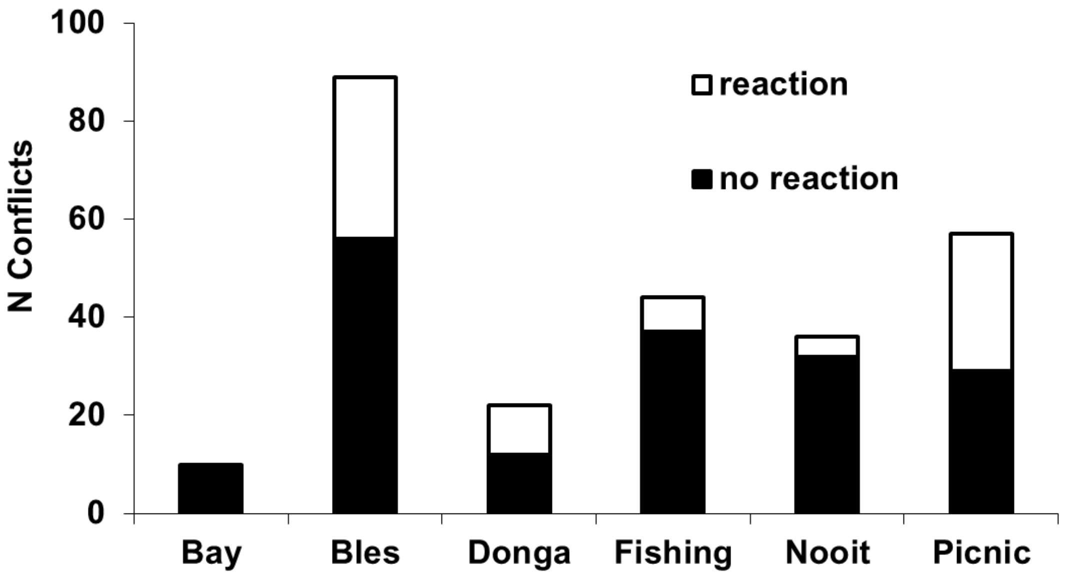
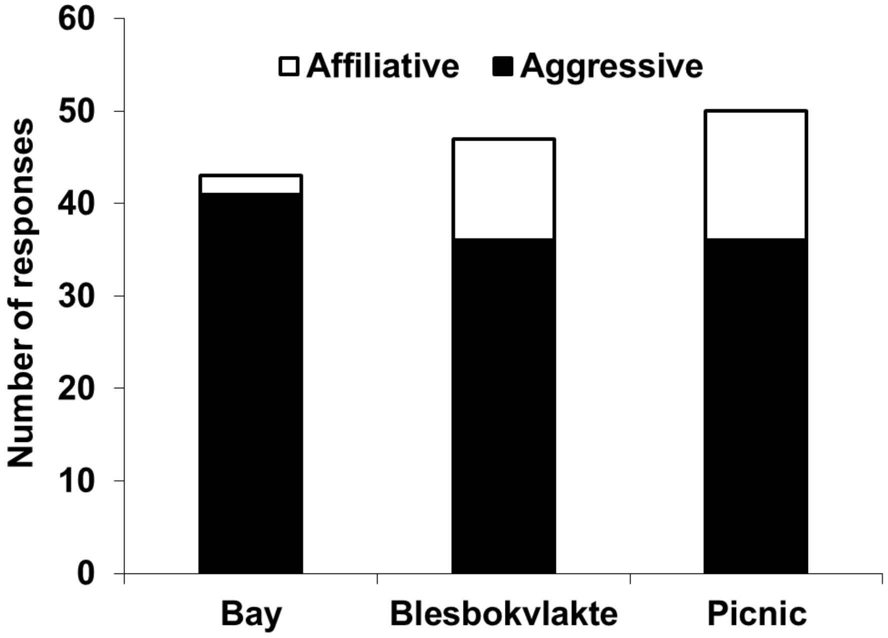


Fig. 6. Response to aggression: preference for an aggressive (black) or affiliative (white) strategy between groups in both natural and experimental context.



Tables:

Table 1.

Data presented in this paper:

Variation studied in :	**Field site**	**N groups**	**References**
Diet	Loskop	6	Tournier et al. 2014
Facial expression (lip smacking) during grooming	Loskop	2	van de Waal et al. 2013a
Social network structure	IVP	3	Borgeaud et al. 2016
Agonistic behaviours	Loskop	6	Unpublished dataset

Legend Table 1:

This table summarize the four research questions discussed in this paper; vervet monkeys were studied in two different field sites: Loskop Dam Nature Reserve (Loskop), or Inkawu Vervet Project (IVP) in Mawana Game Reserve; N groups is the number of studied groups.

Table 2.

Composition of the six studied groups for feeding and agonistic behaviours:

Group	**Adult males**	**Adult females**	**Juveniles**	**Infants**	**Total**
Bay	5	5	6	4	**20**
Picnic	3	3	7	3	**16**
Blesbokvlakte	4	3	4	3	**14**
Donga	5	6	5	5	**21**
Nooitgedacht	3	5	6	3	**17**
Fishing Camp	3	5	12	3	**23**

Legend Table 2:

Group composition of the six studied groups in the middle of the data collection: Individuals are classified as adult males after they have dispersed to another group, adult females if they gave birth, before they are classified as juveniles except if they are less than 1 year old, then they are classified as infants.