

1 **On the neglected behavioural variation among neighbouring primate groups**

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19 **Abstract**

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

35

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

## 38 **Introduction**

39

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

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

54       Studies of between-species variation often correlate variation in aspects such as diet,  
55 group size, body size or sexual dimorphism, with variation in factors such as social structure,  
56 mating system, or brain size across species (Mitani et al. 2012). Due to the scarcity of wild  
57 study groups in each population, these analyses often rely on small sample sizes for each  
58 species, with the risk that data are not particularly representative of the whole species. This can  
59 lead to increased unexplained variance in analyses. The question is then: how much of the  
60 variation observed is really explained by differences between populations rather than variation  
61 present within populations? This issue famously occurred in human studies using the ultimatum

62 game, a two-player bargaining experiment extensively used across disciplines to measure  
63 fairness. One study revealed very high cross-cultural variation in fairness (and thus great  
64 excitement: Henrich et al. 2006), but Lamba & Mace (2013) found a similar amount of variation  
65 between local villages in an Indian sub-culture. Such findings warrant interest in whether a  
66 similar amount of variation can be found between neighbouring groups in other species.

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

73 Studies of variation between populations of a single species have had two main goals:  
74 first, linking diet or social organization with ecology, and second, detecting potential traditions.  
75 Biologists have defined culture as group-typical behavioural patterns, shared by members of a  
76 community, which rely on socially learned and transmitted information (Hoppitt & Laland  
77 2013). Social learning is the mechanism underlying ‘cultural transmission’ (Whiten 2005). This  
78 cultural transmission is an important phenomenon to understand within the Life Sciences as a  
79 whole, because if innovations spread and persist across generations, the result is a ‘second  
80 inheritance system’ (Whiten 2005) that has evolved in addition to genetic inheritance and now  
81 forms a parallel evolutionary stream (Dawkins 1976; Mesoudi et al. 2006). Cultural and genetic  
82 evolution share fundamental characteristics, notably information transmission, mutation,  
83 selection and adaptation (Mesoudi et al. 2006). We now know much about genetic or  
84 ‘biological’ evolution, but still relatively little about cultural evolution.

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

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

108           Intergroup differences in neighbouring groups of primates were first reported when  
109 comparing the diet of three such groups of capuchin monkeys (Chapman & Fedigan 1990). This

110 study found that dietary variation was not linked to food availability and thus the authors  
111 concluded that it was either due to food profitability or to local traditions. Later research on two  
112 neighbouring communities of chimpanzees in the Mahale mountains found variation in hand-  
113 clasp grooming, demonstrating the first such example concerning social customs (McGrew et  
114 al. 2001). A review by Perry & Mason (2013) highlighted that studies on monkey traditions  
115 were focussing essentially on foraging behaviour (food processing or choice) and rarely on  
116 social behaviours, with most research being conducted on one group, some on two, or a  
117 maximum of three groups.

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

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

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

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

151 Since 2005, I have worked with wild vervet monkeys (*Chlorocebus pygerythrus*) in  
152 South Africa, mainly conducting social learning experiments but also collecting baseline data  
153 on natural behaviours. I first worked with six groups of the population living in the Loskop  
154 Dam nature reserve, Mpumalanga, for six years; then on six groups of the population at the  
155 Inkawu Vervet Project (IVP) in the Mawana private game reserve, KwaZulu Natal since 2010.  
156 Here, I review intergroup behavioural variation observed in neighbouring groups (with often  
157 overlapping home ranges) of wild vervet monkeys. First, I report intergroup dietary variation  
158 found through analyses of the amount of foraging on 14 preferred fruiting tree species, in  
159 association with the abundance of these trees in each home range (Tournier et al. 2014). Second,

160 I report results on intergroup variation in the frequency of lip smacking (a facial expression)  
161 during grooming between dyads of adult females (van de Waal et al. 2013a). Third, I describe  
162 intergroup variation in social network structure and dynamics (Borgeaud et al. 2016). Finally,  
163 I present data on agonistic behaviours showing intergroup variation in three respects: 1) conflict  
164 frequency, 2) the number of conflicts followed by a response and 3) the number of aggressive  
165 and affiliative responses used.

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

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



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

188

## 189 **1. Variation in the diet of vervet monkeys**

190

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

205

## 206 **Results**

207 Tournier et al. (2014) analysed scan samples with diet data, and assessed the availability of the  
208 14 most important tree species utilised by the monkeys during the study, using abundance

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

227

## 228 **2. Variation in facial expression (lip smacking) during grooming**

229

230 This data set was already published by van de Waal and colleagues (2013a). To summarize  
231 their methods, lip smacking data were extracted from ad libitum video recordings of grooming  
232 bouts between adult females of two study groups. The Picnic group had three adult females and  
233 the Donga group six. The researchers analysed lip smack frequency (smacks per second) when

234 the groomer groomed with the mouth. Whenever lip smacking occurred and the mouth of the  
235 subject was clearly visible, the frequency of mouth movements was calculated. Lip smacks per  
236 second were counted using slow motion video playback, and correlations between lip smacking  
237 frequency and the recipient's rank were computed. The female rank order was calculated using  
238 Matman (Matrix manipulation and analyses package in The Observer, Noldus). The term "rank"  
239 referred to the place of an individual in the dominance hierarchy of adult females with rank 1  
240 being that of the highest ranking female. The goal was to study communicative signals (body  
241 presentations and lip smacking) produced during grooming between adult females of two  
242 groups of vervet monkeys (van de Waal et al. 2013a).

243

## 244 **Results**

245 The results showed that the frequency of lip smacking did not correlate in any obvious way  
246 with the rank of the groomee, as the sign of the correlation coefficients differed between the  
247 two groups (negative correlation in the Donga group; positive correlation in the Picnic group,  
248 Fig.2). Analyses revealed that individuals of the Picnic group produced significantly more lip  
249 smacks per second than individuals of the Donga group. The reason for intergroup variation in  
250 this signal, observed in the context of an adult female grooming another with her mouth,  
251 remains unclear. The authors explain lip smacking as a request for tolerance when directed to a  
252 higher-ranked individual, or as an appeasement signal when directed to a lower-ranked  
253 individual (van de Waal et al. 2013a), but this did not explain the variation found between the  
254 two study groups. Though the explanation remains unclear, I suggest deeper consideration of  
255 this group level variation. Since all the females in the Picnic group express a higher frequency  
256 of smacks than females in the Donga group, it could be a socially learned trait, akin to another  
257 lip smacking 'dialect' in each group. Should this possibility be confirmed, for example through  
258 more detailed study of more neighbouring groups or study of fissioned groups, vervets would

259 show a social custom, as in the chimpanzee hand-clasp grooming custom that differs between  
260 neighbouring communities limiting a potential genetic base for the observed behavioural  
261 variation (McGrew et al. 2001).

262

### 263 **3. Variation in the social network structure**

264

265 These findings have already been published by Borgeaud et al. (2016). Grooming and 1m and  
266 5m proximity data were collected through scan sampling (Altmann 1974) of three  
267 neighbouring groups (Ankhase: AK; Noha: NH; and Baie Dankie: BD) of wild vervets at the  
268 Inkawu Vervet Project (IVP). During this study, the group size of AK, excluding infants,  
269 ranged from 26 to 33 individuals (including 6 to 8 adult females, 4 to 7 adult males, and 12 to  
270 19 juveniles); BD comprised 36 to 48 individuals (11 to 14 adult females, 4 to 5 adult males,  
271 and 19 to 33 juveniles), and NH varied from 25 to 41 individuals (11 to 12 adult females, 2 to  
272 7 adult males, and 11 to 25 juveniles). In contrast to traditional social network analyses,  
273 which rely on temporally isolated snapshots, this study applied a novel approach to capture  
274 changes over time in both the structure and the dynamics of the relationships of the three  
275 groups using a stochastic actor-oriented model (SAOM; Borgeaud et al. 2016).

276

### 277 **Results**

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

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

295

#### 296 **4. Variation in agonistic behaviours**

297

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

300

##### 301 *Study area*

302 The study was conducted from July 2007 until March 2008 at the ABEERU (Applied  
303 Behavioural Ecology and Ecosystem Research Unit) research site of UNISA (University of  
304 South Africa) in the Loskop Dam Nature Reserve, Mpumalanga Province, South Africa. This  
305 site was chosen for the presence of a tourist road passing through the territories of six groups  
306 of vervet monkeys (*Chlorocebus pygerythrus*) allowing observers to travel easily from one  
307 group to another. The six groups were subject to social learning experiments during the course

308 of this study (van de Waal et al. 2010, 2012; van de Waal & Bshary 2011). All group  
309 compositions are detailed in Table 2.

310

### 311 *Data Collection*

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

322         Behavioural interactions were recorded during (all occurrence sampling) and just after  
323 (focal sampling) a conflict. The context of the conflict (natural or around experiments) was also  
324 recorded. Presence or absence of a conflict management strategy was recorded, and if present,  
325 it was identified as aggressive (redirection of aggression) or affiliative (consolation or  
326 reconciliation). Post-conflict interactions were recorded through focal sampling of both the  
327 victim and the aggressor (if possible) for five minutes after a conflict (post conflict period; PC).  
328 Five minutes were considered sufficient to collect all post conflict behaviours, which occur  
329 mainly in the first minutes after a conflict (Kazem & Aureli 2005). According to the PC and  
330 matched control period (MC) method (de Waal & Yoshihara 1983), every PC observation  
331 requires a corresponding context-matched control observation. The MC was initiated, and a five

332 minute focal sample collected, as soon as the victim or the aggressor was observed in the same  
333 behavioural context but without a prior aggression.

334

### 335 *Data analyses*

#### 336 *Conflict frequency in natural contexts: comparison of six groups*

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

345

#### 346 *Conflict management*

##### 347 a) Reaction after an aggression: Response or no response

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

353

##### 354 b) Affiliative versus aggressive responses

355 To have a large enough sample size they included conflicts recorded during both natural  
356 observations and around experiments. They first compared the absolute frequencies of

357 aggressive versus affiliative responses to conflicts using a  $\chi^2$  test. Using the PC (Post-conflict  
358 period)–MC (Matched control period) method they compared the timing of the first affiliative  
359 interaction between the former opponents during one PC with the corresponding MC. If this  
360 interaction occurred only in the PC or earlier in the PC than in the MC the PC-MC pair was  
361 considered to be “attracted”. Alternatively, if affiliative behaviours occurred sooner or only in  
362 the MC, the pair was considered to be “dispersed”. When no affiliative interactions took place  
363 in either the PC or the MC, or when the interaction occurred at the same time in both, the PC-  
364 MC pair was considered “neutral” (de Waal & Ren 1988).

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

375

### 376 *Statistics*

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

380

### 381 *Ethics Guidelines*



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

386

## 387 **Results**

### 388 a) Conflict frequency in natural context

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

394

### 395 b) Conflict management

#### 396 *Reaction after an aggression: Response or no response*

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

399

#### 400 *Affiliative versus aggressive responses*

401 Two of the three groups were more likely to respond with affiliative behaviour (either through  
402 consolation of the victim from third parties, or through reconciliation between the aggressor  
403 and the victim). In contrast, the third group, reacted more often with an aggressive behaviour

404 such as a coalition or redirection ( $\chi^2$  test,  $n=140$ ,  $X^2=8.9$ ,  $df=2$ ,  $p=0.01$ , Fig. 6). In addition,  
405 groups also differed in their probability to reconcile after a conflict ( $\chi^2$  test, attracted pairs –  
406 dispersed pairs as one column, neutral pairs as the other column,  $n=159$ ,  $X^2=9.1$ ,  $df=2$ ,  
407  $p=0.007$ ).

408

## 409 **Discussion**

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

428 size of conflict occurrence, and by the time over which the data were collected (ideally the data  
429 would have been from multiple years of observation). Nonetheless, this work highlights the  
430 importance of studying particular behaviours at different levels.

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

444         In vervet monkeys, males disperse between the groups at sexual maturity and multiple  
445 times within their lives, creating a continuous gene flow between the study groups, thus limiting  
446 the chances of a genetic cause of the observed group differences. Furthermore, as most of the  
447 neighbouring vervet monkey groups described above have overlapping territories, their ecology  
448 is very similar. Nonetheless, to exclude ecological explanations for the observed behavioural  
449 variation we must confirm that the variation remains just as pronounced in overlap zones as it  
450 is elsewhere in their home ranges. An even more promising way to test whether the observed  
451 intergroup variation is cultural would be through examination of the consequences of recent  
452 group fissions documented in our study population (van de Waal et al. 2017). Fissions provide

453 an opportunity to compare the behaviour of a subgroup of individuals, retrospectively in their  
454 origin group, with the behaviour they exhibit once in their splinter group, with a different social  
455 structure and in a different environment (usually neighbouring their origin home range).  
456 Investigating this specific context offers a promising way to examine whether ecology and  
457 group structure or composition are the only factors contributing to the observed variation. If the  
458 splinter groups continue to exhibit the same behavioural variants to those observed in their  
459 origin group as it was the case in an experimental context (van de Waal et al. 2017), then a  
460 socially learned basis of the observed variation will be the most likely explanation. This would  
461 shed light upon whether intergroup behavioural variation is due to different local traditions or  
462 other socio-ecological factors.

463         Studies of multiple groups of wild primates within single populations have demonstrated  
464 social learning through field experiments (in four groups of lemurs, Schnoell & Fichtel 2012;  
465 in up to 13 groups of marmosets, Gunhold et al. 2014a, 2014b; in up to six groups of vervet  
466 monkeys, van de Waal et al. 2010, 2012, 2013b, 2014, 2015; van de Waal & Bshary 2011).  
467 However, long-term observations of these populations, with the aim of revealing potential  
468 intergroup differences, are to my knowledge lacking, until this present review of behavioural  
469 variation in wild vervet monkeys.

470         In conclusion, this study of four different behavioural domains in up to six neighbouring  
471 groups of wild vervet monkeys contrasts with most studies, which have focussed on a specific  
472 behaviour and drawn a general picture of that behaviour in a particular species only on the basis  
473 of only one or two groups. Results warn scientists about the risks of generalization from data  
474 collected from only a few groups in a population and suggest that, in the future, studies of any  
475 behaviour should include several groups. These data reveal that we should take between-group  
476 differences within a single population seriously for any larger scale evolutionary comparisons  
477 (between populations and/or between species) as well as a potential source for studying animal

478 culture. The intergroup variation found also indicates that establishing species-specific or even  
479 population specific behaviours for later between-species comparisons will be challenging. In  
480 their conclusions, Luncz and Boesch (2012) stated that “Our study shows that cultural  
481 differences in chimpanzees can be found over a very small spatial scale and between  
482 neighbouring communities”. The results presented here on vervet monkeys are consistent with  
483 this finding, and I urge other researchers to investigate behavioural variation between multiple  
484 groups within a single population.

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494

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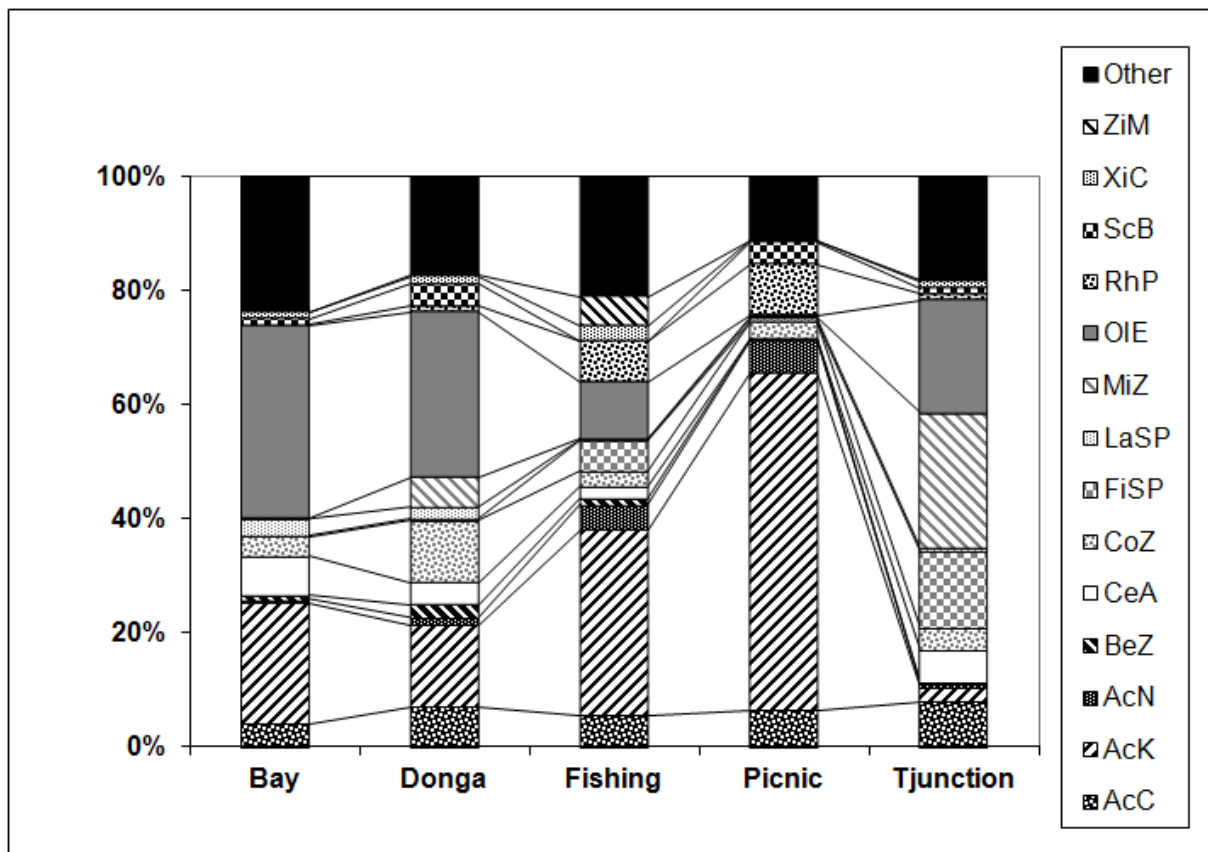
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622

623 **Figures legends**

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

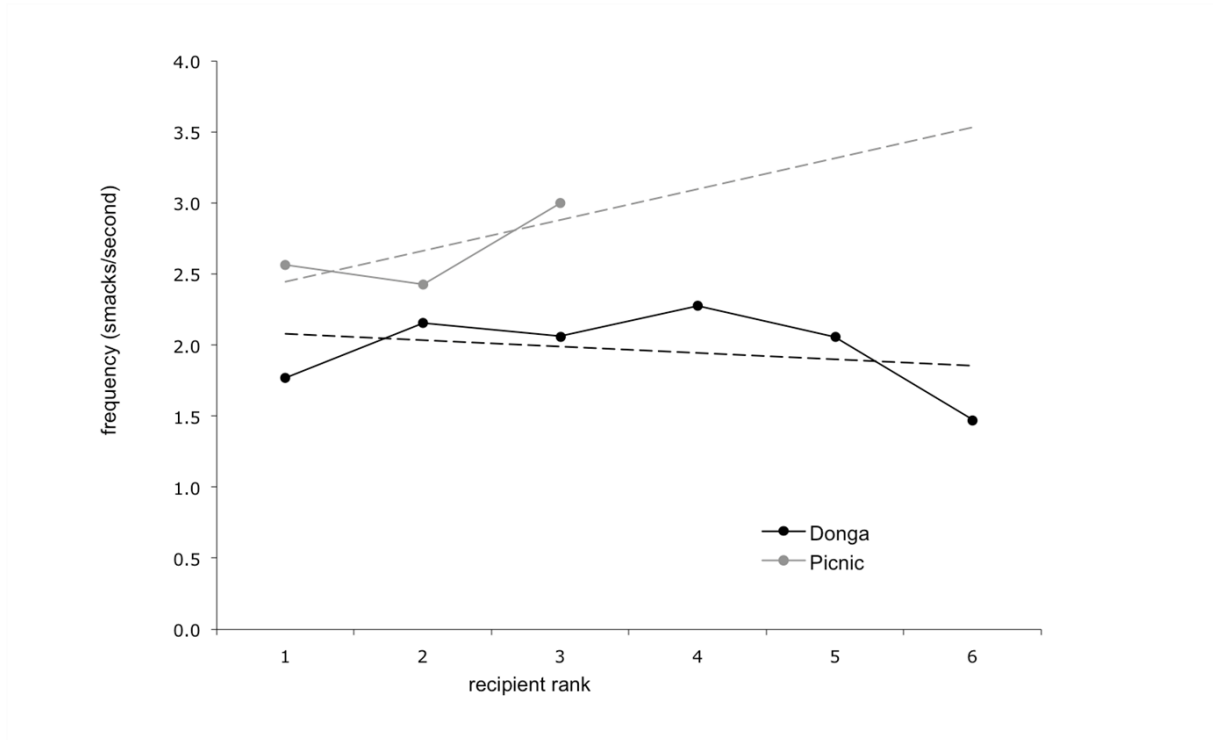
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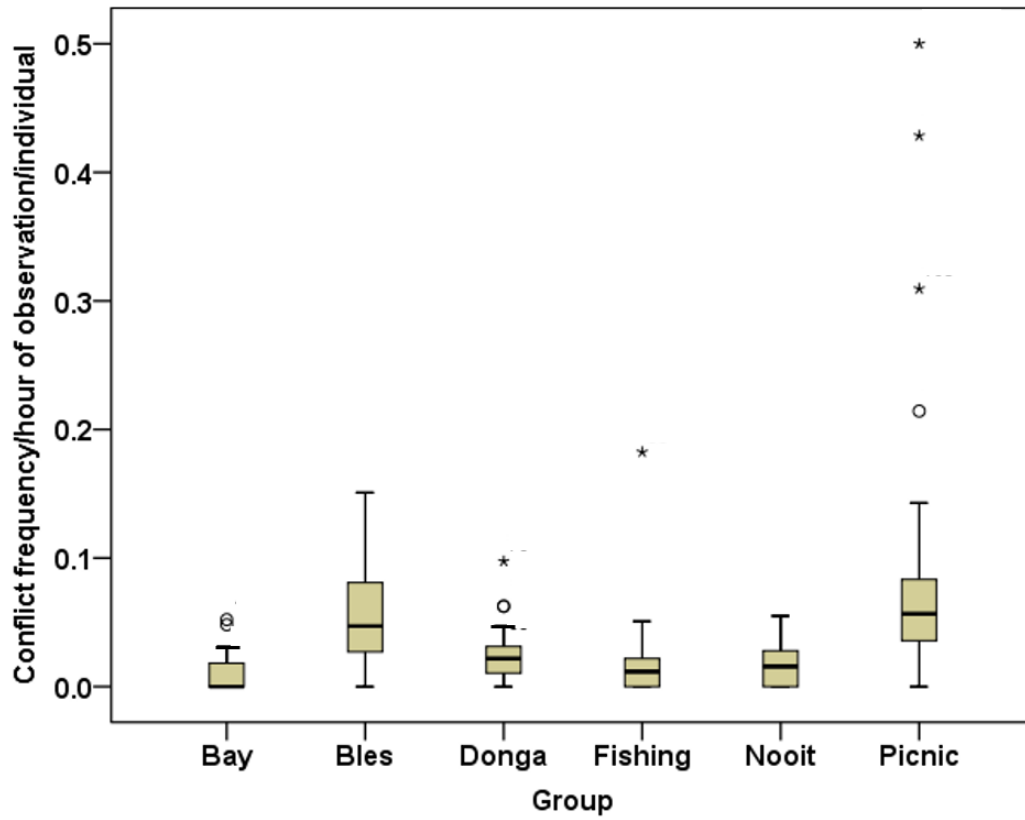
631 Fig. 2. Mean lip-smacks per second performed by groomers during grooming-with-mouth  
632 events in relation to the recipient's rank. The dashed lines represent the linear trend lines (Figure  
633 7 in van de Waal et al. 2013a).



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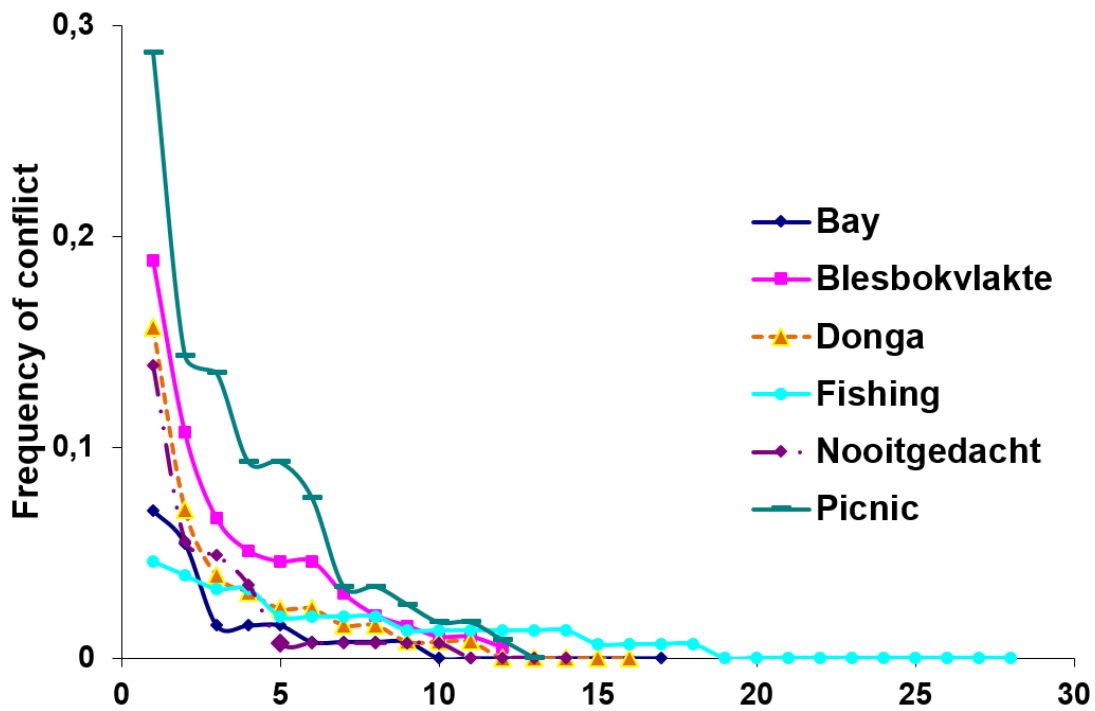
636 Fig. 3. Comparison in conflict frequency per day of observation and per the number of  
637 individuals between the six groups in a natural context.



638

639

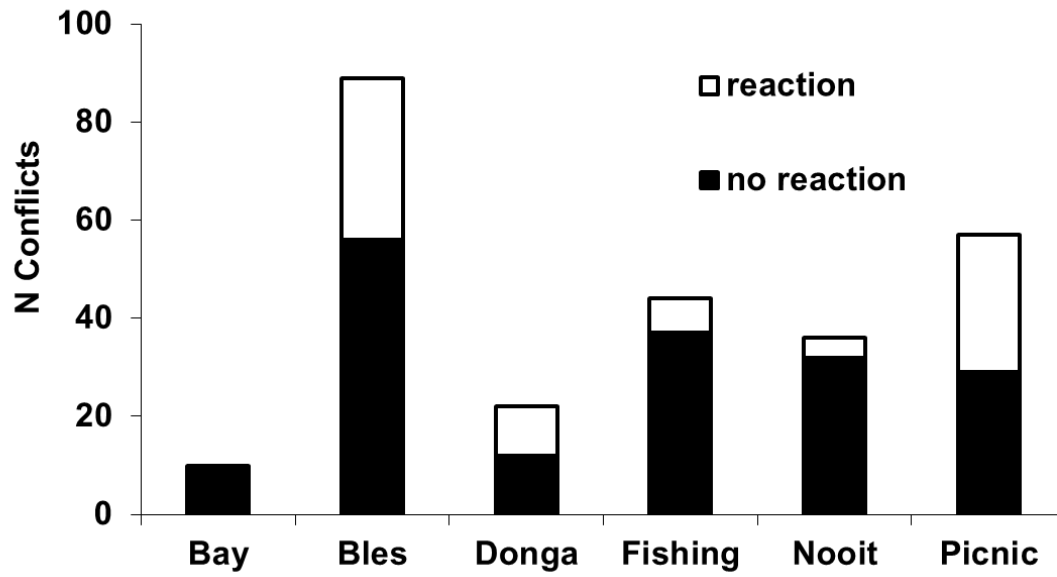
640 Fig. 4. Comparison of conflict frequency (Number of conflict per hour of observation) per  
 641 individual (classified by their rank of aggressiveness within their group) between the six groups  
 642 in natural context. The six groups are represented by different coloured lines and each symbol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



646

647

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

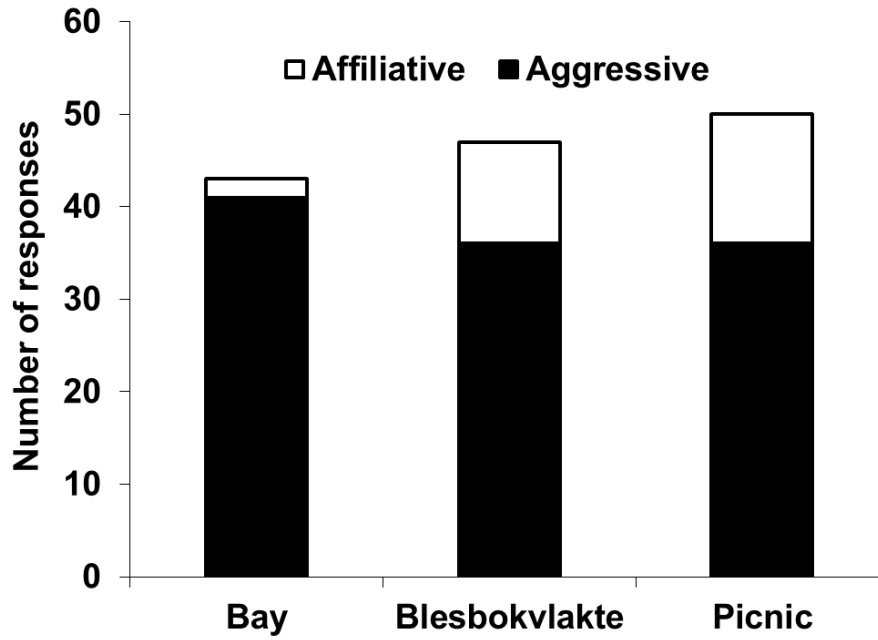


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652 Fig. 6. Response to aggression: preference for an aggressive (black) or affiliative (white)  
653 strategy between groups in both natural and experimental context.



654

655 **Tables:**

656 Table 1.

657 **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

658

659 Legend Table 1:

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

663

664 **Table 2.**

665

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

667

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

668

669 Legend Table 2:

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