

# Differences in Diet Between Six Neighbouring Groups of Vervet Monkeys

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## Abstract

The comparative approach provides a powerful tool to study evolutionary questions on both intra- and interspecific variation. It has been applied to a great variety of taxa, including primates. Primate studies differ from those on most other taxa in two ways: first, data from most study sites contain information about only one group. Second, primatologists have used the comparative approach also to identify local traditions, that is, behaviours that spread through social learning. Here, we evaluate the appropriateness of such data by comparing the diet composition of six neighbouring groups of vervet monkeys, *Cercopithecus aethiops*. We used scan samples to collect diet data, and abundance measures and phenology to assess the availability of the 14 most important tree species utilised during the study. We calculated indices of diet overlap, which were highly variable and could be remarkably low. Furthermore, we found significant differences between group diets with respect to the relative utilisation of 13 of the 14 tree species. For all 13 species, we found positive correlations between local abundance and appearance in the diet, consistent with the importance of local ecology for diet composition. Nevertheless, more detailed comparisons of pairs of groups often revealed significant mismatches between the relative importance of a tree species and its local abundance. In conclusion, local variation merits increased attention by primatologists. While our results are compatible with the possibility that traditions exist on a local (group) rather than population scale, alternative explanations have to be considered.

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## Introduction

Behavioural ecologists aim to explain animal behaviour as a function of the environment. A prominent approach makes use of the diversity of projects to compare data obtained at different locations and/or on different species in order to identify variables that may explain variance in the data. This comparative approach has been applied with great success to a variety of questions (Davies et al. 2012). Some classic examples involve results on primates as a widely studied animal taxon. For example, sexual dimorphism

and relative testes size could be related to the mating system (Clutton-Brock & Harvey 1977; Harcourt et al. 1981). More recently, comparative analyses were used to determine likely factors selecting for large brains in primates but also in other clades (Barton & Dunbar 1997; Deaner et al. 2005; Emery & Clayton 2005; Shultz & Dunbar 2010; van Schaik et al. 2012).

These studies are still based on classic evolutionary theory, which assumes that behaviour is closely tied to genes and the environment and that behavioural adaptations reflect genetic adaptations. However, this

view has been extended when it became obvious that many animal species may socially learn from conspecifics (Tomasello & Call 1997; Heyes & Huber 2000; Franks & Richardson 2006; Shettleworth 2010; Slagsvold & Wiebe 2011; Thornton & Clutton-Brock 2011; Whiten et al. 2011). Social learning is of interest because it forms the basis for behavioural traditions and culture, which are no longer tightly linked to an individual's genome or the constraints of its environment. In the light of evidence for widespread occurrence of social learning, the comparative approach has also been used to compare populations of the same species in order to identify differences in behaviour that appear to be not explicable through differences in ecology or genetics (Whiten et al. 1999; van Schaik et al. 2003; Santorelli et al. 2011).

Despite the widespread use of the comparative approach in primatology, the approach is potentially limited due to constraints on sample sizes within each study population. In contrast to many studies on other taxa such as birds and insects, primate projects typically consist of a single study group in each population. This is because habituation of subjects to the presence of human observers is time intensive. An unfortunate consequence is that we know very little about within population variation in primates, despite its importance for a proper appreciation of between sites or between species variance. An expansion of chimpanzee study groups at Taï National Park, Ivory Coast, demonstrates the pitfalls of small sample size: a tool-use behaviour previously classified as a tradition in the population was present only in the first but not in the second study group (Boesch 2003). These data are in line with a recent model that proposes that different traditions may arise not only between distant populations of the same species but also on a more local scale and even between neighbouring groups (Yeaman et al. 2011). Such group-level traditions are particularly likely to occur if two conditions are met, and which apply to our study species, the vervet monkey. First, social learning rules encompass the use of the mother and members of the philopatric sex as models. Second, females are philopatric while males migrate. The combination of the two factors effectively blocks the transfer of knowledge between groups, as the prior knowledge of immigrated males is ignored (Yeaman et al. 2011). A promising context to test this model's predictions is foraging.

Many experimental studies on traditions deal with foraging behaviours (Whiten & Mesoudi 2008; Slagsvold & Wiebe 2011; Thornton & Clutton-Brock 2011). Also, most candidate behaviours for traditions in chimpanzees and orang-utans concern foraging

behaviour, usually concerning how food is processed and often closely linked to tool use (Whiten et al. 1999; van Schaik et al. 2003). The model's assumptions on social learning rules seem to be largely met. The focus on foraging makes sense because there is plenty of circumstantial evidence that primates in general learn socially what to eat by foraging with their mother (Hauser 1993; van Schaik 2007; Jaeggli et al. 2010). Furthermore, a recent field experiment on vervet monkeys provided evidence that individuals learn socially how to open an artificial foraging device if the model is a member of the philopatric sex (in this case a female) but not if it is a member of the migrating sex (in this case a male: van de Waal et al. 2010). Furthermore, in a food-preference experiment on vervet monkeys, newly immigrated males abandoned their original group preference in favour of their new group habits (van de Waal et al. 2013). Such social learning rules effectively prevent the spread of knowledge over larger distances. At the same time, it is obviously important to study the variation within a population and the role of ecological variables as potential explanation for the variation.

Here, we studied the diet composition of six sympatric groups of vervet monkeys in order to investigate the degree to which food consumption varies on the group level. We studied neighbouring groups, where strong gene flow was documented both through observations of males migrating from one group to another and with genetic data (van de Waal et al. 2012). Genes are thus unlikely to explain inter-group differences. Likewise, general ecological conditions such as temperature, rain or seasonality of fruits can be expected to be very similar, reducing uncontrolled variance between groups. Our data collection and analysis involved three steps. First, we assessed the general diet composition of vervet monkeys. According to previous studies on vervet monkeys, trees provide the major part of the diet (Barrett 2005, 2010). We therefore identified in a second step 14 tree species that should be of major importance for the vervets' diet during our study period and analysed their relative contribution to the diet of each study group. Thirdly and finally, we measured the abundance of each tree species in each home range to analyse how well local abundance predicts consumption. However, we also studied in detail whether a significant dietary difference between each pair of groups is explained by the abundance of the tree species within their two home ranges. With the data, we tested the prediction assumed by comparative studies on primates that within-site variance between groups is negligible. Furthermore, and in accordance with

previous studies, we anticipated that differences in local abundance will largely explain between-group differences in diet composition (Lee & Hauser 1998; Fairgrieve & Muhumuza 2003). In case of evidence for significant unexplained variance, we will discuss the possibility of group-level traditions of food preferences as well as alternative hypotheses such as variation in group composition and group size.

## Methods

### Study Site and Population

We studied six neighbouring groups of habituated wild vervet monkeys (*Chlorocebus aethiops*) at Loskop Dam Nature Reserve, South Africa. The reserve, situated 250 km north-east of Johannesburg, covers 25 000 ha. Foraging data were collected from November 2007 until March 2008, while tree mapping took place in September 2008 or October 2008. Vervet monkeys live in stable family groups which during our study varied from 12 to 27 individuals (Table 1). Groups are typically composed of an alpha male, a few subordinate males and several matriline, that is, females and their offspring. Females remain in their natal group all their life, while males migrate to another group when they are sexually mature, usually at around 4 yr of age. Our six study groups – Bay, Donga, Fishing camp, Nooitgedacht, T-junction (called Blesbokvlakte in previous publications) and Picnic (named after sites on the Park map) – live in contiguous home ranges along a tourist road that allows easy access to each group (van de Waal et al. 2010).

All groups had been exposed to the presence of human researchers for at least 4 mo before data collection started. All individuals were recognised by their faces, and a recognition file with portrait pictures and specific individual features (scars, dots, etc.) was

constructed for each group. Two of the six groups were in regular contact with tourists: the ‘Fishing camp group’ and the ‘Picnic group’.

### Data Collection

The equipment used consisted of Swarovski binoculars EL 8X32, a stopwatch and a handheld computer (Palm Zire 22 or HP travel companion iPAQ rx5935) running PenDragon 5.1 data collection software and ESRI ArcPad 7.0.1 software. Seven observers contributed to data collection. Three pairs of observers were each in charge of two of the six groups while a seventh observer (EvdW) knew all monkeys in the population and helped with data collection on all groups. Observers were previously trained to recognise each targeted tree species and recorded information about the diet through scans every 30 min. Each scan period lasted 10 min during which the observers located as many monkeys as possible (Altmann 1974). As soon as an individual was foraging for the first time during each scan period, the type of food that was eaten was noted. We considered six types: human food, grass, bush, tree, invertebrate and other. The ‘other’ class included bird eggs, maternal milk or salt (on red rocks). If the monkey was feeding on a tree, the species of the tree and the item eaten were recorded as well (fruit, leaf, flower, gum, bark, branch or bud). After the scan, a period of 10 more minutes was allocated to following individuals that had not been observed eating during the scan in order to increase sample size.

For the phenology, we examined 14 species of trees which a prior study had shown to represent a significant portion of two groups’ (Donga and Picnic) food selection, contributing towards 80.1% of their combined (wet and dry seasons) diets (Barrett 2010). These species were *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* (OIE), *Rhus pyroides* (RhP), *Sclerocarya birrea* (ScB), *Ximenia caffra* (XiC) and *Ziziphus mucronata* (ZiM).

After the foraging data collection, we mapped the trees of the 14 preselected species in each home range. We walked the routes used by the monkeys during the 4 mo of data collection and recorded positions of relevant trees with a GPS point taken on the Pocket PC running ArcPad 7.0.1. For (locally) rare tree species, the aim was to find every single individual within each home range. We provide precise counts of found trees per home range up to 50 individuals.

**Table 1:** The composition of the study groups and relative contribution (%) of age/sex class to the data set

Group	Adult male	Adult female	Juvenile	Baby
Blesbokvlakte	2(4)/40	3/36	5/24	3
Nooitgedacht	3/31	5/18	6/52	3
Picnic	3/22	3/29	8/49	2
Bay	4/27	5/30	7/42	5
Donga	5/19	6/51	5/30	5
Fishing	4(6)/15	7/26	16/57	6

Between parentheses is the number of males at the beginning of the 4 mo of study. Adult males and females are older than 4 yr. Juveniles are older than 1 yr and babies younger than 6 mo.

Beyond 50, we considered a tree species simply as ‘abundant’ within a home range and stopped counting, as a complete map was beyond the scope of this study. In total, 3048 trees were mapped.

## Data Analyses

### *Descriptive general diet analyses*

Data were pooled for each group; the relative contribution of age/sex classes to the data is shown in Table 1. In an initial global analysis, we distinguished between the major categories ‘human food’, ‘trees’, ‘bushes’, ‘grass’ and ‘invertebrates’, to calculate food overlap between groups ( $n = 5247$ ), while we excluded the category ‘other’ in our analyses ( $n = 200$ ). We considered the number of times each kind of food was eaten by each group. Using the Bray–Curtis similarity index (also called Steinhaus index), we tested the food overlap between groups, compared two by two, to describe the degree of similarity. We then calculated  $\chi^2$  tests to determine whether there were significant differences between groups. Due to the five calculations for the five food categories, we lowered the  $\alpha$ -value using the Bonferroni method ( $\alpha' = 0.05/5 = 0.01$ ).

In a second analysis, we considered only items eaten off trees ( $n = 2900$ ). We initially distinguished between fruits, leaves, flowers, buds, bark, gum and branch. We considered the number of times each kind of food was eaten by each group. Using the Bray–Curtis similarity index, we tested the food overlap between groups regarding items eaten of trees. We then calculated  $\chi^2$  tests to determine whether there were significant differences between groups. Branches and buds were eaten so rarely that assumptions of a  $\chi^2$  test were violated and hence not further analysed. Due to the five calculations for the remaining five food categories, we lowered the  $\alpha$ -value using the Bonferroni method ( $\alpha' = 0.05/5 = 0.01$ ).

### *Relative importance of 14 key tree species in the groups’ diet*

We calculated the percentage contribution to the diet of each of the 14 key tree species listed earlier. We used the original data to evaluate similarities in diet using the Bray–Curtis similarity index. In addition, we calculated  $\chi^2$  tests to establish whether the groups utilised the 14 species in a significantly different way, without consideration of which items were exactly eaten. Thus, if hypothetically in one group buds of tree species  $x$  contributed  $y\%$  to the diet and in another group leaves of the same tree species  $x$  contributed also  $y\%$  to the diet, our analysis would not

have picked up the difference in item. Our results are therefore conservative in that they favour the null hypothesis that there are no differences between groups in the use of tree species. Sample size for one group (Nooitgedacht) yielded expected values in several cases that were low enough to violate assumptions of the test. Therefore, the data for this group were removed. We reduced the  $\alpha$ -value using the sequential Bonferroni method to determine successively  $\alpha$ -values that could yield significant results. We first tested whether at least one result would be significant with the initial level  $\alpha' = 0.05/14 = 0.0036$ , and if that was the case, we continued to check the remaining results for a value lower than  $\alpha'' = 0.05/13 = 0.0038$ , and so on until no p-value would be below the current critical threshold (Rice 1989).

### *Correlations between local abundance of tree species and consumption*

We investigated for each tree species whether its contribution to a group’s diet was correlated with the abundance of this species in the home range.

### *Statistics*

We used nonparametric statistics using SPSS 17 and Excel for the  $\chi^2$  tests.

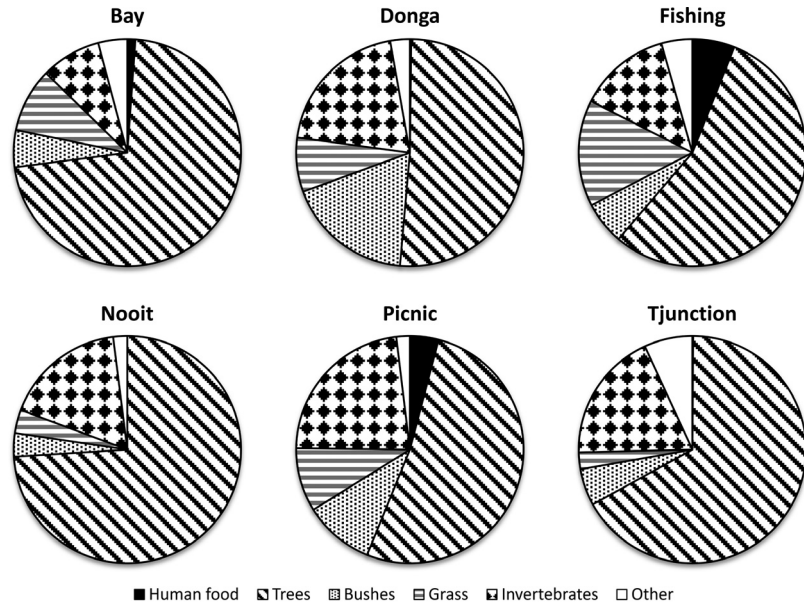
## Ethics Guidelines

We adhered to the ‘Guidelines for the Use of Animals in Research’ of the Association for the Study of Animal Behaviour. Our study consisted only of natural observations and was 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.

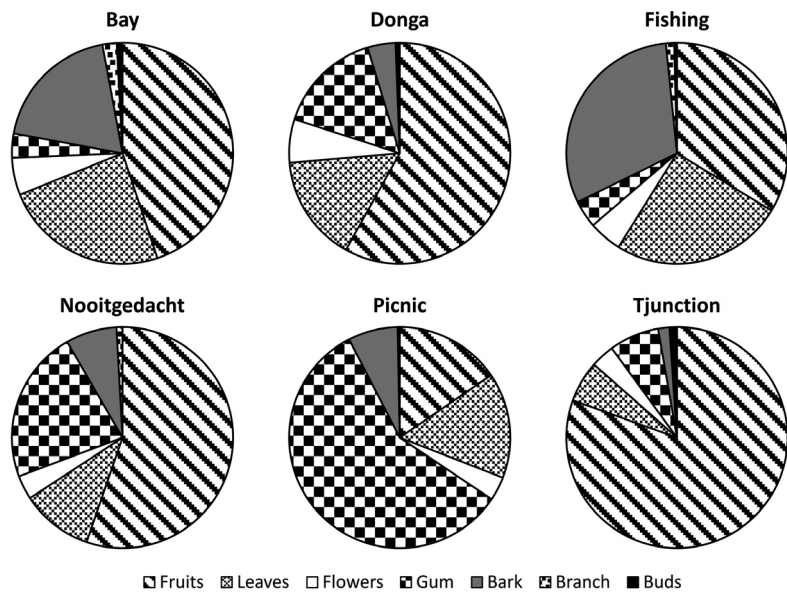
## Results

### General Diet

For brevity, we typically use only the first letter to denote each group in the results section (full names in Fig. 1). Analyses are based on 5247 observations (minimum 450 and maximum 1302 data points per group). Items eaten off tree species comprised more than 50% of the diet in all six study groups (51–75%; Fig. 1). Invertebrates were the second most important food source, followed by bushes and grass. The Bray–Curtis similarity index yielded diet overlaps between pairs of groups that range between 75.65% (B vs. D)



**Fig. 1:** Total partitioning of the diet in six groups of monkeys (group names given above their respective pie chart), distinguishing between human food, trees, bushes, grass, invertebrates and others. Items eaten off trees represent more than half of the diet for each group.



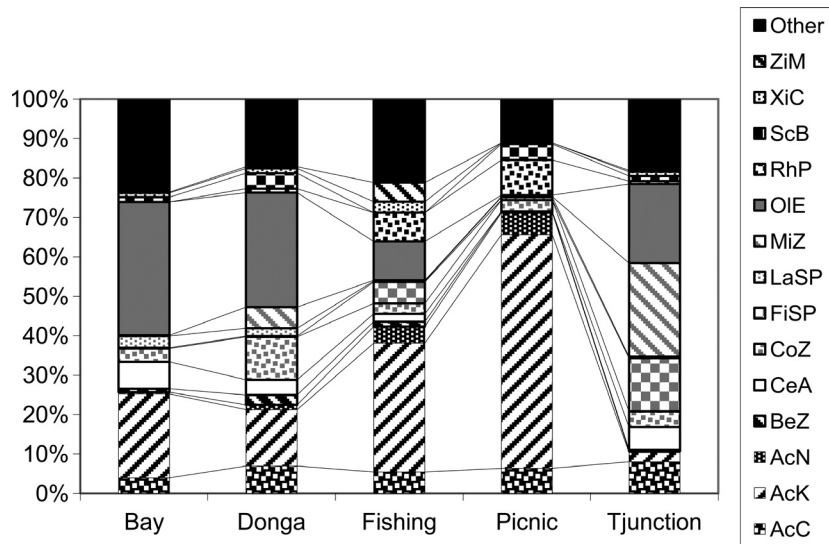
**Fig. 2:** Relative importance of items eaten off trees in six groups of monkeys (group names given above their respective pie chart), distinguishing between fruits, leaves, flowers, gum, bark, branch and buds.

and 94.24% (N vs. T). However, groups differed significantly in their diet composition ( $\chi^2$  test with  $df = 5$ ;  $\chi^2 = 532$ ,  $p < 0.0001$ ). The relative contribution of all five food types to the diets varied significantly between the six groups ( $\chi^2$  tests with  $df = 5$ ; human food:  $\chi^2 = 133$ ; trees:  $\chi^2 = 78$ ; bushes:  $\chi^2 = 146$ ; grass:  $\chi^2 = 109$ ; invertebrates:  $\chi^2 = 66$ ; all  $p < 0.0001$ ).

#### Tree species analyses

A total of 2900 data points are available for items eaten off the 14 species assessed during the study

period (range 228–660). A qualitative inspection of the kind of food items eaten revealed that the monkeys typically ate mostly fruits off trees, with the exception of the Picnic group, which mainly ate gum (Fig. 2). The Fishing camp group, in addition to fruits, ate a lot of bark mainly from *AcK*. The Bray–Curtis similarity index yields pairwise dietary overlaps regarding tree items eaten between 34.2% (P vs. T) and 88.72% (D vs. N). Groups differed strongly with respect to the relative importance of fruits, leaves, gum and bark in their diet ( $\chi^2$  tests with  $df = 5$ ; fruits:  $\chi^2 = 503$ ; leaves:  $\chi^2 = 98$ ; gum:  $\chi^2 = 995$ ; bark:



**Fig. 3:** 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 off the 14 tree species add up to 100%. For abbreviations of tree species, see Methods.

$\chi^2 = 285$ ; all  $p < 0.0001$ ) while they ate flowers at similar levels ( $\chi^2$  test with  $df = 5$ ;  $\chi^2 = 6.7$ ,  $p = 0.24$ ).

#### Quantitative analysis of the relative importance of key tree species

Analysing dietary overlap between groups with respect to the 14 preselected tree species, the Bray–Curtis similarity index yields dietary overlaps between pairs of groups that range between 18.02% (P vs. T) and 76.31% (B vs. D; see Fig. 3).

The relative importance of food trees for the remaining five groups differed significantly in 13 of 14 cases ( $\chi^2$  tests with  $df=4$ ;  $\chi^2$ :AcK = 359,  $\chi^2$ :AcN = 47,  $\chi^2$ :BeZ = 17,  $\chi^2$ :CeA = 55,  $\chi^2$ :CoZ = 51,  $\chi^2$ :FiSP = 197,  $\chi^2$ :LaSP = 25,  $\chi^2$ :MiZ = 384,  $\chi^2$ :OIE = 266,  $\chi^2$ :RhP = 93,  $\chi^2$ :ScB = 28,  $\chi^2$ :XiC = 17,  $\chi^2$ :ZiM = 84, all  $p < \alpha' = 0.05/14 = 0.0036$ ). Only for AcC did we not find significant differences ( $\chi^2$ :AcC = 6.4,  $p > 0.05$ ; Fig. 3).

#### Relationship between local abundance and importance in the diet

Regarding the 13 tree species that had yielded significant differences between groups, we found that three of them (AcN, CoZ and RhP) were invariably highly abundant in all home ranges. For the other ten tree species, we found that the proportion of them in a group's diet was positively correlated with their relative abundance (Spearman rank correlations, Table 2). Using the correlation coefficients for a Wilcoxon one-sample test, local abundance had a

significant positive effect on diet composition (Wilcoxon test,  $N = 10$ ,  $T = 0$ ,  $p = 0.002$ ).

#### Pairwise analyses of the link between local abundance and importance for the diet

In this final analysis, we conducted pairwise comparisons between groups and asked how many significant differences, with respect to a specific tree species utilised, are consistent with differences in local abundance, and how often local abundance predicts the absence of significant differences. The results are summarised in Tables 2 and 3 and described in more detail below.

#### Abundant Tree Species

Three tree species were generally abundant in all home ranges: AcN, CoZ and RhP. Nevertheless, we noted that there were significant differences between groups with respect to the relative importance of these trees for their diets. For AcN, there were several significant differences ( $\chi^2$  tests, P vs. B:  $\chi^2 = 18.26$ ; P vs. T:  $\chi^2 = 23.19$ ; F vs. T:  $\chi^2 = 18.52$ , all  $p < 0.0036$ ). Similarly for CoZ, the Donga group ate significantly more of it than any other group ( $\chi^2$  tests, D vs. B:  $\chi^2 = 16.32$ ; D vs. F:  $\chi^2 = 22.86$ ; D vs. P:  $\chi^2 = 32.03$ ; D vs. T:  $\chi^2 = 16.25$ , all  $p < 0.0036$ ). Finally, regarding RhP, Picnic and Fishing groups ate significantly more of it than the other three groups ( $\chi^2$  tests, P vs. B:  $\chi^2 = 36.79$ ; P vs. D:  $\chi^2 = 28.87$ ; P vs. T:  $\chi^2 = 35.10$ ; F vs. B:  $\chi^2 = 33.698$ ; F vs. D:  $\chi^2 = 24.55$ ; F vs. T:  $\chi^2 = 30.36$ , all  $p < 0.0036$ ).

**Table 2:** Evaluation of the relationship between local abundance and consumption of 14 preselected tree species

Class	Tree sp	r	Eat most	Eat least	Differences <i>entirely</i> explicable from ecology?
Abundant	AcN	\	F + P	B + T	NO?
	CoZ	\	D	F + B	NO?
	RhP	\	P + F	B (do not eat)	NO?
Abundant except in one home range	AcK (less in T)	0.71	P	T	NO
	BeZ (less in P)	0.71	D	B + P + T	NO
	OIE (less in P)	0.71	B + D	P	NO
Quite abundant s	ScB	0.1	P + D	F (do not eat), B + T	NO
	ZiM	0.74	F	P (do not eat)	NO
Quite abundant except in one or two home ranges	CeA (less in F)	0.2	B + T	P (do not eat)	NO
	LaSP (less in P)	0.1	B + D	P + F + T	NO
	MiZ (less in B + P)	0.7	T	B + F + P	NO
	XiC (less in P)	1	F	P	NO
Rare	FISP	0.74	T	P (do not eat)	NO

We grouped trees according to their distribution pattern into five classes: abundant (>50 individuals per home range), abundant but in one home range, quite abundant, quite abundant except in one or two home ranges, and rare. Abbreviations for tree species are given in the methods: abbreviations for monkey groups: B: Bay; D: Donga; F: Fishing camp; P: Picnic; T: T-junction; r: spearman rank correlation coefficients (no values for tree species that were abundant in all home ranges). The next two columns indicate qualitatively which vervet groups ate most or least of each tree species. The final column indicates whether pairwise comparisons between groups invariably yield similarities/differences in consumption that are fully explained by local abundance. '?' for the abundant species acknowledges that there could be variation in abundance that was beyond the precision of our mapping.

**Table 3:**  $\chi^2$  values to test for significant differences in the relative importance of 14 key tree species (shown in letter codes in the left column) in five vervet groups (B: Bay; D: Donga; F: Fishing; P: Picnic; T: T-junction)

	B vs. D	B vs. F	B vs. P	B vs. T	D vs. F	D vs. P	D vs. T	F vs. P	F vs. T	P vs. T
AcC	2.8	0.9	1.4	5.5	0.6	0.5	0.5	0.02	2.1	2.1
AcK	9.7	10	<b>65.4 (-)</b>	<b>89.1</b>	<b>39.8 (-)</b>	<b>125 (-)</b>	<b>45.3</b>	<b>26.3 (-)</b>	<b>149</b>	<b>264.8</b>
AcN	1.6	14.5	<b>18.3 (-)</b>	0.04	8.9	12.9	2.4	0.3	<b>18.5 (-)</b>	<b>23.2 (-)</b>
BeZ	3.2	0.3	2.0 (+)	1.2	1.8	11.7 (+)	8.2	4.1 (+)	2.6	0.07 (+)
CeA	5.3	13.9 (+)	<b>52.9 (-)</b>	1.2 (+)	2.5 (+)	<b>27.5 (-)</b>	1.8	15 (+)	8.1 (+)	<b>40.5 (-)</b>
CoZ	<b>16.3 (-)</b>	0.5	0.8	0.1	<b>22.9 (-)</b>	<b>32 (-)</b>	<b>16.3 (-)</b>	0.01	1.2	1.8
FISP	0.01	<b>22.5 (-)</b>	1.6	<b>57.6</b>	<b>25.1 (-)</b>	1.5	<b>63.9 (-)</b>	<b>40.5 (-)</b>	<b>15.9 (-)</b>	<b>96.7</b>
LaSP	1.1	12.2	10.0 (+)	11.7	7.1 (+)	4.2 (+)	6.21	1.4 (+)	0.2 (+)	0.6 (+)
MiZ	<b>20.7</b>	0.002	0.1	<b>103.2</b>	<b>22.3 (-)</b>	<b>34.4</b>	<b>59.2 (-)</b>	0.08 (+)	<b>110 (-)</b>	<b>166.7</b>
OIE	4.1	<b>68.3 (-)</b>	<b>252.7</b>	<b>23.6 (-)</b>	<b>42.1 (-)</b>	<b>199</b>	8.1	<b>66.9</b>	<b>15.8 (-)</b>	<b>137.3</b>
RhP	4.5	<b>33.7 (-)</b>	<b>36.8 (-)</b>	3.3	<b>24.6 (-)</b>	<b>28.9 (-)</b>	0.2	0.2	<b>30.4 (-)</b>	<b>35.1 (-)</b>
ScB	5.5	6.4 (+)	5.7 (+)	0.01 (+)	<b>18.3 (-)</b>	0.004	6.9	18 (-)	6.1	7.2
XiC	0.02	3.7	3.2	0.001	3.5	3.9 (+)	0.03	15.1 (+)	4.4	3.3 (+)
ZiM	0.2	<b>19.7 (-)</b>	1.6	0.2	<b>19.4 (-)</b>	2.9	0.01	<b>36</b>	<b>21.9 (-)</b>	2.6 (+)

Significant differences are indicated by bold formatting.  $\alpha = 0.0036$ ;  $\chi^2$  critical = 15.6. Bold values followed by (-): consumption significantly different while local abundance NOT significantly different (35 cases). Values followed by (+): consumption NOT significantly different while local abundance significantly different (23 cases).

### Abundant tree species except in T-junction home range

Three tree species were abundant in all but one home range: AcK, BeZ and OIE. For AcK, we noted that the group with access to fewer trees (T-junction group) ate the least of it. However, the Picnic group ate significantly more of this tree than the other three groups that had access to many trees ( $\chi^2$  tests, P vs. B:  $\chi^2 = 65.41$ ; P vs. D:  $\chi^2 = 125.47$ ; P vs. F:  $\chi^2 = 26.31$ ,

all  $p < 0.0036$ ). In addition, D was significantly different from F ( $\chi^2$  tests,  $\chi^2 = 39.80$ ,  $p < 0.0036$ ). For BeZ, we noted that it was rare in the Picnic home range and therefore expected that this group would eat less of this tree than the other groups. However, we failed to find any significant differences between Picnic and the other groups ( $\chi^2$  tests,  $\chi^2$  between 0.07 and 11.68, all non-significant). For OIE, we expected and found that the Picnic group ate less of this tree as it was rare

in their home range but abundant in the other home ranges. However, when comparing the groups that had access to many OIE trees, we also found that the Fishing group ate OIE significantly less than the other three groups ( $\chi^2$  tests, F vs. B:  $\chi^2 = 68.28$ ; F vs. D:  $\chi^2 = 42.08$ ; F vs. T:  $\chi^2 = 15.81$ , all  $p < 0.0036$ ), and the Bay group ate significantly more of it than the T-junction group ( $\chi^2$  tests,  $\chi^2 = 23.598$ ,  $p < 0.0036$ ).

#### Quite Abundant Tree Species

Two tree species, ScB and ZiM, were generally quite abundant in the home ranges but without reaching >50 individuals per home range. For ScB, Picnic and Donga fed on significantly more of it than the Fishing group did ( $\chi^2$  tests, F vs. D:  $\chi^2 = 18.34$ ; F vs. P:  $\chi^2 = 17.98$ , both  $p < 0.0036$ ). We never noticed any fruits in the Fishing home range, and fruits were the main food items eaten off this tree species, so these differences may be expected. ZiM was generally quite abundant except in the Picnic home range. The Fishing group ate significantly more of it than any other group ( $\chi^2$  tests, F against B, D, T and P,  $\chi^2$  between 19.69 and 36.03, all  $p < 0.0036$ ).

#### Tree Species of Variable Abundance Across Home Ranges

The remaining five tree species were quite variable in their local abundance. For CeA, we noted that its abundance was similar in the Picnic home range compared with Bay, Donga and T-junction, but the Picnic group ate significantly less of it than the other three groups ( $\chi^2$  tests,  $\chi^2$  between 27.54 and 52.93, all  $p < 0.0036$ ). For LaSP, one could have expected that the Picnic group would eat less of it as this tree species was rare in its home range. However, this was not the case ( $\chi^2$  tests,  $\chi^2$  between 0.62 and 9.9, all  $p > 0.0036$ ). MiZ was quite abundant except in the Bay and Picnic home ranges. While these two groups rarely ate MiZ, we found significant differences between the three groups which had similar access to MiZ. T-junction ate significantly more of it than Donga, which in turn ate significantly more of it than Fishing ( $\chi^2$  tests, T vs. D:  $\chi^2 = 59.19$ ; D vs. F:  $\chi^2 = 22.28$ , both  $p < 0.0036$ ). The Fishing group did not eat significantly more of the tree than the two groups that had restricted access to MiZ ( $\chi^2$  tests,  $\chi^2 = 0.002$  and 0.08, all non-significant). XiC was significantly less abundant in the Picnic home range than in the other home ranges. However, except for Fishing, the other groups did not make use of the trees and

ate significantly less of it than the Picnic group ( $\chi^2$  tests,  $\chi^2$  between 3.23 and 3.87, all NS).

#### Rare Tree Species

Finally, FiSP was generally rare with the exception of the T-junction home range. Accordingly, T-junction fed significantly more in FiSp than any other group ( $\chi^2$  tests,  $\chi^2$  between 15.94 and 96.74, all  $p < 0.0036$ ). However, we found cases where local abundance was similar in two home ranges, but the consumption was significantly different ( $\chi^2$  tests, B vs. F:  $\chi^2 = 22.48$ ; D vs. F:  $\chi^2 = 25.07$ ; F vs. P:  $\chi^2 = 40.53$ , all  $p < 0.0036$ ).

#### Discussion

The main aims of our study were to determine how strongly neighbouring groups of vervet monkeys differ in diet composition and whether variation in the local abundance of major, measurable food sources (trees) can explain these results. We found large variation in diet composition that we could largely explain with variation in local abundance of food sources. Nevertheless, there was also widespread and unexplained, significant variance due to mismatches between local abundance and consumption. We will therefore discuss in how this might indicate the existence of local traditions based on the transmission of foraging preferences within vervet groups.

#### General Aspects of Diet

On a global level, our study groups showed strong overlaps in diet. All groups ate mostly items off trees, which has also been found in previous studies on the same population as well as in other populations of vervet monkeys (Eisenberg et al. 1972; Wrangham & Waterman 1981; Whitten 1988; Dunbar & Barrett 2000; Barrett 2005, 2010). Clear differences were obvious with respect to the consumption of human food, which reflects the fact that only two groups had regular access to human facilities. Given that data were collected only over a 4-mo period, we did not test for seasonal variation in diet composition. Such variation is generally well documented (Dasilva 1992; Nakagawa 2000; Barrett 2010) and not relevant to the research questions pursued here. The importance of trees for the vervets' diet gives justification to our focus on trees in order to assess the scope of local variation in abundance to explain variation in the vervet groups' diet.

Similarities in diet were more variable when we considered what main food items were consumed.

Most groups ate primarily fruits, as found in previous study of same population (Barrett 2010). Nevertheless, the Picnic group mainly ate gum, and the fishing group showed similar consumption of fruits, bark and leaves. We did not include item identification in our analyses of the relative importance of tree species to avoid sample sizes too small for statistical analysis (see Discussion section on methodological considerations for likely consequences for our conclusions). We consider it promising for future studies to investigate more explicitly whether differences in food item composition could be based on social learning leading to local traditions.

### Use of Different Tree Species

Our study groups differed considerably in the consumption of items from the 14 tree species we had chosen due to their importance during our study period. In fact, differences were the norm, with the only exception being *AcC* that was consumed at similar rates. Differences were partly linked to a focus on different food items. For example, the Picnic group ate much from *AcK*, and the main eaten item was gum. The other groups rarely ate gum and hence little of *AcK*. On the level of tree species, our main conclusion is that data obtained from any one group cannot be taken as representative for this study population. Thus, a major shortcoming of many primate studies is that typically data are collected from one group per site. Given the variance we observed in our study groups, it seems clear that only very gross patterns will be revealed in any comparative literature review study that compares diets of different populations of the same species, or even compares diet overlaps between different species.

### Explanations for Differences in Tree Species Utilisation

Overall, differences in tree diet composition between groups were strongly linked to differences in the local abundance of tree species. This result is in line with several previous studies on vervet monkeys (Harrison 1984; Fedigan & Fedigan 1988; Lee & Hauser 1998; Barrett 2010) as well as, for example, in blue monkeys (Fairgrieve & Muhumuza 2003). In addition, despite this overarching, important role of ecology, we consistently found results in direct comparisons between pairs of groups that are not consistent with a purely ecological interpretation. In our total of 140 comparisons, we found that groups would often either eat similar amounts of a tree species despite significantly different abundances in the respective home ranges

(23 cases) or would eat significantly different amounts of a tree species despite similar abundances in the respective home ranges (35 cases). Thus, such ‘irregularities’ were found in 41% of the pairwise comparisons. We acknowledge that there may be complex ecological processes underlying these irregularities that could not be detected with our analyses. For example, a more detailed study on the Picnic and Donga groups (Barrett 2010) detected a more homogeneous distribution of trees in the Picnic group home range, and a variety of different and more preferred tree species in the Donga group home range. Nevertheless, the large amount of observed mismatches warrants further examination.

### Unexplained Differences, a Case for Group-Level Traditions?

Colleagues who have compared groups belonging to different populations have argued that any behavioural differences that do not seem to be linked to any ecological differences between the sites provide good candidates for local traditions (Whiten et al. 1999; Santorelli et al. 2011). Following their logic, the large amount of mismatches between local tree species abundance and consumption by vervet groups allows for the possibility that local traditions may play an additional role in the formation of overall diets in vervet monkey groups. However, this conclusion has to remain largely preliminary because of some uncontrolled variables. Most importantly, our diet data per group are pooled over all individuals in each group. Therefore, there may be some uncontrolled biases in the data sets due to unequal sampling of individuals. These biases may be of particular importance if age/sex classes differ in their diets as their relative contribution differed between groups (see Table 1). A recent experiment suggests that males may adjust their diet to local preferences, at least in vervet monkeys (van de Waal et al. 2013). Thus, the effects may be of relatively little importance but clearly, further data are necessary. Another potentially confounding variables are group size and composition. Most but not all females had infants during the observation period, and also sex ratio and group size varied between groups (Table 1). In addition to alternative explanations based on sampling and group composition, there is also the possibility that social learning may lead to traditions but less on the group level but on the matriline level. In fact, a recent experiment on the same vervet monkeys demonstrated that with respect to foraging techniques, most similarities are found on the level of matrilines rather than entire groups (van

de Waal et al. 2012). Finally, some significant results may simply be due to stochastic variation in the data, as often emphasised by ecologists (May & Oster 1976). Thus, our study needs to be followed up by experimental tests in which the relative preferences of neighbouring groups for local food items are explicitly evaluated.

### Further Methodological Considerations

Our exploratory study has some inevitable shortcomings. First, data were collected over a relatively brief period, while ideally one would like to have data for at least two different years in order to evaluate consistency in the findings. On the other hand, our concerted effort provided data on six groups in parallel, which has rarely been achieved in other studies. Second, some trees were so abundant that our methods were insufficient to detect possible significant differences between home ranges. Counterbalancing these concerns, we note that significant differences were observed multiple times and also for tree species for which precise counts in all home ranges existed. Also, we obtained many mismatches, particularly if we ignore the Picnic group because they lack several key species in their home range (*FiSP*, *OIE*, *MiZ* and *LaSP*) which may have had cascading effects on the relative importance of the other tree species in their diet. The consistency of our results for different tree species suggests that differences between groups with respect to diet are real and that they cannot entirely be explained by variation in local abundance. As a final remark on methods, we note that the lack of consideration for the actual items eaten on each tree species makes our results relatively conservative (more likely to be in line with the hypothesis that differences in local abundance may explain differences in local consumption). Any case in which the number of items eaten from a tree by two groups corresponded to the tree species' local abundance, while the two groups mainly ate different items from the same tree species, would have been classified as 'can be explained ecologically' in our analyses.

In conclusion, our data provide strong support for the notion that in order to be able to properly interpret variation between study sites or between species, one has to determine within-site variation within a species. We appreciate that this demands a major effort by primatologists but otherwise the risk of false positives and negatives is very high. In addition, our results provide some preliminary correlational evidence in support of the hypothesis that local foraging traditions may contribute to variation in the diet of

neighbouring vervet groups. Our study complements previous research on foraging traditions in primates that has focussed on between-population comparisons (Whiten et al. 1999; van Schaik et al. 2003; Santorelli et al. 2011). We also note that due to detailed information on tree distribution and the use of neighbouring groups, we could compare directly the diet, while the studies on chimpanzees (Whiten et al. 1999) and orang-utans (van Schaik et al. 2003) focussed strongly on the use of tools. Tool use is a very convenient indicator for local traditions but it is restricted to relatively few primate species, while our approach could be used more generally. Our results are in line with predictions of a model that takes sex-biased dispersal into consideration (Yeaman et al. 2011). On the other hand, neighbouring chimpanzee groups may differ with respect to socially learned behaviour (Boesch 2003). Thus, we predict that future research on group-level traditions is likely to yield positive evidence in a great variety of social species. Nevertheless, potentially confounding variables such as group size and composition have to be controlled for in order to exclude alternative hypotheses. Furthermore, recent experiments on vervet monkeys provide evidence for socially transmitted similarities within matrilineages rather than on the group level (van de Waal et al. 2012). These results suggest that future studies should investigate this additional layer as well, especially because young individuals should be most likely to learn what to eat from their mother. Most importantly, we think that future studies can test explicitly whether general differences in food preferences exist on the level of groups or lower social units. Candidate food items can be offered directly in a choice experiment. In addition, in species like vervet monkeys, the diet of immigrated adult males of known origin could reveal whether these individuals continue to have a diet that is more similar to their group of origin than to the current group (as observed recently in a food colour experiment on vervet monkeys; van de Waal et al. 2013). This approach would nicely control for differences in local food tree distribution.

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