

# Socioecological correlates of inter-individual variation in orangutan diets at Ketambe, Sumatra

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**Abstract** The diet of great apes consists of several hundred plant species. The factors determining diet differences have been examined between populations but not within a population, probably due to the confounding effect of seasonal fluctuations on fruit availability. In Sumatran orangutans (*Pongo abelii*), fruit availability appears to be sufficiently high year round to have little influence on diet composition, which in turn allows for addressing this question. We examined the diet of eight adult female orangutans at Ketambe, Sumatra, and investigated whether fig and non-fig fruit availability, association time, and/or home range measures influenced dietary overlap between female dyads. Between most pairs, females' diets were different: 16 out of

23 pairs had a significantly low diet species overlap. Only fig diet overlap was influenced (negatively) by the availability of non-fig fruit. Association time only influenced (positively) fig diet overlap. Hence, orangutans gathered in fig trees when non-fig fruit availability was low. Home range measures did not influence overall diet overlap. To our knowledge, this is the first study showing that, while controlling for confounding factors, individuals with similar energetic requirements, from the same population and sharing the same area, make different dietary choices relatively to their preferred (non-fig) fruit constituting the majority of their diet. Social transmission, with putative matrilineal diet traditions, suitably explains these results. We discuss the implications of the findings for orangutan conservation, namely on reintroduction and the felling of fig trees.

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## Introduction

Non-human primates (hereafter primates) living in tropical rainforests are surrounded by thousands of plant species. Primates rely heavily on these resources, but their diet is composed of only a fraction of the total resources available in the environment (Robbins and Hohmann 2006). In great apes, a species' diet may consist of several hundred plant species (Russon et al. 2009). Among the factors that can influence primate diets, food availability plays an imperative role since an individual can only consume what is available (Chapman 1988; Doran 1997; Knott 1998; Buij et al. 2002; Matsumoto-Oda 2002; Stanford and Nkurunungi 2003). Several studies have described how differences in food availability lead to dietary differences between conspecific populations and/or communities (Nishida et al. 1983; Boesch et al. 2006; Morrogh-Bernard et al. 2009; Bastian

et al. 2010) and even between age–sex classes within a population of the same species (Ganas et al. 2004; Wich et al. 2006). Interestingly, though, food availability has been shown to have little influence on the diet composition (fruit, leaves, flowers, etc.) of Sumatran orangutans (Wich et al. 2006). Across substantial fluctuations in food availability, Sumatran orangutans can maintain a high percentage of fruit in their diet year round (Wich et al. 2006). This is likely possible due to the fact that, despite fluctuations, fruit availability is always relatively high throughout the year on the island (Morrogh-Bernard et al. 2009; Harrison et al. 2010; Wich et al. 2011). This offers the possibility to investigate the influence of other important diet determinants that remain masked, such as fruit nutritional quality (Janson et al. 1986; Leighton 1993; Wasserman and Chapman 2003) and social learning (Rapaport and Brown 2008; Bastian et al. 2010; Jaeggi et al. 2010) and that may predispose individuals to favor particular fruits that have the highest energy yield or those chosen by a demonstrator, respectively. The hypothesis that diet composition depends mostly on fruit nutritional quality predicts that individuals living in a habitat offering sufficient fruit choices (like Ketambe) will have very similar diets, as they will come to prefer the same fruit (those that give the highest energy returns) through individual learning. The social learning hypothesis predicts that individuals in a habitat offering sufficient variation in fruit choices do not strictly align with what others eat because their past social interactions bias their fruit choices toward those of models from whom they have learned. Such biases could occur without substantial energetic compromises given that fruit favored by orangutans tends to be relatively high in energy. Different individuals could thus exhibit different diets, particularly so in dispersed fission–fusion communities such as orangutans' (e.g., Singleton et al. 2009), where individuals are not equally connected within social networks (e.g., van Noordwijk et al. 2012). Social effects on feeding behavior have been described across the animal kingdom, including fish (e.g., Lachlan et al. 1998), birds (e.g., Rowley and Chapman 1986; Slagsvold and Wiebe 2007), non-primate mammals (e.g., Galef and Giraldeau 2001; Ratcliffe and ter Hofstede 2005), and primates (e.g., Visalberghi and Addessi 2001; Rapaport and Brown 2008). In particular, social learning has been shown to give rise to distinct differences in the fallback food eaten by two different orangutan populations (Bastian et al. 2010). However, to our best knowledge, no study has yet been dedicated to documenting the extent of dietary variation among individual orangutans while taking variation in food availability into account and then assessing how well ecological versus social factors might account for the variation (cf., Bastian et al. 2010; Jaeggi et al. 2010).

Here, we use data on the individual diets of all adult parous female orangutans residing in the Ketambe area

(Indonesia) between 2003 and 2009 to examine differences in the use of fig and non-fig fruit species, which comprise the majority of the diet of Sumatran orangutans (Wich et al. 2006). First, we asked whether overall fruit availability influenced time spent feeding on all fruit including figs (hereafter fruit), on figs specifically and on non-fig fruit specifically (cf., Wich et al. 2006). Second, we investigate the relationship between the availability of particular fig and non-fig fruits from particular species (hereafter species availability) and time spent feeding on these species. Third, we calculate overlap between the diets of all female dyads, where overlap was measured both in terms of feeding time devoted to particular species and in terms of the number of species shared in common. Fourth, we investigate whether diet overlap between female dyads could be explained by fruit, fig, and non-fig fruit availability, association time, home range overlap, or distance to home range centroid between females. Finally, we assess whether dietary variation among females was compatible with the hypothesis in which fruit nutritional quality has the greatest effect on food choice or with the hypothesis that social transmission is the most important source of individual dietary variation at Ketambe.

## Methods

### Study site

This study was conducted in the Ketambe research site (3°41'N, 97°39'E), Gunung Leuser National Park, Leuser Ecosystem (Aceh, Sumatra, Indonesia). Most of the research area is covered by pristine tropical rainforest at elevations of 350–1,000 m above sea level, with the area having been subjected to high levels of encroachment since 1999 (Rijksen 1978; van Schaik and Mirmanto 1985; Wich et al. 1999; Wich and Utami Atmoko 2010; Hardus et al. 2012). The orangutan population in the study area is well known and has been studied since 1971 (Rijksen 1978; Schürmann and van Hooff 1986; Sugardjito et al. 1987; Utami Atmoko 2000; Wich et al. 2004b).

### Data

Field assistants recorded monthly fruit availability data from 25 phenology plots (25×25m, average 52 trees per plot; van Schaik 1986; Wich and van Schaik 2000) between August 2003 and June 2005. On each tree, the number of fruits was scored in classes (see Wich and van Schaik 2000 for details), but in the analyses presented in this paper, only the presence or absence of fruits was used. All species were identified to species; a local name was given in the event that the Latin name was not known. Plant species were identified by

botanists from several international herbaria and the main Indonesian Herbarium in Bogor. We calculated fruit availability as the percentage of trees bearing fruit. Phenology plots consisted of orangutan and non-orangutan fruits; however, this could not have influenced the analyses involving overall fruit availability because a strong correlation between orangutan fruit availability and overall fruit availability was found ( $r=0.99$ ; Wich et al. 2006). Fruit availability was subsequently calculated per species per month (species availability), and correlated with the time orangutans spent feeding on each of these (fig or non-fig fruit) species. For all correlations between species availability and behavioral data, only behavioral data collected during the same time period (i.e., August 2003–June 2005) was considered. However, not all species comprising orangutan diets were found to exist within the phenology plots, and thus, only species present in the phenology plots were included in the analyses.

Feeding data and association data were collected from August 2003 till June 2005 (2807.4/1767.3 total/feeding observation hours) and July 2005 till June 2009 (5729.8/3690.2 total/feeding observation hours) by field assistants and other researchers using standardized behavioral data collection techniques (van Schaik 1999; Morrogh-Bernard et al. 2002). A minimum follow length of 3 h was used to calculate percentages of time spent feeding on a certain species per month. These data were highly correlated with data based on full day follows (Spearman's  $\rho=0.973$ ). We thus chose a minimum follow length of 3 h because this provided a better assessment of individuals' diet composition and variety, preventing biases toward individuals (who could be) followed more frequently during full days (e.g., more habituated individuals, individuals ranging close to camp). Furthermore, data were only used when the focal individual was followed for more than 3 days per month. For comparisons between two individuals, we included an additional requirement to decrease possible influence of seasonality: data were only used when focal individuals were followed within 15 days of each other during a specific month. This study is based on eight individuals, and we solely considered adult parous females because they share similar energetic requirements, have smaller home ranges than males, their ranges can greatly overlap with each other (Singleton and van Schaik 2001; Singleton et al. 2009), and this age–sex class is the one for which the largest comparative dataset is available. The number of months per female for which there was availability (phenology) data and feeding data were 15, 14, 14, 10, 9, 6, and 4. Thus, for correlation analyses between availability and feeding data, only seven females could be used. Concerning feeding data, only fig and non-fig fruits were considered, as these foods are preferred by orangutans (e.g., Bastian et al. 2010) and constituted the bulk of orangutan diet at Ketambe (e.g.,

Wich et al. 2006), for which the largest amount of observation hours was available across individuals. Overlap of feeding time was calculated as percentage of overlap for time spent feeding on a particular species between two individuals. For instance, when individual A spent 20 % of feeding time on species 1 and individual B spent 15 % of feeding time on this same species, overlap in time spent feeding on species 1 between individual A and B was considered 15 %.

Home range overlap and distance between home range centroids were calculated per dyad of individuals for the period August 2003 till June 2009 in ArcGIS 9.3.1 (ESRI 2009). Cumulative annual home ranges per individual were calculated in the form of fixed kernel density estimates (KDE) (Worton 1989) generated through the Home Range Tools extension (Rodgers et al. 2007). Biased cross validation was used to select smoothing parameters, with cell size set at 50 m, and 90 % volume contours chosen to include the overall home range of each individual. Home range overlaps were then calculated through measuring with ArcGIS Analysis Tools (ESRI 2009), the area of intersection for each orangutan dyad.

#### Statistical analyses

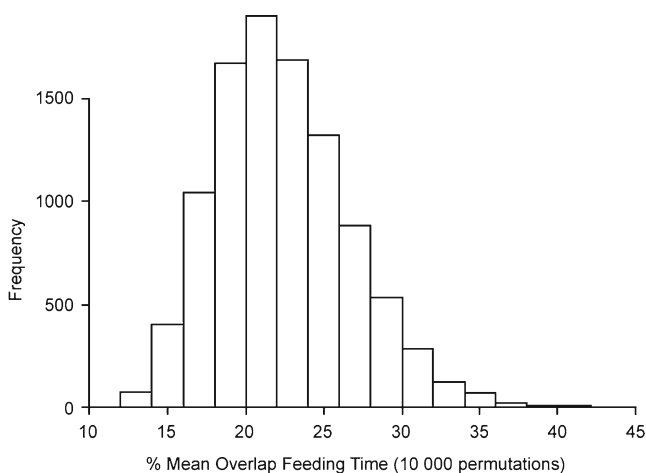
Correlation analyses were conducted using Spearman's rho correlation test. Correlations between overall fruit availability and time spent feeding on fig and non-fig fruits were replicated using generalized linear mixed model (GLMM) analyses to control for sampling biases among individuals (i.e., orangutan ID was used as random effect).

We developed a permutation test procedure in R version 2.13.0 (R Development Core Team 2011) to assess the statistical significance of (1) percentage of time spent feeding on particular species by two individuals (feeding time overlap) and (2) the proportion of identical species in the diets of two individuals (diet species overlap). These tests were carried out at the plant species level for fruits including figs, and conditional upon all observed percentages of foraging time spent on similar and/or different fruit species by two individuals in the months they were followed. Hereafter, we will explain in detail the two statistical test procedures using the Ketambe data set from the orangutan dyad Ans and Chris as an example.

First, the average overlap in feeding time on identical species across the 8 months during which Ans and Chris were followed was 47.2 %. To perform the permutation test, the percentages of feeding time spent by each of the two orangutans on the different fruit species were randomly permuted for each month separately. We chose this procedure based upon the null hypothesis that each of the observed percentages of time spent feeding on some fruit species by an orangutan could just as likely have been spent

feeding on another fruit species. By creating 10,000 sets of randomly permuted sequences of monthly percentages of feeding time for each of the two individuals, a null distribution of the average overlap in feeding time was generated (Fig. 1). Subsequently, the probability of obtaining an average overlap in percentage of feeding time on identical species greater than or equal to 47.2 (i.e.,  $P_{\text{right}}$ ) was calculated and was 0.0001 (based on 10,000 permutations). Thus, the average overlap in feeding time on identical species was significantly high for Ans and Chris, meaning that they spent a significantly larger amount of feeding time on identical fruit species than was expected under the null hypothesis.

Second, Ans and Chris foraged on six identical fruit species in August 2003. The total number of fruit species foraged on by at least one of them in this month was 27. Accordingly, the diet species overlap was  $6/27=0.22$  for this month. The average diet species overlap, calculated across all months during which both individuals were followed, was 0.35. After running a permutation test, similarly as described above, it was found that  $P_{\text{left}}$  was 0.0001 (based on 10,000 permutations). Thus, the diet species overlap (i.e., 0.35) was significantly low for Ans and Chris, meaning that the proportion of identical fruit species foraged on by these two orangutans was significantly less than expected by chance. We applied a Bonferroni correction for multiple comparisons (Hochberg 1988) for each of the two sets of permutation tests, as we tested multiple dyads. This constituted a conservative approach to the data as testing for differences between female dyads could possibly be considered an exploratory analysis rather than rigorous hypothesis testing, and, thus, Bonferroni corrections were not strictly necessary (Roback and Askins 2005). The critical significance level was set at 0.05; all tests were two sided.



**Fig. 1** Frequency histogram of random feeding time overlap for the orangutan dyad Ans and Chris, generated under the null hypothesis (see text)

## Results

### Fruit availability

Overall fruit availability was not correlated with time spent feeding on figs ( $\rho=-0.180$ ,  $p=0.131$ ;  $n=72$  months) and non-fig fruit ( $\rho=0.046$ ,  $p=0.701$ ;  $n=72$  months). Replication of the analyses confirmed that overall fruit availability had no significant effect on time spent feeding on figs (GLMM:  $F_{(1, 70)}=2.862$ ,  $p=0.095$ ), together with no significant effect due to orangutan ID ( $Z=1.403$ ,  $p=0.16$ ). Similar results were found between overall fruit availability and time spent feeding on non-fig fruit (GLMM:  $F_{(1, 70)}=3.335$ ,  $p=0.072$ ), with no effect due to orangutan ID ( $Z=0.961$ ,  $p=0.336$ ). However, species availability was significantly correlated with time spent feeding on fig species ( $\rho=0.415$ ,  $p=0.049$ ;  $n=6$  fig species) but not on non-fig fruit species ( $\rho=-0.038$ ,  $p=0.602$ ;  $n=43$  fruit species).

### Diet differences and diet overlap

Percentage of time spent feeding on a species was significantly higher than expected by chance for only 4 out of 23 dyads (Table 1). In contrast, diet species overlap was significantly lower than expected by chance for 16 out of 23 dyads (Table 1). Solely, the percentage of time spent feeding on identical fig species was negatively correlated with non-fig fruit availability (Table 2). Similarly, fig species overlap was also negatively correlated with non-fig fruit availability (Table 2). Fig diet overlap (time spent feeding on identical species and species overlap) was positively correlated with association time (Table 2). Time spent feeding on identical fruit was correlated with home range overlap, but when we examined this significance separately for time spent feeding on identical fig and non-fig fruit species, no correlation was found with home range overlap. Time spent feeding on identical species and diet species overlap was not correlated with distance to home range center (Table 2).

## Discussion

We confirmed that overall fruit availability did not influence feeding time on fruit, figs, and non-fig fruits for female orangutans, and our data sample was not biased toward any particular individual. This stands in contrast to the positive trend between overall fruit availability and feeding time on non-fig fruit for the same sex–age class that has been reported by Wich and colleagues (2006) for the same population during an earlier study. Although this trend could not be replicated with our data, we did find an effect at the plant species level for fig species. When investigating the effect of species availability and the respective representation of these species in

**Table 1** Dietary overlap between female orangutans

Dyad	Mean feeding time overlap (%)	Range (%)	Two-sided <i>p</i> value	Mean diet species overlap (P)	Range (P)	Two-sided <i>p</i> value
Ans–Binjei	34.3	[0.6–61.1]	0.116	0.19	[0.07–0.32]	<b>0.0006</b>
Ans–Chris	47.2	[29.7–60.6]	<b>0.0002</b>	0.35	[0.22–0.50]	<b>0.0002</b>
Ans–Elisa	19.7	[3.9–40.7]	0.7	0.09	[0.07–0.11]	<b>0.0002</b>
Ans–Pluis	33.7	[9.1–58.3]	0.32	0.12		0.0172
Ans–Yet	31.4	[6.6–58]	0.036	0.27	[0.17–0.36]	<b>0.0002</b>
Binjei–Chris	19.9	[11.3–30.6]	0.96	0.25	[0.22–0.30]	<b>0.0008</b>
Binjei–Elisa	13.8	[5.8–21.8]	0.34	0.16	[0.06–0.25]	<b>0.0002</b>
Binjei–Pluis	5.8		0.08	0.08		0.084
Binjei–Yet	20.0	[4.5–41.1]	0.66	0.16	[0.10–0.21]	<b>0.0002</b>
Chris–Elisa	23.8	[7–51.8]	0.3	0.28	[0.12–0.50]	<b>0.0002</b>
Chris–Pluis	43.5	[26.2–57.1]	<b>0.0002</b>	0.30	[0.19–0.39]	<b>0.0002</b>
Chris–Puji	25.6	[25–26.1]	0.13	0.26	[0.21–0.31]	<b>0.0002</b>
Chris–Sina	17.0	[0.2–44.3]	0.66	0.23	[0.05–0.45]	<b>0.0002</b>
Chris–Yet	34.8	[3–70.3]	<b>0.0002</b>	0.30	[0.04–0.50]	<b>0.0002</b>
Elisa–Pluis	36.0	[9.7–63.6]	0.076	0.31	[0.18–0.45]	0.86
Elisa–Sina	3.6		0.2	0.11		<b>0.0026</b>
Elisa–Yet	48.9	[11.5–98]	0.007	0.30	[0.13–0.40]	<b>0.0002</b>
Pluis–Puji	76.6		<b>0.0002</b>	0.55		0.18
Pluis–Sina	20.2	[1.3–39.1]	0.98	0.18	[0.15–0.22]	0.074
Pluis–Yet	35.9	[15.6–55.1]	0.0088	0.33	[0.22–0.43]	<b>0.0002</b>
Puji–Sina	36.8		0.172	0.21		<b>0.0042</b>
Puji–Yet	37.0		0.094	0.44		0.024
Sina–Yet	66.2	[34.7–88.1]	0.0066	0.34	[0.27–0.43]	0.96

*Bold p values* indicate significance from the permutation test and after applying the Bonferroni correction for multiple comparisons (Hochberg 1988)  
*P* proportion of species

orangutan diet, we found that orangutans proportionally increase their feeding time on figs when fig availability increases. This was not found for non-fig fruit species.

In addition, our results indicate that the diet of orangutan females (measured as time spent feeding on identical fruit

species) was more similar than expected by chance for only a minority of individuals. In contrast, in terms of fruit species constituting their diet (measured as diet species overlap), the diet of orangutan females was significantly different for the majority of individuals. Thus, the diets of

**Table 2** Correlations between diet overlap and several variables

	Fruit (including figs) availability ( <i>n</i> =50)		Fig availability ( <i>n</i> =50)		Non-fig fruit availability ( <i>n</i> =50)		Association time ( <i>n</i> =50)		Home range overlap ( <i>n</i> =23)		Distance to home range center ( <i>n</i> =23)	
Spearman's rho correlation tests	Rho	<i>p</i>	Rho	<i>p</i>	rho	<i>p</i>	Rho	<i>p</i>	Rho	<i>p</i>	Rho	<i>p</i>
Ft overlap fruit (including figs)	−0.261	0.068 <sup>a</sup>	−0.351	<b>0.012</b>	−0.261	0.067 <sup>a</sup>	0.475	< <b>0.001</b>	0.426	<b>0.043</b>	−0.269	0.214
Ft overlap figs	−0.213	0.137	−0.266	0.062	−0.337	<b>0.017</b>	0.463	<b>0.001</b>	0.289	0.182		
Ft overlap non-fig fruit	0.016	0.914	−0.073	0.614	0.228	0.112	0.04	0.785	0.292	0.177		
Diet species (fruit including figs) overlap	−0.309	<b>0.029</b>	−0.159	0.270	−0.274	0.055 <sup>a</sup>	0.282	<b>0.047</b>	0.293	0.174	−0.331	0.122
Fig species overlap	−0.305	<b>0.031</b>			−0.349	<b>0.013</b>	0.435	<b>0.002</b>				
Non-fig fruit species overlap	−0.142	0.324			0.051	0.723	0.015	0.917				

*Ft* feeding time

*Bold* values indicate significance with  $p \leq 0.05$

<sup>a</sup> When  $0.05 < p < 0.07$  at fruit (including figs) level, correlations are also conducted between availability and Ft/species overlap for fig and non-fig fruits

the eight female orangutans were substantially different from each other. Non-fig fruit species availability influenced negatively overall diet overlap for fig species, that is, the higher the abundance of non-fig fruit in the forest, the lower the overlap of fig species in the diet between orangutans and the lower the amount of time spent feeding on identical fig species. This suggests that during periods of lower availability of non-fig fruit, orangutans very likely search for and depend on similar species of figs, perhaps even on specific fig trees (see also Sugardjito et al. 1987), which agrees with previous assertions that figs represent important fallback foods for these primates (Wich et al. 2006; Marshall and Wrangham 2007; Marshall et al. 2009b). Fig tree density has been suggested to determine orangutan carrying capacity in the dryland forests of Sumatra (van Schaik et al. 2001; Wich et al. 2004a; Marshall et al. 2009a; Morrogh-Bernard et al. 2009). Particularly, the high orangutan density at Ketambe has been suggested to be the result of the area's exceptionally high fig tree density. We found that orangutans consume a larger variety of fig species during periods of non-fig fruit abundance, and this is in line with the observation at other sites that orangutans travel more when fruit is abundant (Morrogh-Bernard et al. 2009). We also found that association time was significantly correlated with both time spent feeding on identical species and species overlap for figs but not for non-fig fruit. This can be understood from the observation that orangutans at Ketambe form feeding aggregations at large fig trees (Sugardjito et al. 1987; Utami et al. 1997). At Ketambe, figs likely bear the largest crop sizes within this forest area (Hardus, Lameira, and Wich, personal observation), which may strongly influence the visit rate by orangutans in the area (Leighton 1993) and time spent feeding at each fruiting fig tree (as our results indicate, see above). Overall, these findings suggest that, at Ketambe, dietary overlap (expressed as percentage of time spent feeding on identical species and as diet species overlap) is mainly the result of the feeding associations in large fig trees. This suggests that orangutans likely use tracking skills during such periods of low non-fig fruit availability. Recently, Normand et al. (2009) have shown that chimpanzees possess an extensive and a precise spatial memory that they use to improve their foraging efficiency. Orangutans probably also have such abilities. However, orangutans probably do not need to rely on tracking abilities during other seasons with sufficient non-fig fruit abundance; if they did, one would expect relatively high coefficients of diet overlap.

The observation that large diet differences may occur between individuals with similar energetic requirements in an essentially availability-independent way may be surprising, particularly so when no significant correlations were found with home range overlap or distance between home range centers. Moreover, orangutan ranges are several

hundred hectares large (Singleton and van Schaik 2001) and individuals co-use the same multi-hectare forest blocks (Dellatore unpublished data, Singleton and van Schaik 2001), diluting potential differences in availability due to micro-habitat variations. Such potential differences may even be smaller in forests with relatively high fruit availability year round, such as in Ketambe. However, overall fruit availability is lower throughout the year in many other areas where orangutans have been studied (Husson et al. 2009; Marshall et al. 2009a; Wich et al. 2011). In forests with lower density of figs (Morrogh-Bernard et al. 2009) or lower levels of overall fruit availability (Harrison et al. 2010), such as in Borneo, individuals may be forced to revisit the same currently available fruit sources regularly and track fruit availability more closely than at Ketambe, leading to high diet similarity among individuals, with all concentrating on fruits with the highest energy yields. Hence, within such populations, availability may represent a major driver of diet differences/similarity between individuals. A similar role of fruit availability has been observed in comparisons between orangutan populations (Morrogh-Bernard et al. 2009; Bastian et al. 2010; Campbell-Smith et al. 2011). Altogether, our results suggest that when fruit availability does not limit the ability of orangutans to obtain a suitable diet, other factors act as the most important determinants of dietary similarity among individuals.

The demonstration of large dietary individual differences at Ketambe is consistent with the view that social learning represents one such major factor, as previously proposed (Bastian et al. 2010). Indeed, our results parsimoniously explain why, until now, differences in diet traditions between neighboring Bornean populations have been found only for fallback foods (e.g., leaves, bark), which are constantly available and not for fruit, which are comparatively less available and experience larger fluctuations during the year on this island (Wich et al. 2011). We expect that our results would not be substantially different if we had also considered non-fruit items, such as leaves and bark. Our results also suggest that overlap in the fallback component of orangutan diets may not be always constant but instead vary as a function of the energy yield of the fallback foods in question: diet overlap should be high for high quality fallback foods (e.g., figs, this study) and low for low quality fallback foods (e.g., leaves, bark; Bastian et al. 2010). However, relatively to preferred food (i.e., non-fallback), such as non-fig fruit, diet overlap at Ketambe may not be strongly influenced by energy content because if individuals foraged optimally, their diets would converge on highly nutritious non-fig fruits, irrespectively of the high availability of other non-fig fruits. At Ketambe, individuals only form feeding aggregations during periods of non-fig fruit scarcity and only at large fig trees; such aggregations are

probably not suitable contexts, nor do they occur at suitable times, for the transmission of information about the potential dietary suitability of non-fig fruits. Hence, our results suggest that fruit-related learning occurs within mother–infant dyads. Such learning has been suggested to occur at Tuanan, in Borneo (Jaeggi et al. 2008, 2010) and also has been deduced from inter-population comparison of diets (Bastian et al. 2010). This is, to our knowledge, the first study providing supporting evidence that, once fruit availability no longer constrains individual food sources, preferential social learning (Bastian et al. 2010) can become a critical influence on those foods that constitute the bulk of the diet. Each individual may then make different major diet choices to satisfy her own energetic or other nutritional needs. The influence of social learning may be further investigated in the future by assessing the ontogeny of individuals' diet and by measuring diet similarity between adult mother–daughter dyads.

To our knowledge, dietary differences between individuals of the same group/community have only been examined in one other primate species, weanling baboons (*Papio hamadryas anubis*; Altmann 2000). This study examined time spent feeding on the same species and found individual differences in approximately more than a third but less than half of the items consumed by a group of baboons during their first year of age. Several of these differences were attributable to seasonal differences in birth date between yearlings, age difference between yearlings, mothering characteristics, or phenological differences between years. Moreover, differences found were not consistent nor persisted across ages. Hence, the study by Altmann (2000) does not allow a direct comparison with the present study due to the strong influence of diet determinants which are only relevant at very young ages (e.g., birth date) and the uncertainty about how the differences found at young age express potential differences between adult diets. However, it is unlikely that dietary differences among (adult) individuals are as extensive among more gregarious primate species as they are among orangutans at Ketambe. Local enhancement and observational conditioning (sensu Whiten et al. 2004) contribute to diet similarity among members of a cohesive social group because individuals in the same group have similar learning opportunities. Indeed, computer models of gregarious entities show high diet similarity within groups as a side effect of grouping (van der Post and Hogeweg 2008). In a patchy (i.e., not uniform) environment, trial-and-error (individual) learning is sufficient to bring about diet convergence within groups, where the fact that individuals share the same local opportunities for learning about food items automatically lead them to consume similar items (van der Post and Hogeweg 2008). The sole requirement for spontaneous emergence of diet similarity within groups was

that individuals foraged in the proximity of two other conspecifics, independently of the fact that each individual established its own dietary preferences. This grouping effect created an inheritable system of dietary repertoire composition, where diet similarity remained high and constant within a group even after generational substitution (van der Post and Hogeweg 2008). As such, gregariousness may passively hamper the emergence of substantial diet differences between primate individuals. Nevertheless, a number of dietary differences can exist that affect individuals' fitness (Altmann 2000).

The findings of this study have two implications for orangutan conservation. First, it is relevant for reintroduction practices to know that an individual's diet is largely formed before their independence. Reintroduction of confiscated individuals back into the wild is one of Indonesia's main orangutan conservation strategies (Soehartono et al. 2009). Released individuals are, nevertheless, frequently unfamiliar with their new habitat and the fruit resources therein, and years after release, fruit sources which are important for their wild counterparts can remain ignored by reintroduced orangutans (Russon 2009). Therefore, exposing individuals to numerous plant species present in their future release area before release and allowing them to become familiar with these would likely assist in the success of the reintroduction process. Secondly, our findings reemphasize the importance of large fig trees in mixed dipterocarp forests for orangutan diets and population viability. Accordingly, in agreement with recent published guidelines for minimized impact logging (Hardus et al. 2012), trees with attached climbing figs should not be felled.

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**Ethical standards** The experiments complied with the current laws of Indonesia.

**Conflict of interest** The authors declare to have no conflict of interest.

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