A Direct Comparison of Scan and Focal Sampling Methods for Measuring Wild Chimpanzee Feeding Behaviour

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ABSTRACT

Focal sampling is the most accurate method for measuring primate activity budgets, but is sometimes impractical. An alternative is scan sampling, in which the behaviour of the group is recorded at regular intervals. The simplest technique is to record whether at least one animal is engaged in the behaviour of interest. By direct comparison with focal data collected simultaneously on the same population, we assess the validity of this simple group-level sampling method for studying chimpanzee (*Pan troglodytes schweinfurthii*) feeding behaviour. In a 13-month study at Kanyawara, Kibale National Park, Uganda, group-level scan sampling provided statistically similar measures of broad diet composition to those produced by focal data, despite considerable seasonal variation. Monthly means of the percentage of time spent consuming non-fig fruit calculated from group-level scan sampling were highly correlated with those from focal sampling. This validates previous methodology used to identify periods of high energy availability. However, group-level scans tended to overestimate the percentage of observation time spent feeding, particularly for adult males. We conclude that this method of group-level scan sampling provides valuable data for characterising broad diet choice in chimpanzees and other species, but may be of limited use for estimating individual feeding time.

INTRODUCTION

Focal sampling is generally considered to be the most accurate method for measuring primate activity budgets, and is therefore the preferred method when observation conditions permit it [Altmann, 1974]. However, collecting focal data is often a challenge for primatologists working in thick vegetation. It is particularly difficult when studying animals that are not fully habituated to human observers (e.g. snub-nosed monkeys (*Rhinopithecus roxellana*) [Guo et al., 2007]), or arboreal species in which individuals cannot be quickly or reliably identified (e.g. woolly monkeys (*Lagothrix lagotricha*) [Di Fiore and Rodman, 2001]; Sulawesi crested black macaques (*Macaca nigra*) [O'Brien and Kinnaird, 1997]). One alternative to focal animal sampling is scan sampling [Altmann, 1974], which involves recording the behaviour of all visible individuals at pre-determined intervals. Numerous variants of scan sampling have been used to calculate basic parameters such as activity budgets and diet composition in many primate populations.

At our study site at Kanyawara, Kibale National Park, Uganda, scan sampling has repeatedly been used to identify seasonal variation in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) [e.g. Conklin-Brittain et al., 1998; Gilby and Wrangham, 2007; Emery Thompson and Wrangham, 2008]. The chimpanzees in this community rely on ripe fig fruits (*Ficus spp.*) as a 'fall-back' food [Wrangham et al., 1993; Marshall and Wrangham, 2007] which they consume during periods of low food availability. Their 'preferred' foods (defined as those that are selected disproportionately often relative to their abundance [Leighton, 1993; Marshall and Wrangham, 2007]) are ripe drupe fruits, also referred to as 'non-fig fruits' (NFF). In these studies, the relative contribution of NFF (or other foods) to the diet was assessed from scans in which observers recorded whether at least one chimpanzee in the group was feeding on a given item. This simple

measure of feeding behaviour is similar to one used by Fragazy et al. [1992], who classified squirrel monkeys as 'foraging together' if at least one individual in the social group was 'engaged in a food-related activity'. NFF consumption by the Kanyawara chimpanzee community, as assessed by this sampling method, appears to be a salient correlate of behaviour, probably because it indexes energy availability. Thus it has been linked to higher food quality [Conklin-Brittain et al., 1998], higher C-peptide production [Emery Thompson et al., 2009], larger subgroups [Wrangham, 2002], increased reproductive function in females [Emery Thompson and Wrangham, 2008] and higher rates of hunting and killing red colobus monkeys (Procolobus *spp.*) [Gilby and Wrangham, 2007]. We suspect that NFF consumption is also important in other chimpanzee communities as well as other frugivorous primates. Before this claim can be tested, however, our simple group-level measure of NFF diet composition must first be validated.

Group-level scan sampling is vulnerable to various potential problems. First, if feeding activity is not synchronous for all members of a group, group-level scans will over-estimate the total time an average individual spends feeding. Second, if the behaviour of some individuals is over-sampled, and there is substantial individual variation in diet choice, group-level scans would be unrepresentative of individual food intake. Therefore, group-level scan sampling would neither capture intraspecific variation in feeding behaviour (such as variation associated with age or sex class), nor represent a meaningful average (across ages or sexes). For chimpanzees these effects are plausible because compared to males, females often feed in smaller groups and visit large feeding parties for shorter periods (Wrangham and Smuts 1980). If the strength of such an

effect varies among food types, group-level scans might lead to a distorted picture of seasonal variation in food intake.

Here we assess the importance of such problems by comparing the results of group-level scan sampling with data collected using focal sampling during the same period. We assume that focal sampling provides accurate and reliable data. We assess the validity of group-level scan data by comparison with focal data collected on (A) overall feeding time, and (B) diet composition. We use these data to test the hypothesis that a group-level sampling protocol is sufficient for identifying temporal variation in feeding behaviour.

METHODS

The study population

The Kanyawara chimpanzee community resides within Kibale National Park Uganda, and has been studied continuously by Richard Wrangham and colleagues since 1987 [Wrangham et al., 1991; Wrangham et al., 1992]. The chimpanzees were habituated to the presence of researchers without provisioning. The community composition has remained relatively stable over the course of the long-term study, averaging 40-50 individuals, with 9-12 adult males and 12-15 adult females [e.g. Gilby and Wrangham, 2008].

Party-level scan sampling

Since 1987, the Kibale Chimpanzee Project (KCP) has conducted daily follows of the Kanyawara chimpanzees. For the current study, we used data collected by KCP researchers between June 1, 2004 and June 30, 2005. Most days, a team of observers consisting of at least

two Ugandan field assistants, typically accompanied by graduate students, the project manager or visiting scientists, located a party of chimpanzees by using the previous day's nesting data, checking recent feeding trees and/or listening for calls. Chimpanzees have a fission-fusion social organization in which individuals form fluid groups (parties, hereafter) containing a subset of the community [Nishida, 1968; Wrangham and Smuts, 1980; Goodall, 1986]. The research team followed the party for as long as possible, usually from dawn until dusk. If the party split, the observers followed the larger subgroup, unless there were enough researchers to follow both parties. In that case, both parties were followed simultaneously.

At 15 minute intervals, one observer used instantaneous scan sampling [Altmann 1974], ('*party-level scans*', hereafter) to record party composition and feeding behaviour. If at least one chimpanzee in the party was feeding (consuming food), the observer recorded the species and part (e.g. fruit, leaf, etc) that was being eaten. This method was designed to capture broad dietary patterns, therefore the observer did not record which chimpanzees were feeding. In cases in which members of the party were feeding on different food items, the observer recorded the food eaten by the majority of the individuals that were feeding. All data were digitised and stored in a relational database in the Department of Human Evolutionary Biology at Harvard University.

From these data, we calculated two monthly measures of feeding behaviour. First, we calculated *time spent feeding* – the percentage of all party-level scans in which at least one chimpanzee was feeding. Second, we calculated *non-fig-fruit (NFF) diet composition* – the percentage of all feeding scans in which chimpanzees were consuming NFF [Gilby and Wrangham, 2007; Emery Thompson and Wrangham, 2008].

Focal sampling

During the same time period (June 1, 2004 – June 30, 2005), one of the authors (AP) conducted focal sampling [Altmann, 1974] of individual chimpanzees as part of a concurrent study on sex differences in feeding behaviour [Pokempner, 2009]. Focal individuals included five adult males and five non-cycling (i.e. pregnant or lactating) adult females. During full-day focal follows, the activity of the individual was recorded using instantaneous scan sampling [Altmann, 1974] at one minute intervals. When the focal individual was feeding, the species, plant part, and phytophase (e.g. ripe, unripe, young, mature) of the food were recorded. Due to the nature of fission-fusion grouping it was not always possible to rotate focal individuals in a systematic fashion. A field assistant was therefore assigned to follow a selected individual until the end of the day in order to locate them as a focal for the following day. This strategy was intended to reduce the potential bias of following larger parties and resulted in focal follows that were sometimes conducted in the absence of KCP observers. Focal follows averaged 9.2 hours and were distributed evenly by sex and season.

We calculated time spent feeding and NFF diet composition using the focal data in the manner described for the party-level scans.

Analysis

First, we used linear regression to examine whether monthly means of time spent feeding and NFF diet composition calculated from party-level sampling data were predicted by those calculated from focal sampling. We assumed that a statistically significant association, a slope of 1, and a high R^2 value indicated that data collected by party-level scan sampling provided a

meaningful estimate of data collected by focal sampling. Second, for each of the two variables (time spent feeding and NFF diet composition), we calculated the difference between the monthly means derived from party-level and focal sampling, and used a one-sample T-test to ascertain whether the difference was significantly different from zero. This allowed us to evaluate the magnitude of any discrepancy between the two data collection methods. Finally, we used logistic regression to estimate the probability that if at least one member of the party was feeding on NFF (as determined by a party-level scan), the focal individual was also doing so. This provided a means of evaluating the degree to which members of a feeding party were consuming the same type of food. We ran our analyses on both sexes together as well as separately.

We conducted all statistical analyses using SAS 9.2 (SAS Institute, Cary, NC).

RESULTS

The KCP research teams conducted 15602 15-min party-level scans during the 13 month study period, equaling 3900.5 hours of observation. There were 103 instances when two research teams sampled the same chimpanzee party, usually when two simultaneously-followed parties briefly came together. For each of these, we randomly deleted one of the observations, resulting in 15499 party-level scans (Table 1). At least one chimpanzee was feeding in 58.2% (9025) of these scans. Chimpanzees were feeding on non-fig fruit (NFF) in 39.6% (3577) of feeding scans. Monthly values of time spent feeding are displayed in Table 1.

81294 1-min focal scans were conducted during the study period, equaling 1354.9 hours of observation (Table 1). The focal chimpanzee was feeding in 32.9% (26748) of these scans. NFF was being consumed in 37.4% (10010) of focal feeding scans.

5424 of the 1-min focal scans occurred on the quarter-hour (hh:00, hh:15, hh:30, hh: 45). The focal chimpanzee was in a party being sampled by a KCP research team for 3650 (67.3%) of these 15-minute scans (Table 2). These are our 'simultaneous' data points for which data could be matched between the focal and party-level scans. Our statistical analyses used these data points.

According to the KCP party-level data, at least one chimpanzee was feeding in 63.2% (2308/3650) of the simultaneous scans. By contrast the focal chimpanzee was feeding in 33.7% (1230/3650) of the simultaneous scans. Estimates of NFF diet composition based on party-level and focal sampling were similar, however. The focal chimpanzee was feeding on NFF in 39.8% (490/1230) of focal feeding scans, while at least one chimpanzee was feeding on NFF in 41.2% (951/2308) of the party-level feeding scans.

These data suggest that our party-level scans provided a close approximation of broad diet composition but not of individual time spent feeding. Below we use the monthly variation to assess this claim.

Time spent feeding

There was no correlation between monthly means of time spent feeding when party-level and focal data were compared ($F_{1,12} = 0.12$, $R^2 = 0.01$, $P = 0.74$, Figure 1, open circles). The mean difference between time spent feeding calculated from party-level data and focal data was 29.7

(range 15.9 – 50), which was significantly greater than zero (one-sample T-test, $T_{1,12} = 12.44$, $P < 0.0001$, (Figure 2, open circles)). This indicates that our party-level sampling method consistently overestimated individual feeding times.

When the focal chimpanzee was male, there was no correlation between estimates of time spent feeding calculated from party-level and focal data ($F_{1,12} = 1.12$, $R^2 = 0.01$, $P = 0.31$, Figure 3A, open circles). For females, however, this relationship was statistically significant ($F_{1,12} = 4.83$, $R^2 = 0.24$, slope = 0.50 ± 0.23 (SE), $P = 0.05$, Figure 3B, open circles).

Diet composition

There was a strong positive correlation between estimates of monthly non-fig fruit (NFF) diet composition (percent of feeding time eating NFF) calculated from focal and party-level sampling ($F_{1,12} = 121.4$, $R^2 = 0.91$, Slope = 1.02 ± 0.09, $P < 0.0001$, Figure 1, solid diamonds). The estimated slope of the NFF regression line (range 0.93 - 1.11) includes 1, indicating that party-level scan sampling corresponded well with focal-based data on seasonal variation in food choice. The mean difference between values of NFF diet composition determined by the two methods was -2.4 (range -24.1 – 6.7), which was not significantly different from zero (one-sample T-test, $T_{1,12} = -1.26$, $P = 0.23$, Figure 2, solid diamonds). Finally, party- and focal-based estimates of NFF diet composition were very strongly correlated when the focal chimpanzee was an adult male ($F_{1,12} = 316.7$, $R^2 = 0.96$, slope = 0.98 ± 0.06, $P < 0.0001$, Figure 3A, solid diamonds). When the focal chimpanzee was a female, the correlation between party- and focal-based estimates of NFF diet composition was also highly significant, but not as tight ($F_{1,12} = 25.74$, $R^2 = 0.67$, slope = 0.87 ± 0.17, $P = 0.0004$, Figure 3B, solid diamonds). The lower R^2 was

due to a single month (June, 2004) in which the focal-based NFF diet composition (70%) was more than 4 times greater than the party-based NFF diet composition (16%). During this month, there were only 18 simultaneous focal- and party-level feeding scans when the focal chimpanzee was an adult female. This is more than 1 standard deviation below the mean number of such scans during the other months of the study (38 ± 16). Nine (50%) of the scans occurred during a single feeding bout in which the party was recorded as eating terrestrial herbaceous vegetation, and focal female BL was recorded to be eating *Uvariopsis congensis*, an important NFF. When we removed June, 2004 from the analysis, the R^2 value increased to 0.92 ($F_{1,11} = 135.22$, slope = 0.99 ± 0.085, $P < 0.0001$).

There were 1021 instances in which both the party and the focal individual were classified as feeding. In this sample, the focal chimpanzee was significantly more likely to be feeding upon NFF if we had classified the group as feeding on NFF (an "NFF feeding party") than if the party was feeding on something else (GEE logistic regression, $\chi^2_1 = 545.2$, $P < 0.0001$, repeated measure = focal). However, in 40 (10.3%) of the 388 instances in which the party was consuming NFF, the focal was eating another food item. As the size of an NFF feeding party increased, this discrepancy increased (multiple logistic regression, Odds ratio = 1.04, $\chi^2_1 = 4.33$, $P < 0.0001$, repeated measure = focal). In the largest NFF feeding parties (19 adults), there was an 86% chance that the focal chimpanzee was also eating NFF (Figure 4). Note that in NFF feeding parties containing only one adult, the probability that the focal individual was consuming NFF was only 93% (not 100%). This is likely due to the fact that our party-level scan samples included subadults, which may have been eating NFF while the focal adult was consuming something else. When included in the multiple logistic regression, the focal individual's sex did

not have a significant effect on the probability that s/he was feeding upon NFF ($\chi^2_1 = 1.2$, P = 0.27).

DISCUSSION

We found that a broad group-level measure of chimpanzee diet composition correlated closely with data collected on focal individuals. Specifically, monthly measures of non-fig fruit (NFF) diet composition derived from group-level scan sampling (in which a group was classified as 'feeding' if at least one chimpanzee was doing so) were highly correlated with those derived from focal sampling. This finding validates previous methodology used to identify periods of high energy availability at Kanyawara [Gilby and Wrangham, 2007; Emery Thompson and Wrangham, 2008]. However, our data suggest that this correlation should be interpreted with caution. While the difference between monthly values derived from group-level scans and focal data were not significantly different from zero, there were some months in which there was a considerable discrepancy. For example, in June 2005, the group-level data yielded an estimate of NFF diet composition (14.6%) that was more than 9 times greater than that based on focal data (1.6%). However, in other months, the estimates were almost identical (e.g. November 2004 and May, 2005). This variability is likely due to the possibility that members of a social group may be feeding upon different food items. While the focal chimpanzee was highly likely to be consuming NFF if the group was classified as doing so, s/he was eating another food item roughly 10% of the time. This discrepancy increased with adult group size. Whether or not this level of accuracy is acceptable will depend on the nature of the question being addressed.

Data from group-level scan sampling did not provide an accurate estimate of an individual's time spent feeding, as determined by focal animal sampling. Similarly, Fragaszy et al. [1992] found that in comparison to focal sampling, group scan sampling overestimated the amount of time spent feeding by wedge-capped capuchins (*Cebus olivaceus*) and squirrel monkeys (*Saimiri oerstedi*). In our study, this result is not surprising, since a group was classified as 'feeding' if a minimum of one chimpanzee was feeding at the time of the scan. However, the group-level scan data provide a rough idea of female feeding times. One possible explanation for this is that sampling of females might have been more likely in smaller parties, in which the chances are higher that all group members are engaged in the same behaviour. This possibility remains to be tested.

In sum, our data showed that group-level scan sampling provided accurate measures of broad diet composition, including seasonal variation. It did not closely predict the percentage of time spent feeding however, suggesting that when possible, focal sampling should be used for estimating individual feeding rates. While our results are derived from a single chimpanzee community, their fit to expectation suggests that they may have wide applicability to primate studies. In circumstances where focal sampling is impractical, a simple group scan sampling protocol is valuable for identifying broad temporal variation in individual diet composition.

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TABLES

Table 1. Summary of the complete data set. Party-level scans occurred at 15-minute intervals, and were classified as "Feeding" if at least one chimpanzee in the party was feeding at the time of the scan, and as "Non-fig Fruit Feeding" if non-fig fruits were being consumed. Focal observations took place at 1-minute intervals, and were classified in the same manner as party-level scans.

Year	Month	Party-level scans (15 min intervals)						Focal scans (1 min intervals)					
		Observation		Feeding		Non-fig Fruit Feeding		Observation		Feeding		Non-fig Fruit Feeding	
		Scans	Hours	Scans	% Total Scans	Scans	% Feeding Scans	Scans	Hours	Scans	% Total Scans	Scans	% Feeding Scans
2004	June	1118	279.5	703	62.9	460	65.4	2448	40.8	649	26.5	481	74.1
2004	July	1316	329	754	57.3	289	38.3	7421	123.7	3037	40.9	943	31.1
2004	August	1417	354.3	939	66.3	157	16.7	7165	119.4	3318	46.3	482	14.5
2004	September	1439	359.8	870	60.5	595	68.4	5159	86.0	1573	30.5	1040	66.1
2004	October	1289	322.3	790	61.3	553	70.0	10163	169.4	3130	30.8	2122	67.8
2004	November	1045	261.3	587	56.2	249	42.4	2584	43.1	859	33.2	357	41.6
2004	December	881	220.3	455	51.6	108	23.7	6711	111.9	2010	30.0	699	34.8
2005	January	1212	303	739	61.0	178	24.1	9200	153.3	3050	33.2	888	29.1
2005	February	1161	290.3	670	57.7	161	24.0	5551	92.5	1691	30.5	583	34.5
2005	March	1114	278.5	637	57.2	429	67.3	6214	103.6	2048	33.0	1303	63.6
2005	April	1118	279.5	517	46.2	281	54.4	6572	109.5	1575	24.0	1003	63.7
2005	May	1279	319.8	720	56.3	23	3.2	8327	138.8	2471	29.7	88	3.6
2005	June	1110	277.5	644	58.0	94	14.6	3779	63.0	1337	35.4	21	1.6
All Months		15499	3874.8	9025	58.2	3577	39.6	81294	1354.9	26748	32.903	10010	37.4

Table 2. Simultaneous 15-minute focal and party-level scans of the same chimpanzee party, by month. "Feeding Scans, Focal" = the number (and percentage) of total scans when the focal chimpanzee was feeding. "Feeding Scans, Party" = the number (and percentage) of total scans when at least one chimpanzee in the party was recorded as feeding, according to party-level scan sampling. "NFF Feeding Scans, Focal" = the number (and percentage) of feeding scans when the focal chimpanzee was consuming non-fig fruit (NFF). "NFF Feeding Scans, Party" = the number (and percentage) of feeding scans when at least one chimpanzee was recorded as eating NFF.

Year	Month	Total Scans	Feeding Scans				NFF Feeding Scans			
			Focal		Party		Focal		Party	
			Scans	% Total Scans	Scans	% Total Scans	Scans	% Feeding Scans	Scans	% Feeding Scans
2004	June	128	33	25.8	97	75.8	26	78.8	53	54.6
2004	July	276	117	42.4	161	58.3	42	35.9	65	40.4
2004	August	360	163	45.3	259	71.9	18	11.0	46	17.8
2004	September	295	94	31.9	193	65.4	71	75.5	147	76.2
2004	October	460	140	30.4	308	67.0	101	72.1	222	72.1
2004	November	99	34	34.3	58	58.6	23	67.6	34	58.6
2004	December	206	70	34.0	116	56.3	26	37.1	35	30.2
2005	January	447	147	32.9	286	64.0	37	25.2	65	22.7
2005	February	274	85	31.0	185	67.5	28	32.9	43	23.2
2005	March	311	103	33.1	201	64.6	70	68.0	149	74.1
2005	April	266	71	26.7	131	49.2	47	66.2	87	66.4
2005	May	366	115	31.4	204	55.7	1	0.9	3	1.5
2005	June	162	58	35.8	109	67.3	0	0.0	2	1.8
All Months		3650	1230	33.7	2308	63.2	490	39.8	951	41.2

FIGURE LEGENDS

Figure 1. Correlation between monthly means calculated from simultaneous focal- and party-level scans. Solid diamonds represent non-fig-fruit (NFF) diet composition, which equals the percentage of feeding scans in which NFF was being consumed. Open circles represent time spent feeding, which equals the percentage of scan samples in which feeding was recorded. See text for details.

Figure 2. Differences between monthly means derived from party-level and focal sampling. Solid diamonds represent NFF diet composition values derived from party-level sampling minus those derived from focal data. Open circles represent time spent feeding (party-level sampling) minus time spent feeding (focal data).

Figure 3. Correlations between monthly means calculated from simultaneous focal- and party-level data for A) male focals, and B) female focals. Solid diamonds represent non-fig-fruit (NFF) diet composition, and open circles represent time spent feeding.

Figure 4. Graphical representation of the results of a multiple logistic regression modeling the probability that the focal chimpanzee was feeding on NFF. The focal individual was significantly more likely to be feeding upon NFF in parties that were classified as feeding on NFF (Solid diamonds), than in parties that were consuming another type of food (Open circles). As party size increased, however, the focal individual

was significantly less likely to be feeding upon the same broad food category as the party. Error bars represent 95% confidence intervals of the regression lines.

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