

Title: Evaluating the efficacy of a consumer-centric method for ecological sampling: Using bonobo (*Pan paniscus*) feeding patterns as an instrument for tropical forest characterization

Running headline: Consumer-centric sampling of food availability

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Abstract

- 1 1. Characteristics of food availability and distribution are a key component of a species ecology. Objective
2 measurement of food resources, such as vegetation plot sampling, do not consider aspects of selection
3 by the consumer and therefore may produce imprecise measures of availability. Further, in most animal
4 ecology research, traditional ecological surveying often is time-intensive and supplementary to ongoing
5 behavioral observation. We propose a method to integrate ecological sampling of an animal's
6 environment into existing behavioral data collection systems by using the consumer as the surveyor.
7 Here, we introduce the consumer-centric method (CCM) of assessing resource availability for its ability
8 to measure food resource abundance, distribution, and dispersion. This method catalogues feeding
9 locations observed during behavioral observation and uses aggregated data to characterize these
10 ecological metrics.
- 11 2. We evaluated the CCM relative to traditional vegetation plot surveying using accumulated feeding
12 locations across three years visited by a tropical frugivore, the bonobo (*Pan paniscus*), and compared
13 it with data derived from over 200 vegetation plots across their 50km²+ home range.
- 14 3. We demonstrate that food species abundance estimates derived from the CCM are comparable to
15 those derived from traditional vegetation plot sampling after approximately 600 observation days or 60
16 spatially explicit feeding locations. The agreement between the methods further improved when
17 accounting for aspects of consumer selectivity in objective vegetation plot sampling (e.g., size minima).
18 Estimates of density from CCM correlated with plot-derived estimates and were relatively insensitive to
19 home range inclusion and other species characteristics, but were sensitive to sampling frequency (e.g.,
20 consumption frequency). Agreement between the methods in relative distribution of resources
21 performed better across species than expected by chance, although measures of dispersion correlated
22 poorly.
- 23 4. We demonstrate that while providing a robust measure to quantify local food availability, the CCM has
24 an advantage over traditional sampling methods as it incorporates sampling biases relevant to the
25 consumer. Therefore, as this method can be incorporated into existing observational data collection

26 and does not require additional ecological surveying, it serves as a promising method for behavioral
27 ecological data collection for animal species who re-use space and consume immobile food items.

28

29 **Keywords:** dispersion | distribution | food availability | resource selection | species abundance |
30 vegetation plot

31

32 **1. Introduction**

33 The abundance, dispersion, and distribution of food resources not only determines species
34 distribution but also has a strong impact on many aspects of an animal's life-history, physiology, and
35 sociality (e.g., Anholt and Werner 1995; Chapman et al. 2015; Davies and Deviche 2014; Hutto 1990;
36 Lambert and Rothman 2005; Rogers 1987; van Schaik et al. 1993; Vogel and Janson 2007). Due to the
37 core importance of food to an organism, the quantification of food availability and distribution are key
38 considerations across studies and disciplines. Methods used to estimate food resource abundance,
39 distribution, and dispersion are just as varied as the questions which necessitate these quantifications
40 (Szigeti et al. 2016).

41 Measurement of food resource **abundance or density** (i.e., estimation of the amount of a resource
42 available in a landscape) depends heavily on the type of resource and scale of interest (Bowering et al.
43 2018; Morrison 2016). Large scale analyses of abundance typically rely on remotely derived proxies via
44 satellite imagery, but for questions related more immediately to the individual or social group scale, direct
45 measurement of exploitable resources offer more direct insights into the resources available to a consumer
46 (e.g., Foerster et al. 2016; Wessling et al. 2020). While mobile resources may be measured via consumer
47 behavior (e.g., attack rates: Hutto 1990), for static food resources like plants, **abundance** is commonly
48 estimated by sampling subsets of the area of interest. Example methods include transects or vegetation
49 plots/quadrats (Baraloto et al. 2013; Ståhl et al. 2017; Vogel and Janson 2007), with the latter being the
50 most common sampling method in studies of frugivorous or folivorous animals. To then estimate
51 **distribution**, that is, a calculation of relative resource abundance or density across space within a
52 landscape, sampling may be further stratified across a given area relevant from individuals to populations
53 (e.g., home range, landscape, or region).

54 Measures of *dispersion* (i.e., patterns of clustering or patchiness), such as Morisita's index
55 (Morisita 1962), are used to quantify the clustering of resources over space within a landscape (Krebs 1999;
56 Stephens and Krebs 1986), often used in the contexts of understanding resource competition and socio-
57 ecological behavior (e.g., Vogel and Janson 2011). Quantifications of food species dispersion are perhaps
58 even more varied in practice and sensitive to the scale relevant to the consumer (e.g., Myers 1978; Vogel
59 and Janson 2011). Dispersion metrics may also require distinct sampling methods tailored to specific
60 questions (e.g., Vogel and Janson 2007), thus potentially requiring supplementary surveying effort to food
61 abundance surveying.

62 Despite its centrality to animal ecological research, ecological sampling design frequently does not
63 conform to recommended standards nor is adequately validated by animal ecologists (Mortelliti et al., 2010;
64 Szigeti et al. 2016). For example, sampling effort can substantially impact measures of resource
65 abundance, but it is rarely validated whether efforts are sufficient to adequately measure the intended
66 metrics. Further, ecological data collection often requires research effort additional to ongoing behavioral
67 observations and is time intensive and thus infrequently conducted. Snapshots of abundance derived from
68 these efforts in a landscape may therefore be used even many years after they have been collected or may
69 fail to account for temporal variation.

70 The problem of insufficient quantifications of resource availability may also extend to sampling
71 design. While traditional sampling methods in animal ecology may offer an objective measure of the
72 resources potentially accessible to a consumer, these methods are by design blind to aspects of resource
73 selection by the consumer. Given these disadvantages, the question arises whether there is a way to
74 conduct ecological sampling that is time-efficient within existing behavioral data collection systems and also
75 integrates resource selection criteria of the consumer? Behavioral observation has been used previously
76 as a measure of food availability (Lovette and Holmes 1995; Hutto 1990), dispersion (Vogel and Janson
77 2011), and preference (Forester et al. 2009), however these methods are either limited in application or still
78 necessitate ecological data collection.

79 We therefore introduce a consumer-centric method (CCM) for animal behavioral ecology studies
80 which uses the consumer as the survey vehicle to potentially quantify food resources in a landscape. With
81 this method, researchers catalogue food resource locations as they are consumed during the process of

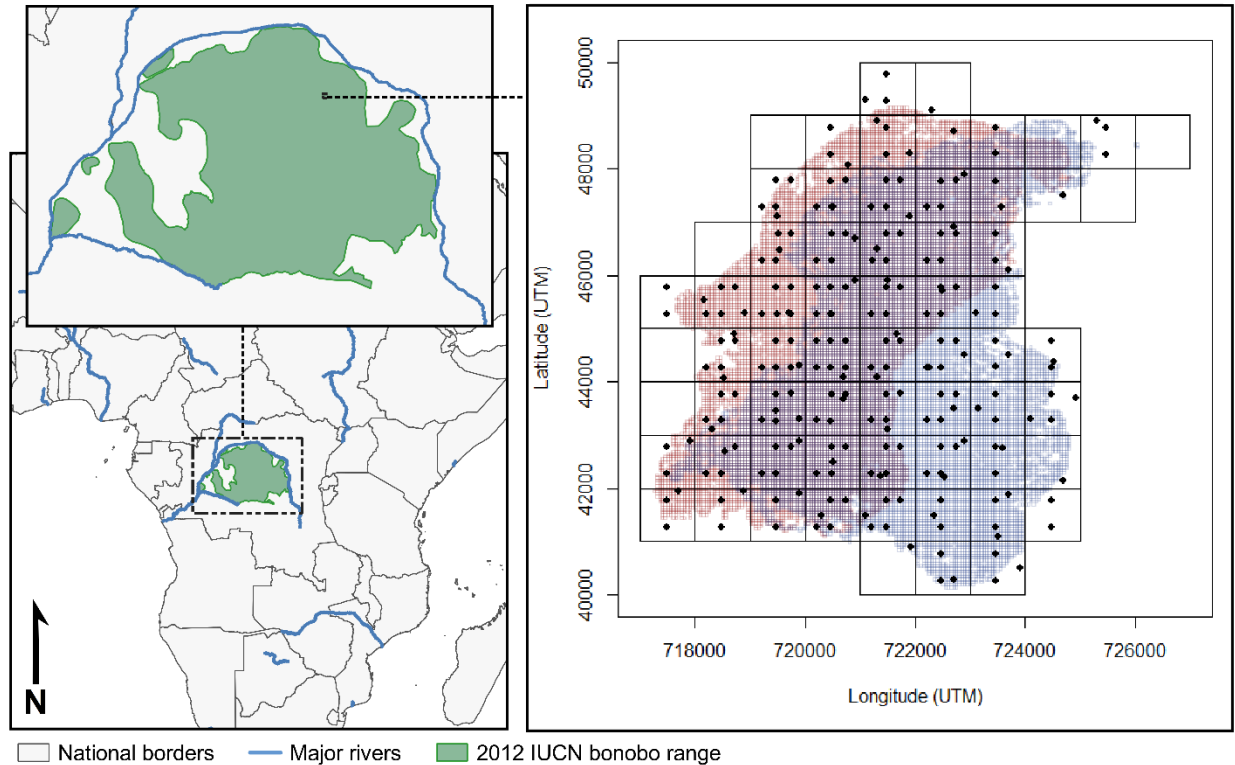
82 behavioral observation. Here, we evaluate the CCM relative to traditional habitat plot data collection using
83 accumulated feeding locations from two social groups of a tropical frugivore, the bonobo (*Pan paniscus*),
84 as a case study. Specifically, we investigated whether behavioral data on feeding locations (trees and
85 lianas) provide a reliable dataset allowing inference about food species' (1) densities, (2) distribution and
86 (3) dispersion. We additionally assess (4) the minimum sampling effort required and (5) for what
87 characteristics of a food species this method can be considered most reliable.

88

89 **2. Methods**

90 **2.1 Study Species and Behavioral Observation**

91 Data were collected at the Kokolopori Bonobo Reserve (Fig. 1) on two social groups of bonobos
92 (Ekalakala: EKK, Kokoalongo: KKL) between May 2016 and December 2019. Groups were followed daily
93 for behavioral data collection, during which we collected group feeding locations using a GPS (Garmin
94 GPSMAP 62), and circumference at breast height (synonymous with and hereafter referred to as DBH) of
95 feeding trees ≥ 20 cm diameter and lianas ≥ 5 cm DBH (SI 2.1, 2.2). Due to GPS measurement error and
96 consequently an inability to distinguish individual trees on a small scale, we summarized feeding tree
97 locations of each group into presence or absence of each species in 50 x 50 m cells. We used location data
98 collected with the GPS tracklog function to calculate the home range of both bonobo groups using kernel
99 density estimates (see SI 2.1). These groups share overlapping areas of their home ranges, including 64%
100 and 66% of the home ranges of EKK and KKL, respectively (Samuni et al. 2020). We evaluated whether
101 feeding location datasets were sufficiently sampled and stable by considering accumulation patterns of data
102 per species over time (SI 2.3).



103 National borders Major rivers 2012 IUCN bonobo range

104 **Fig. 1.** (Left) Location of the study site relative to global bonobo distribution. (Right) 50 x 50m habitat plots
105 (black dots; not to scale) within 1 km² grid cells (black square) overlaid upon all visited 50x50 cells within
106 the 95% home range kernels for Ekalakala (red) and Kokoalongo (blue) bonobo groups.

107

108 2.2 Vegetation plots

109 We conducted vegetation plot sampling by overlaying 1x1 km grid cells over the whole ranging
110 area and aimed to conduct plot sampling in every grid cell utilized by at least one of the groups (Fig. 1; SI
111 1.2). Like the observational cells, all habitat plots were 50 x 50m in size, within which data were collected
112 on all trees meeting the minima defined for observational cells. In total, we sampled 236 plots within these
113 grid cells, of which 214 plots fell within the 95% home range of either group, with 162 and 170 within the
114 95% range of EKK and KKL, respectively (Fig. 1). Plot sampling averaged 4.1 ± 1.6 (SD) plots per km²
115 (range: 1 to 7) and was determined to be of sufficient sampling depth (SI 1.3).

116

117 **2.3 Comparison of datasets**

118 2.3.1 Density

119 To compare estimated species abundances derived from each dataset (CCM or vegetation plots),
120 we derived three different indices. 1) We used the bonobo observational data to create a ‘presence index’
121 based on bonobo feeding locations for each food species, estimated as the number of 50x50m cells in
122 which each species was present divided by the total number of cells within the 95% kernel home range of
123 each group (see Fig. S5 for an example). 2) We calculated species density estimations using the vegetation
124 plot data as the total number of individuals observed per area surveyed (num. individuals / km², hereafter
125 “Plot Density”). 3) We calculated the number of 50x50m plots in which each species was present per total
126 number of plots sampled for more direct comparison with the CCM (hereafter “Plot Presence”).

127 To evaluate method agreement, we created pair-wise sets of comparisons of the three density
128 indices by means of Pearson’s correlation tests and used the correlation coefficient (r) as a measure of
129 strength of agreement between methods. We conducted the pair-wise comparisons while assessing the
130 influence of sampling effort on method agreement by varying levels of home range usage (kernel % range
131 from 20 until 95 % in increments of 1%) and dietary inclusion (top 10 most consumed species until full diet)
132 for each group. We only considered comparisons with at least 10 species in at least 10 vegetation plots.
133 We additionally created a moving window over the kernel home range from 20% to 95% for which to
134 compare methods more directly according to home range location. This window accounts for variation in
135 area coverage by adjusting window radius to impose similarly sized datasets for comparison over the range
136 of % kernel inclusion (i.e., for agreement from home range core to periphery; SI 3.1).

137 Finally, to identify potential dataset minima required for reliable and stable density indices derived
138 from the CCM, we evaluated the pattern of correlation strength between indices from each method as the
139 dataset grew over time (i.e., day of data collection), and set the minimum as the point from which the
140 correlation coefficient remains relatively stable. We describe p -values for these correlations in our
141 summaries below, however as these correlations require independent data and because we evaluated
142 thousands of correlation coefficients per group ($n_{EKK}=15075$ and $n_{KKL}=12834$), we do not draw inference
143 based on p -values but instead focus only upon correlation coefficients.

144

145 2.3.2 Dispersion

146 To evaluate agreement between methods in characterizing food species dispersion, we used
147 Morisita's index (Morisita 1962). To allow for standardized and directly comparable sample units from which
148 to calculate this index for both methods, we aggregated number of individuals per species visited by the
149 bonobos across three different grid cell sizes (500x500m cells, 1000x1000m cells, and 1500x1500m cells),
150 and calculated the average number of individuals for each species in each of these grid cells using the
151 vegetation plot dataset. For both datasets, we then calculated the Morisita's index using the *dispindmorisita*
152 function of the package 'vegan' (Oksanen et al. 2019) for each species. We further accounted for an unusual
153 distribution of Morisita's indices deriving from the vegetation plot dataset by transforming the data to allow
154 for a more normal distribution (SI 3.2).

155

156 2.3.3 Distribution

157 To evaluate the efficacy of the CCM to reliably quantify the distribution of food species in a
158 landscape, we aggregated data by grid cell as in our dispersion comparison. We compiled the abundance
159 data for both bonobo and vegetation plot datasets in two ways: by either i) aggregating (CCM) or averaging
160 (plot dataset) the number of individuals per species per grid cell or ii) by marking the presence/absence of
161 a given species per grid cell size. We chose to average rather than aggregate plot data because greater
162 plot sampling in a grid cell will inherently increase species abundances, whereas sampling biases in CCM
163 could be accounted for by controlling for location within each group's home range (i.e., % kernel home
164 range). We then fitted model sets separately for each cell size and group (six sets of up to 70 species each),
165 using each food species as a dataset and each cell as a datapoint. We used the estimated bonobo feeding
166 data abundance per cell (a measure of distribution) as the response and the plot abundance as the test
167 predictor using zero inflated Poisson models (500x500m grid size) or simple linear models for (1000x1000
168 and 1500x1500m grid sizes). Within these models, to account for variation in home range utilization by the
169 bonobos we controlled for the % kernel home range of each cell by averaging the % kernel value assigned
170 to each of the vegetation plots used to estimate the species abundance within that cell. We then calculated
171 average Nagelkerke's R^2 (500x500m) or r^2 (1000x1000m and 1500x1500m) for each model set across
172 levels of dietary inclusion (see SI 3.3 for detailed descriptions of the fitted models and model checks).

173 To also evaluate agreement between methods on simple presence of a species in a cell, we fitted
174 a generalized linear mixed model with binomial error structure (Baayen 2008) for each grid cell size and
175 each social group. The response in this model was the presence or absence of a species in a given cell as
176 predicted by the bonobo observational data (with one datapoint per species per cell), and presence as
177 measured by vegetation plot and % kernel as test predictors. In these (six total) binomial models we
178 included cell ID and species as random effects and included random slopes for presence/absence in the
179 plots and their correlation within the random effect of species (SI 3.3 for details and model checks). As a
180 last validation of distribution agreement, we identified when bonobos missed the presence of a species in
181 a cell that had been identified in habitat plots and calculated a proportion of missed species occurrences
182 out of all cells per species, as well as evaluated potential sources of biases in likelihood to miss a species
183 in a cell (see 2.4).

184

185 **2.4 Identifying sources of bias**

186 If a consumer is selective in which resources it uses within a landscape, then measurements from
187 vegetation plots may not accurately measure the relevant resources to that consumer. To evaluate these
188 potential discrepancies, we compared food tree and liana sizes (strongly tied to variability in food crop
189 production: Chapman et al. 1992; SI 4) between CCM and vegetation plot data as an example of a potential
190 selective characteristic. We then quantified seven characteristics of each species to evaluate how they
191 contribute to rates of data accumulation and agreement between our sampling methods. Specifically, we
192 considered the lifeform (tree or liana), patterns of dispersion, consumed food item (fruit or non-fruit),
193 seasonality of consumption, density in the landscape, DBH variability, and frequency of consumption (SI
194 4.1) as test predictors in models with the following responses (SI 4.2): (1) the speed at which data
195 accumulate in the CCM dataset (2) a measure of difference between estimates of density between the
196 methods, and (3) likelihood for bonobos to miss the presence of a species in a cell (SI 4.2).

197

198 **2.4 General Analyses**

199 All data analyses were conducted in R (version 4.0.2; R Core Team 2020), and models were fitted
200 using functions of the 'lme4' package (1.1.23; Bates et al. 2015). We report *p*-values between 0.05 and 0.1

201 as a 'trend' for all models to ease issues of dichotomization of significance (Stoehr 1999). To avoid issues
202 of multiple testing when identical models were run across responses which varied only in their summary
203 method (e.g., grid cell size) or dataset (e.g., social group), we describe only patterns which are stable and
204 significant or trending across at least half of each model set; full results for all models as well as further
205 description of all methods and model checks can be found in the SI. We used log transformation to help
206 return predictor (e.g., species density, consumption frequency) and response (all density indices) variables
207 to a roughly normal or symmetric distribution when they were right-skewed.

208

209 **3. Results**

210 **3.1 Consumer Centric Dataset**

211 The bonobo groups visited (i.e., fed in) a total of 12430 (EKK) and 13827 (KKL) 50x50m cells,
212 amounting to an area 'surveyed' of 31.1 (EKK) and 34.6km² (KKL). This amounts to 58.6km² total area
213 surveyed, as 46.7% of this area occurred within the home range overlap of both communities. Bonobos
214 from EKK and KKL fed on a total of 78 tree and liana species (88.6% occurring in the diets of both groups)
215 from trees and lianas, of which 96% of feeding occasions could be identified to a local name. These
216 observations amounted to 8818 (EKK) and 9140 (KKL) unique feeding tree/liana locations (50x50m)
217 consisting of 76 (EKK) and 72 (KKL) species, of which 58 (EKK) and 55 (KKL) species were consumed in
218 at least 10 locations. The diets of both groups were strongly skewed towards a few frequently consumed
219 species (SI 2.4). The groups visited a similar number of locations each day, with a mean of 10.0 ± 5.5 (KKL)
220 and 8.9 ± 5.0 (EKK) locations visited. On average, 4.5 ± 2.0 (KKL) and 4.3 ± 1.8 (EKK) species were
221 consumed per day by the bonobos.

222 Bonobos visited 60% (EKK) and 56% (KKL) of all visited cells within the first year of data collection,
223 with gradual declines in the accumulation of newly visited cells over the 3+ year study period in both groups
224 and a clear approach towards an asymptote for most of the top 30 species (Fig. S2). We found that the
225 speed at which new feeding locations were added to the dataset also decreased across species (i.e., longer
226 accumulation times) with each passing year for both groups, and that much of the observed decrease in
227 new locations visited over time was likely driven by significant gains early within the dataset (Figs. S2, S3;
228 SI 2.3). Data on species more variable in size (DBH) accumulated slower in EKK than species more uniform

229 in size (but no such relationship was found in KKL), and accumulation was also slower in species consumed
230 for their fruits and in more abundant species in the landscape in both groups (SI 4.3, Tables S2 and S3).

231

232 **3.2 Vegetation Plot Dataset**

233 In total, 14855 trees and lianas were measured across 214 habitat plots (SI 1.1), thus exceeding
234 plot surveying minima (124 plots, SI 1.3). Plot surveying required a cumulative total of 146 team days,
235 averaging to 1.7 ± 0.6 (SD) plots completed per team day (range: 1 – 4). Trees comprise the majority
236 (66.9%) of the individuals measured. This dataset averages to 277.7 individual tree and lianas /ha in across
237 the habitat of these two groups, with 196.1 indiv./ha for food species, and 168.2 indiv./ha for potential food
238 trees that meet bonobo size minima (see below) for the EKK and KKL home ranges collectively.

239 Seventy-five of the 200 taxa identified in the plots were consumed by at least one of the two groups,
240 with 67 of 72 (EKK) and 70 of 75 species (KKL) in the diet occurring in the plots. Like the bonobo diet, the
241 forest is heavily biased towards a few species, with one species accounting for over 10% of the dataset
242 ('Bofili', local name for *Scorodophloeus zenkeri*), and the top 10 most common tree species accounting for
243 almost 40% of all trees and lianas (n=6375, 39.2%). Correspondingly, only 16 species account for over
244 50% of the individuals in the plots, of which 11 occur in the diet of both groups. Species in the bonobo diet
245 accounted for 67% of the total number of trees or lianas observed in the Kokolopori landscape.

246

247 **3.3 Dataset comparison**

248 3.3.1 Consumer selectivity of tree sizes

249 Trees visited by bonobos were significantly larger on average than trees measured in the plots
250 (EKK: $t=-17.71$, $p<0.001$; KKL: $t=-20.38$, $p<0.001$), but by only an average of less than 1cm in both groups
251 (Table S1). For 23.1% of consumed species, we found more individuals in the plots that did not reach the
252 minimum size consumed than those who did exceed this minimum threshold. We subsequently restricted
253 all analyses to trees/lianas that met this threshold, consequently reducing the number of individuals
254 included in plot dataset by approximately 18% in both groups (8891 individuals in EKK and 8685 in KKL;
255 SI 4). Reducing the dataset had a measurable effect on the correlation strengths between estimates of
256 density (see below), with an average improvement of 0.04 for comparison (r) of the CCM estimate with the

257 Plot Presence estimates, and 0.07 improvement in correlation coefficient in the comparison of the CCM
258 estimate with Plot Density.

259

260 3.3.2 Density

261 We found that the density estimates from the CCM and vegetation plots were comparable in both
262 groups (Table 1 and Fig. 2). Patterns of correlational strength between the methods stabilized and
263 smoothed from approximately 50% kernel home range inclusion and above, and when approximately a
264 minimum of 15 species was included in the dataset of both groups. Statistical significance of the correlation
265 was reached in both groups when including ca. 20 of the top species or more. Inclusion of less frequently
266 used areas of the home range to the comparison did not appear to considerably affect the strength of
267 agreement between methods but correlation strength decreased with greater number of species included
268 in the comparison (Fig. 2; Table 1). While we did observe that peripheral areas of the home range generally
269 resulted in lower methodological agreement (Fig. S6), bonobo data appeared largely insensitive to inclusion
270 of the outer reaches of the home range in both groups when included alongside more intensively surveyed
271 areas (i.e., the core range).

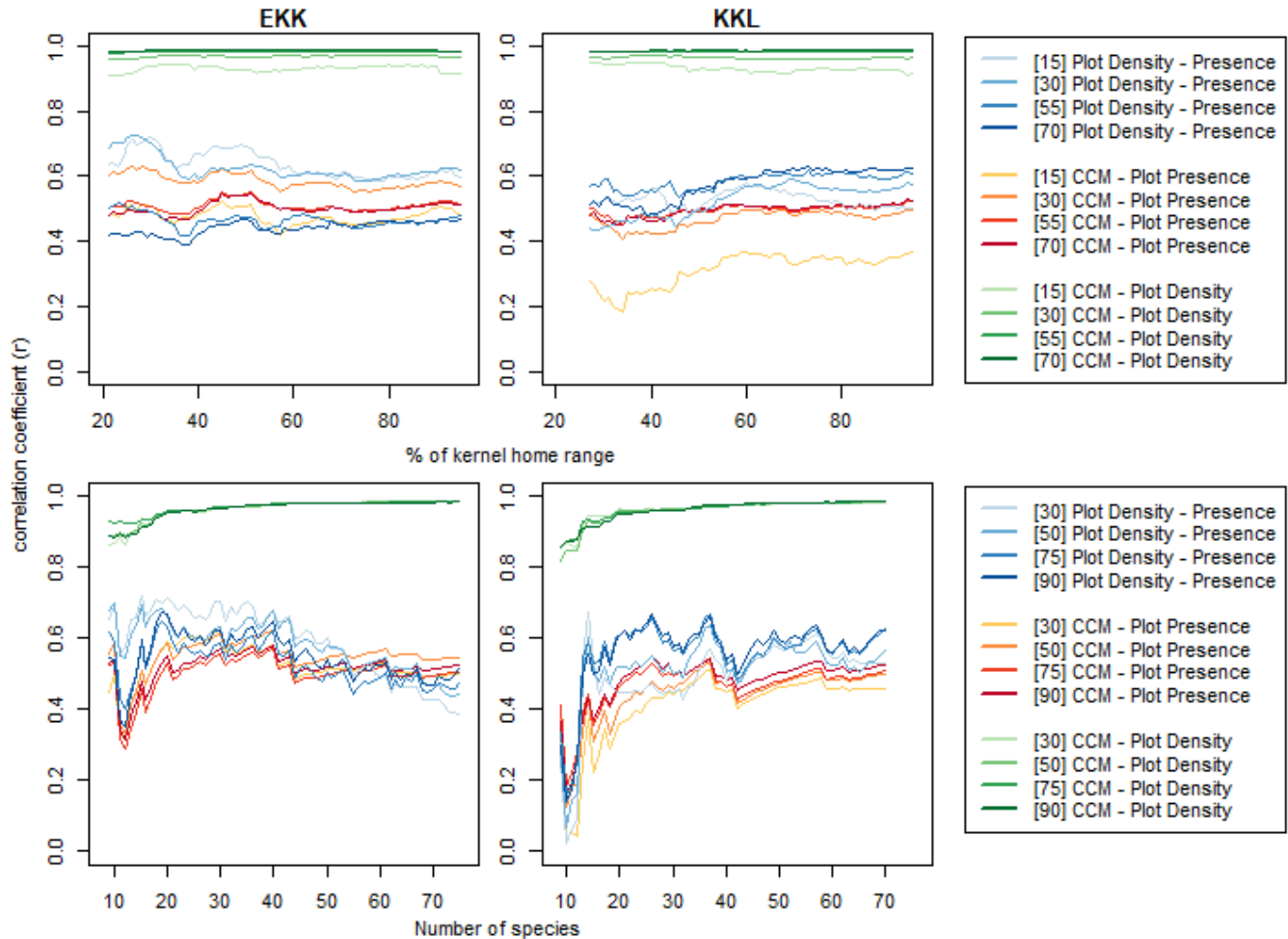
272 Broadly, the CCM more closely matched estimates of Plot Density relative to Plot Presence.
273 However, for both comparisons we observed a decrease in the correlation coefficient the greater the
274 number of species included in the EKK dataset (Fig. 2, blue lines in bottom left panel). For both groups, we
275 found highest agreement between methods when restricting the comparison to the top 36-40 species (i.e.,
276 approximately half of the species in the diet), with one exception that only slightly outcompeted the r of the
277 same range (KKL CCM vs. Plot Density). As expected, comparison between Plot Density and Plot Presence
278 remained consistently high regardless of location within the home range of the bonobo groups, although
279 correlations were lower when fewer species were included.

280 **Table 1.** Summary of correlation coefficients (*r*) between density estimates derived from the CCM and
 281 vegetation plot sampling for all significant comparisons above 50% kernel home range and of at least 10
 282 species.

(a) Kokoalongo	$r_{\text{mean}} \pm \text{SD}$ (all combinations)	r_{range} (all combinations)	Number of species with highest r_{mean} (r_{mean}^*)	Number of species at r_{max}	% kernel with highest r_{mean}^{**}	% kernel at r_{max}
Plot Presence and Plot Density	0.96 ± 0.02	0.82 - 0.99	-	-	-	-
Plot Presence and CCM	0.48 ± 0.04	0.31 - 0.55	36 species (0.53)	10	94 % (0.50)	58
Plot Density and CCM	0.58 ± 0.04	0.46 - 0.69	36 species (0.65)	71	69 % (0.60)	51
(b) Ekalakala	$r_{\text{mean}} \pm \text{SD}$ (all combinations)	r_{range} (all combinations)	Number of species with highest r_{mean} (r_{mean}^*)	Number of species at r_{max}	% kernel with highest r_{mean}^{**}	% kernel at r_{max}
Plot Presence and Plot Density	0.97 ± 0.06	0.88 - 0.99	-	-	-	-
Plot Presence and CCM	0.52 ± 0.02	0.31 - 0.63	40 species (0.58)	48	51 % (0.56)	95
Plot Density and CCM	0.54 ± 0.03	0.42 - 0.70	19 species (0.66)	26	50 % (0.58)	95

283 *averaged across all combinations of % home range inclusion per number of species included

284 **averaged across all combinations of number of species included per % home range inclusion



285

286 **Fig. 2.** Correlation coefficients of density estimates between sampling methods (i.e., CCM and vegetation
287 plots) for EKK (left) and KKL (right), according to home range percentage (top) and dietary inclusion
288 (bottom). Color groups depict the three comparisons in this study (see legend), with numbers in brackets
289 indicating number of species included (top legend) or percent home range included (bottom legend).

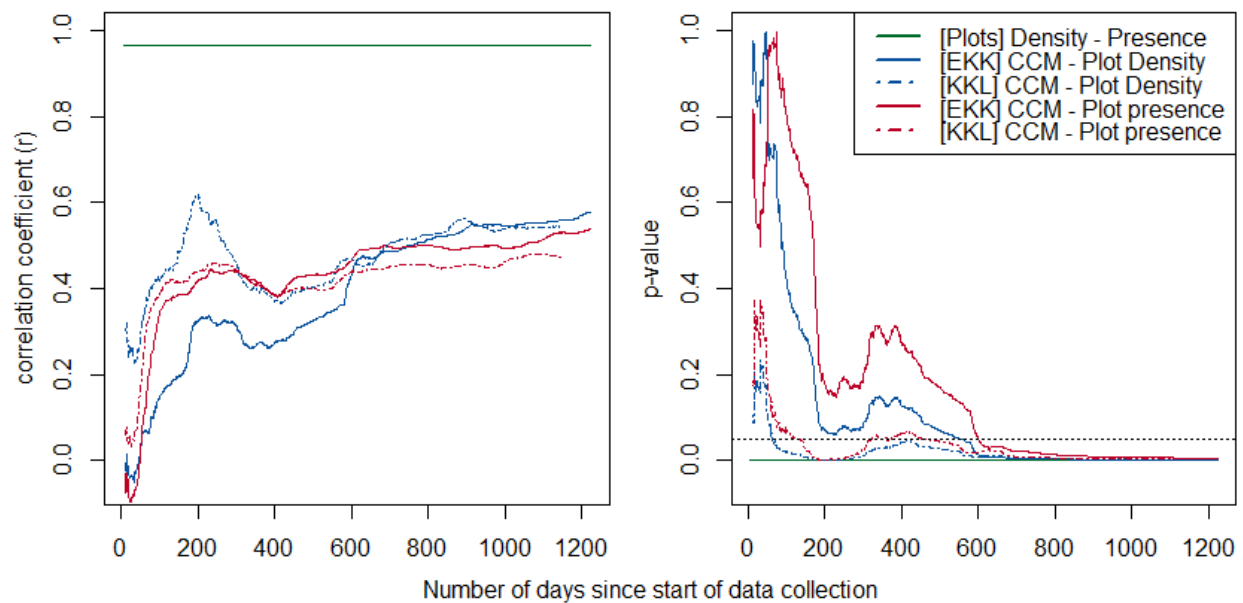
290

291 Once our moving window reached the dataset minimum of 20 plots at ca. 30% kernel, the
292 correlation coefficient of the CCM with plot estimates increased until they reached a maximum around 60%
293 kernel home range in both groups (Fig. S6). Peripheral areas of the home range were generally lower in
294 agreement than more central areas but did not show persistent decreases with increasing peripheralization
295 in a manner that would suggest consistently poorer sampling in peripheral areas. Sampling agreement was

296 strongest within our moving windows for the most frequently consumed species (e.g., 15 or 30 species)
297 relative to more comprehensive subsets of the two groups' diets (e.g., 55 and 70 species).

298 The density of the species in the landscape and the variability in size significantly impacted
299 agreement between the methods (Table S4); specifically, lower species density in the plots (estimate
300 average: 0.57 ± 0.11 [SE]) and lower size variability (-1.29 ± 0.62 [SE]) improved method agreement.
301 Further, in KKL only, greater seasonality, non-fruit item consumption, and greater consumption frequency
302 decreased agreement between methods.

303 Correlation strength between the two methods reached significance and stabilized across methods
304 and groups once exceeding 600 days (i.e., ca. 5300 [KKL] to 6000 [EKK] total visited locations) and
305 continued to improve as data was collected until the end of our data period (Fig. 3; EKK_{max} : 1222 days,
306 KKL_{max} : 1151 days).



307
308 **Fig. 3.** Pearson's r (left) and p -value (right; dashed line indicates 0.05 alpha level) of all three methods
309 comparisons (see legend) for Ekalakala (full line) and Kokoalongo (dashed lines) over the duration of the
310 dataset.

311

312 3.3.3 Dispersion

313 Overall, Morisita's indices from the CCM correlated weakly and non-significantly to vegetation plot
314 indices, regardless of grid cell size used or bonobo group (Table 2a).

315

316 **Table 2.** Average (a) correlation coefficients (*r*) and (b) proportion of variance explained (*r*; 500x500m) or
317 Nagelkerke's *R* (1000x1000m and 1500x1500m) between the CCM and plot datasets across three different
318 grid cell sizes for (a) dispersion and (b) distribution estimates.

(a) Dispersion					
	EKALAKALA		KOKOALONGO		
Cell size	Mean +SD (range)		Mean +SD (range)		
500	0.08 + 0.17 (-0.54, 0.55)		0.00 + 0.16 (-0.35, 0.61)		
1000	0.00 + 0.19 (-0.8, 0.25)		-0.03 + 0.14 (-0.65, 0.13)		
1500	-0.17 + 0.14 (-0.86, 0.07)		-0.20 + 0.14 (-0.83, -0.01)		
(b) Distribution					
	EKALAKALA		KOKOALONGO		
Cell size	Mean ± SD (range)	Num species p<0.05 (% of total species)	Mean ± SD (range)	Num species p<0.05 (% of total species)	Significant species in both groups
500	0.25 ± 0.05 (0.21, 0.38)	15 (29%)	0.23 ± 0.04 (0.20, 0.36)	13 (28%)	11
1000	0.23 ± 0.02 (0.20, 0.30)	13 (19%)	0.24 ± 0.02 (0.20, 0.31)	8 (11%)	7
1500	0.23 ± 0.03 (0.14, 0.27)	8 (12%)	0.24 ± 0.02 (0.21, 0.27)	6 (9%)	3

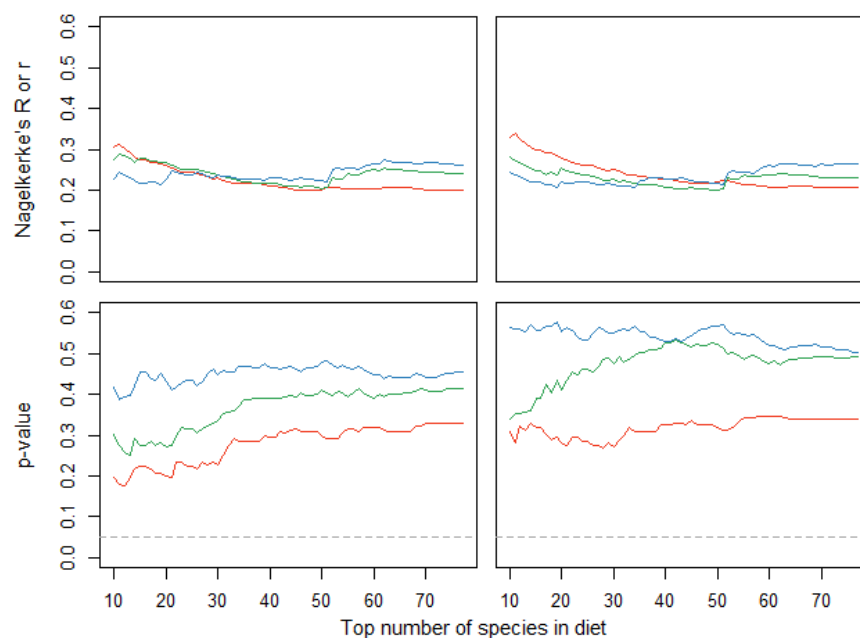
319

320 3.3.4 Distribution

321 Across both bonobo groups and all three grid cell sizes, we found that more species significantly
322 correlated between the two methods for individual abundances across cells than would be expected by
323 chance, with an average of 18% of species significantly correlated between methods across the three cell
324 sizes (Table 2b). Percentage of species with significant correlations across methods declined as grid cell
325 sizes increased, as did the number of significant species which remained consistent across both groups.
326 Generally, proportion variance explained (*r* or Nagelkerke's *R*) by abundance per cell based on plots

327 averaged 0.25 ± 0.32 [SD] across species in all grid cell sizes and groups for predicting abundance per cell
328 based on CCM. Average r did not vary substantially with cell size or between groups (Fig. 5).

329 The presence of a species in a cell as measured by plots significantly predicted the presence of
330 that species in the cell as identified with CCM (estimate: 0.60 ± 0.20 (SD), range: 0.32 – 0.81; Table S5).
331 The location of a cell within the home range appeared to play a consistent role, with food species less likely
332 to be identified by CCM in more peripheral cells (average estimate: -0.05 ± 0.01 (SD), range: -0.05 – -0.04 ;
333 Table S5). Bonobos missed presence of a species on average in $17.5\% \pm 16.3\%$ (SD; range: 0 – 68.4%)
334 of the 500x500m cells and in $18.4\% \pm 16.5\%$ (SD; range: 0 – 61.2%) of the 1000x1000m cells. Increases
335 in species abundance correlated with an increase in the likelihood for bonobos to miss the presence of
336 species in a cell irrespective of cell size or group but species were less likely to be missed in a cell if they
337 were more frequently consumed. We additionally found some support for species consumed for their fruits
338 to be more likely to be missed in smaller cell sizes (Table S6).



339
340 **Fig. 5.** Averaged proportion variance explained (r) or Nagelkerke's R (top) and p -values for the estimate
341 (bottom; dashed line indicates 0.05 alpha level) for correlations between estimated abundances per cell of

342 *species (i.e., distribution agreement) as derived from CCM and vegetation plots for EKK (left) and KKL*
343 *(right) and for three grid cell sizes (red: 500x500m, green: 1000x1000m, blue: 1500x1500m).*

344

345 **4. Discussion**

346 Here we demonstrate the applicability of the consumer-centric method (CCM) for measuring
347 resource density and distribution in an animal's landscape. We demonstrate that food species estimates
348 derived from the CCM method are comparable to estimates derived from traditional vegetation plot
349 sampling following a relatively short data collection timeframe, including before data have reached
350 saturation. The method also seems promising for characterizing distribution of food patches within a
351 landscape. Furthermore, we demonstrated that the CCM has an advantage over traditional sampling
352 methods as it incorporates sampling bias important to the consumer into quantification of the ecological
353 landscape.

354

355 **4.1 Robustness of the CCM**

356 The CCM estimates of abundance showed strong similarity to estimates from traditional ecological
357 sampling. Behavioral ecologists have previously used consumption rates to infer about the abundance of
358 food resources (Hutto 1990; Lovette & Holmes 1995; Watts & Mitani 2015). These methods are particularly
359 susceptible to handling time, consumer motivation, and/or dependence of preference from resource
360 availability and are subsequently difficult to validate (Lovette & Holmes 1995). The key advantage of the
361 CCM is that rather than quantifying availability from occurrences of consumption (frequency dependent) it
362 depends on independent locations (spatially dependent), thereby allowing validation with traditional
363 vegetation plot sampling.

364 Although we found a significant but minor periphery effect on agreement between methods in the
365 presence/absence of species, the correlation of abundance estimates between methods were unaltered by
366 % of home range inclusion. The lack of a spatial effect on agreement between the methods is in some part
367 likely to be a result of home range selection on the part of the consumer (e.g., second-order selection *sensu*
368 Johnson 1980), i.e., bonobos may have already selected their home range based upon resource availability
369 hence no sampling biases therewithin. In absence of home range use biases, the CCM therefore reliably

370 estimates resource availability across the entirety of a group's space use, although future studies should
371 verify absence of sampling biases on agreement between the CCM and traditional methods in their own
372 study species.

373 Further, we found consumption frequency to impact likelihood to miss species presences.
374 Consequently, restricting estimation to only the top half of the consumed species (by frequency) appears
375 to offer a compromise between maintenance of dietary relevance while maximizing fidelity with density
376 estimates as assessed by objective plot measurements. This minimum translated to species consumed in
377 approximately at least 60 locations over our three-year dataset. A general consequence of sampling
378 frequency by a consumer is that estimates improve in precision as data accumulate over time. While
379 species in our dataset were variable in "saturation level", rates of new locations sampled by the bonobos
380 slowed over the course of data collection and inter-method correlation of species abundances stabilized
381 after fewer than two years of data collection (approx. 600 days). As our results indicate that sampling rate
382 affects stability of estimates (e.g., frequency of consumption), we anticipate that this general minimum will
383 be higher for species with slower sampling frequency, i.e., for less frequently consumed species, as well
384 as masting species or species which are consumed aseasonally.

385 Generally, species distribution (i.e., relative abundance) correlated weakly between the methods
386 across species regardless of scale of comparison (i.e., cell size). A greater proportion of species reached
387 significant agreement between methods in smaller rather than larger cell sizes, potentially as a function of
388 proximity, i.e., the larger the cell size used the greater the potential distance between bonobo feeding
389 locations and comparatively small plot areas. Nevertheless, our finding that correlations of distribution within
390 species was significant across a greater proportion of food species than expected by chance (i.e., 5%) and
391 that the rates at which bonobos missed the presence of a species in a cell is likewise better than common
392 rates of species misses between multiple observers in single plot (Millberg et al. 2008) provides hope that
393 reliable estimates of sub-landscape abundances may improve with greater sampling depth.

394 While detectability is rarely 100% in either method (Morrison 2016), the miss rates by a consumer
395 in the CCM may rather carry additional information about the nature of resource selection (and the
396 individuals which are subsequently ignored). This is especially likely to be the case in consumers who have
397 the capacity to keep track of spatiotemporal patterns of resource availability. Bonobos likely have a concept

398 of where and when resources become available, and therefore are also capable of targeting resources that
399 are rare (Janmaat et al. 2013; Normand et al. 2013). Consequently, the CCM mimics *ad hoc* sampling
400 (Foster et al. 1998, Gordon & Newton 2006, Hopkins 2007), and our results indicate that the CCM more
401 closely matches plot density estimates at capturing rare species relative to more abundant species.

402 Nonetheless, in absence of full censusing, we cannot differentiate between which sampling method
403 produced a more precise representation of food species availability, dispersion, and distribution patterns.
404 Ideally, methodological sampling biases could be identified by simulating both sampling schemes from a
405 simulated 'forest'. Unfortunately, we rarely understand the complexity of consumer movement and resource
406 selection patterns (Buskirk & Millspaugh 2006). Therefore, subsequent conclusions drawn from simulated
407 sampling behavior would be just as arbitrary as the decisions made to simulate them (Johnson 1980).

408

409 **4.2 Measuring different phenomena**

410 We argue that the CCM, with adequate evaluation, may be a more appropriate tool for most
411 applications in behavioral ecology than traditional inventory methods. Traditional plot sampling quantifies
412 the total amount of potential resources which also include inaccessible, unattractive, or otherwise
413 unpalatable resources to a consumer. Only a subset of these resources comprises true resource
414 availability, i.e., resources with potential to be selected (Alldredge et al. 1998; Buskirk & Millspaugh 2006;
415 Johnson 1980), and although correlated, each represents inherently two separate phenomena (Hutto
416 1990). Because we rarely understand the processes of food selection by which consumers filters objective
417 resource abundance into availability, the CCM provides the advantage of using the consumer as a means
418 to avoid arbitrary decisions as to how to best sample the landscape (Johnson 1980). We detail examples
419 of this selectivity and the resulting advantages of the CCM below.

420 First, we observed significant differences between average sizes of trees/lianas visited by bonobos
421 relative to what was available in the landscape of consumed species (as measured in vegetation plots).
422 Reducing our plot dataset to sizes selected by the consumer increased the correlations between CCM and
423 vegetation plot measures and demonstrates the inadequacies of consumer-objective plots in mirroring
424 consumer behavior. Second, that bonobos missed or ignored certain food resources in cells identified to
425 contain them underlines further how researchers are likely unaware of relevant selection criteria that impact

426 measurement of true resource availability. Because apes possess mental maps of their environments and
427 are known to adjust travel to target preferred food sources (Janmaat et al. 2013; Lucchesi et al. 2021), they
428 are unlikely to consistently miss potentially important food resources within their home range at the scale
429 observed in our study. Third, we found that CMM estimates of density and distribution differed between
430 bonobo social groups, even with largely overlapping home ranges. This conforms to previous findings of
431 group-specific feeding selection criteria in bonobos (Samuni et al. 2020), independent of local abundance.
432 If resource availability for a consumer in a given landscape is dependent on group identity, then only
433 methods like the CCM incorporating these criteria allow comparable estimates for comparative studies
434 across social groups.

435 Altogether, by accounting for consumer selection, the accumulation of data on food patch location
436 are inherently less subjective than datasets dependent upon arbitrary decisions by the investigator
437 (Johnson 1980). Biases in resource measurement occur via multiple sources including selection of
438 sampling method, metric, effort, as well as through unavoidable systematic or random measurement errors
439 (Baraloto et al. 2013; Milberg et al. 2008; Morrison 2016; Ståhl et al. 2017; Wessling et al. 2020). The CCM,
440 however, accounts for several of these issues because consumers are knowledgeable and motivated
441 surveyors who actively target resources, with apparently negligible impact of scale variation (e.g., cell size)
442 or abundance on fidelity of CCM estimates to plot-derived estimates.

443 Therefore, estimates derived from the CCM provide accurate measures of availability once data
444 have reached a sufficient depth. Our spatially explicit CCM further allows for data accumulation and
445 consequential improvement of the accuracy of estimates over time until otherwise removed due to
446 irrelevance (e.g., patch loss). Nevertheless, if rapid abundance assessment is preferable for a project,
447 traditional ecological sampling may remain a preferable method due to a 600 person-day burn-in time
448 required (this study) by the CCM before estimates become reliably stable per social group relative to 150
449 person days of plots for both groups. However, these 150 person days are supplementary to observational
450 data, insomuch as person-days necessary to collect both sets of data must be considered additive to
451 observational data collection. Yet, if databases of feeding locations are already available, adapting these
452 data to CCM estimation of resource density or distribution save researchers from needing to collect
453 additional data to quantify resource abundance.

454 While this method is best applied to estimate the availability of discrete, immobile, and spatially
455 explicit resources, these advantages transcend application beyond bonobos and allow researchers to
456 evaluate the strengths of the method for their investigations across all potential consumers who meet these
457 criteria (further discussed in Table S7). Functionally, assumptions of the CCM are similar to studies
458 investigating resource preference, a method which also combines objective habitat measures with
459 subjective animal-centric data (Manly et al. 2002). For example, this method can only be applied to
460 consumers which re-use space over time, like a consistent home range, and assumes that consumers have
461 equal access to all the areas of this space (Alldredge et al. 1998). Nonetheless, researchers must verify
462 CCM sampling is of sufficient sampling depth and absent of biases (e.g., sampling biases or characteristics
463 of food items) for their consumer before the CCM can be applied as a means of resource availability. When
464 applied correctly, the CCM will enable many behavioral ecologists to quantify aspects of food availability by
465 using existing data, in a manner that is more suitable to its application as well as allows for more precise
466 comparison ways that make this data comparable across social groups, subsequently promising new
467 insights in the interplay between an animal and its environment.

468

469 **Author contributions**

470 EW, LS conceptualized the manuscript, EW, LS, MS designed the analyses, EW, LS, RM performed the
471 analyses; EW, MAP, SL, BK, MS provided data; EW wrote the manuscript with input from all co-authors.

472

473 **Statement of where you intend to archive your data**

474 All necessary data to reproduce this study will be submitted to the Dryad Digital Repository.

475

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485

486 **References**

- 487 Alldredge, J. R., Thomas, D. L., & McDonald, L. L. (1998). Survey and comparison of methods for study
488 of resource selection. *Journal of Agricultural, Biological, and Environmental Statistics*, 237-253.
489 <https://doi.org/10.2307/1400580>
- 490 Anholt, B. R., & Werner, E. E. (1995). Interaction between food availability and predation mortality
491 mediated by adaptive behavior. *Ecology*, 76(7), 2230-2234. <https://doi.org/10.2307/1941696>
- 492 Baayen, R. H. (2008). *Analyzing Linguistic data: A Practical Introduction to Statistics Using R*. Cambridge:
493 Cambridge University Press. <https://doi.org/10.1017/CBO9780511801686>
- 494 Baraloto, C., Molto, Q., Rabaud, S., Hérault, B., Valencia, R., Blanc, L., Fine, P.V. & Thompson, J. (2013).
495 Rapid simultaneous estimation of aboveground biomass and tree diversity across Neotropical
496 forests: a comparison of field inventory methods. *Biotropica*, 45(3), 288-298.
497 <https://doi.org/10.1111/btp.12006>
- 498 Bates, D. Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4.
499 *Journal of Statistical Software*, 67(1), 1-48. <https://doi.org/10.18637/jss.v067.i01>
- 500 Bowering, R., Wigle, R., Padgett, T., Adams, B., Cote, D., & Wiersma, Y. F. (2018). Searching for rare
501 species: A comparison of Floristic Habitat Sampling and Adaptive Cluster Sampling for detecting
502 and estimating abundance. *Forest Ecology and Management*, 407, 1-8.
503 <https://doi.org/10.1016/j.foreco.2017.10.016>
- 504 Buskirk, S. W., & Millspaugh, J. J. (2006). Metrics for studies of resource selection. *The Journal of Wildlife*
505 *Management*, 70(2), 358-366.
- 506 Chapman, C. A., Chapman, L. J., Wingham, R., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of
507 fruit abundance of tropical trees. *Biotropica*, 527-531. <https://doi.org/10.2307/2389015>
- 508 Chapman, C. A., Schoof, V. A., Bonnell, T. R., Gogarten, J. F., & Calmé, S. (2015). Competing pressures
509 on populations: long-term dynamics of food availability, food quality, disease, stress and animal

- 510 abundance. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1669),
511 20140112. <https://doi.org/10.1098/rstb.2014.0112>
- 512 Davies, S., & Deviche, P. (2014). At the crossroads of physiology and ecology: food supply and the timing
513 of avian reproduction. *Hormones and Behavior*, 66(1), 41-55.
514 <https://doi.org/10.1016/j.yhbeh.2014.04.003>
- 515 Dobson, A. J., and Barnett, A. (2008). *An Introduction to Generalized Linear Models*, 3rd Ed. Boca Raton:
516 CRC Press.
- 517 Foerster, S., Zhong, Y., Pinteá, L., Murray, C. M., Wilson, M. L., Mjungu, D. C., & Pusey, A. E. (2016).
518 Feeding habitat quality and behavioral trade-offs in chimpanzees: A case for species distribution
519 models. *Behavioral Ecology*, 27(4), 1004–1016. <https://doi.org/10.1093/beheco/arw004>
- 520 Forester, J.D., Im, H. K., & Rathouz, P. J. (2009). Accounting for animal movement in estimation of
521 resource selection functions: sampling and data analysis. *Ecology*, 90(12), 3554-3565.
522 <https://doi.org/10.1890/08-0874.1>
- 523 Foster, R.B., Hernandez, N.C., Kakudidi, E.K., & Burnham, R.J. (1998). Rapid assessment of tropical
524 plant communities using variable transects: an informal and practical guide. Field Museum of
525 Chicago.
- 526 Gordon, J.E., & Newton, A.C. (2006). Efficient floristic inventory for the assessment of tropical tree
527 diversity: A comparative test of four alternative approaches. *Forest Ecology and Management*,
528 237(1-3), 564-573. <https://doi.org/10.1016/j.foreco.2006.10.002>
- 529 Hopkins, M.J.G. (2007). Modelling the known and unknown plant biodiversity of the Amazon Basin. *J.*
530 *Biogeogr.* 34: 1400–1411. <https://doi.org/10.1111/j.1365-2699.2007.01737.x>
- 531 Hutto, R. L. (1990). Measuring the availability of food resources. *Studies in Avian Biology*, 13, 20-28.
- 532 Janmaat, K. R., Ban, S. D., & Boesch, C. (2013). Chimpanzees use long-term spatial memory to monitor
533 large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, 86(6),
534 1183-1205. <https://doi.org/10.1016/j.anbehav.2013.09.021>
- 535 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.
536 B., Gavin, X., Simpson, L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H.
537 (2019). *vegan: Community Ecology Package*. R package version 2.5-6.

- 538 Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource
539 preference. *Ecology*, 61(1), 65-71. <https://doi.org/10.2307/1937156>
- 540 Krebs, C. (1999). *Ecological methodology* (2nd ed., pp. 114–115). Menlo Park: Addison-Wesley.
- 541 Lambert, J. E., & Rothman, J. M. (2015). Fallback foods, optimal diets, and nutritional targets: primate
542 responses to varying food availability and quality. *Annual Review of Anthropology*, 44, 493-512.
543 <https://doi.org/10.1146/annurev-anthro-102313-025928>
- 544 Lovette, I. J., & Holmes, R. T. (1995). Foraging behavior of American Redstarts in breeding and wintering
545 habitats: implications for relative food availability. *The Condor*, 97(3), 782-791.
546 <https://doi.org/10.2307/1369186>
- 547 Lucchesi, S. Cheng, L., Wessling, E.G., Kambale, B., Lokasola, A.L., Ortmann, S., & Surbeck, M. 2021.
548 Importance of subterranean fungi in the diet of bonobos in Kokolopori. *American Journal of*
549 *Primatology*, e23308. <https://doi.org/10.1002/ajp.23308>
- 550 Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007). Resource
551 selection by animals: statistical design and analysis for field studies. Springer Science & Business
552 Media.
- 553 Milberg, P., Bergstedt, J., Fridman, J., Odell, G., & Westerberg, L. (2008). Observer bias and random
554 variation in vegetation monitoring data. *Journal of Vegetation Science*, 19(5), 633-644.
555 <https://doi.org/10.3170/2008-8-18423>
- 556 Morisita, M. (1962). I σ -Index, a measure of dispersion of individuals. *Researches on Population*
557 *Ecology*, 4(1), 1-7.
- 558 Morrison, L.W. (2016) Observer error in vegetation surveys: a review. *Journal of Plant Ecology*, 9, 367–
559 379. <https://doi.org/10.1093/jpe/rtv077>
- 560 Mortelliti, A., Amori, G. & Boitani, L. (2010) The role of habitat quality in fragmented landscapes: a
561 conceptual overview and prospectus for future research. *Oecologia*, 163, 535–547
- 562 Myers, J. H. (1978). Selecting a measure of dispersion. *Environmental Entomology*, 7(5), 619-621.
563 <https://doi.org/10.1093/ee/7.5.619>
- 564 Normand, E., Ban, S. D., & Boesch, C. (2009). Forest chimpanzees (*Pan troglodytes verus*) remember
565 the location of numerous fruit trees. *Animal Cognition*, 12(6), 797-807.

- 566 R Core Team (2020). R: A language and environment for statistical computing. R Foundation for
567 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 568 Rogers, L. L. (1987). Effects of food supply and kinship on social behavior, movements, and population
569 growth of black bears in northeastern Minnesota. *Wildlife Monographs*, 3-72.
- 570 Samuni, L., Wegdell, F., & Surbeck, M. (2020). Behavioural diversity of bonobo prey preference as a
571 potential cultural trait. *eLife*, 9, e59191. <https://doi.org/10.7554/eLife.59191>
- 572 Ståhl, G., Ekström, M., Dahlgren, J., Esseen, P. A., Grafström, A., & Jonsson, B. G. (2017). Informative
573 plot sizes in presence-absence sampling of forest floor vegetation. *Methods in Ecology and*
574 *Evolution*, 8(10), 1284-1291. <https://doi.org/10.1111/2041-210X.12749>
- 575 Stephens, D., & Krebs, J. (1986). Foraging theory. Princeton University Press.
- 576 Stoehr, A. M. (1999). Are significance thresholds appropriate for the study of animal behaviour? *Animal*
577 *Behaviour*, 57(5), F22–F25. <https://doi.org/10.1006/anbe.1998.1016>
- 578 Szigeti, V., Körösi, Á., Harnos, A., Nagy, J., & Kis, J. (2016). Measuring floral resource availability for
579 insect pollinators in temperate grasslands—a review. *Ecological Entomology*, 41(3), 231-240.
580 <https://doi.org/10.1111/een.12298>
- 581 van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: adaptive
582 significance and consequences for primary consumers. *Annual Review of Ecology and*
583 *Systematics*, 24(1), 353-377. <https://doi.org/10.1146/annurev.es.24.110193.002033>
- 584 Vogel, E. R., & Janson, C. H. (2007). Predicting the frequency of food-related agonism in white-faced
585 capuchin monkeys (*Cebus capucinus*), using a novel focal-tree method. *American Journal of*
586 *Primatology*, 69(5), 533-550. <https://doi.org/10.1002/ajp.20368>
- 587 Vogel, E. R., & Janson, C. H. (2011). Quantifying primate food distribution and abundance for
588 socioecological studies: an objective consumer-centered method. *International Journal of*
589 *Primatology*, 32(3), 737-754. <https://doi.org/10.1007/s10764-011-9498-7>
- 590 Watts, D. P., & Mitani, J. C. (2015). Hunting and prey switching by chimpanzees (*Pan troglodytes*
591 *schweinfurthii*) at Ngogo. *International Journal of Primatology*, 36(4), 728-748.
592 <https://doi.org/10.1007/s10764-015-9851-3>

593 Wessling, E. G., Dieguez, P., Llana, M., Pacheco, L., Pruetz, J. D., & Kühl, H. S. (2020). Chimpanzee
594 (*Pan troglodytes verus*) density and environmental gradients at their biogeographical range edge.
595 *International Journal of Primatology*, 41(6), 822-848. [https://doi.org/10.1007%2Fs10764-020-](https://doi.org/10.1007%2Fs10764-020-00182-3)
596 [00182-3](https://doi.org/10.1007%2Fs10764-020-00182-3)