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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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

Abstract

1. Characteristics of food availability and distribution are a key component of a species ecology. Objective measurement of food resources, such as vegetation plot sampling, do not consider aspects of selection by the consumer and therefore may produce imprecise measures of availability. Further, in most animal ecology research, traditional ecological surveying often is time-intensive and supplementary to ongoing behavioral observation. We propose a method to integrate ecological sampling of an animal's environment into existing behavioral data collection systems by using the consumer as the surveyor. Here, we introduce the consumer-centric method (CCM) of assessing resource availability for its ability to measure food resource abundance, distribution, and dispersion. This method catalogues feeding locations observed during behavioral observation and uses aggregated data to characterize these ecological metrics.

2. We evaluated the CCM relative to traditional vegetation plot surveying using accumulated feeding locations across three years visited by a tropical frugivore, the bonobo (*Pan paniscus*), and compared it with data derived from over 200 vegetation plots across their 50km^2+ home range.

3. We demonstrate that food species abundance estimates derived from the CCM are comparable to those derived from traditional vegetation plot sampling after approximately 600 observation days or 60 spatially explicit feeding locations. The agreement between the methods further improved when accounting for aspects of consumer selectivity in objective vegetation plot sampling (e.g., size minima). Estimates of density from CCM correlated with plot-derived estimates and were relatively insensitive to home range inclusion and other species characteristics, but were sensitive to sampling frequency (e.g., consumption frequency). Agreement between the methods in relative distribution of resources performed better across species than expected by chance, although measures of dispersion correlated poorly.

4. We demonstrate that while providing a robust measure to quantify local food availability, the CCM has an advantage over traditional sampling methods as it incorporates sampling biases relevant to the 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 $\geq$20cm diameter and lianas $\geq$5cm 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).
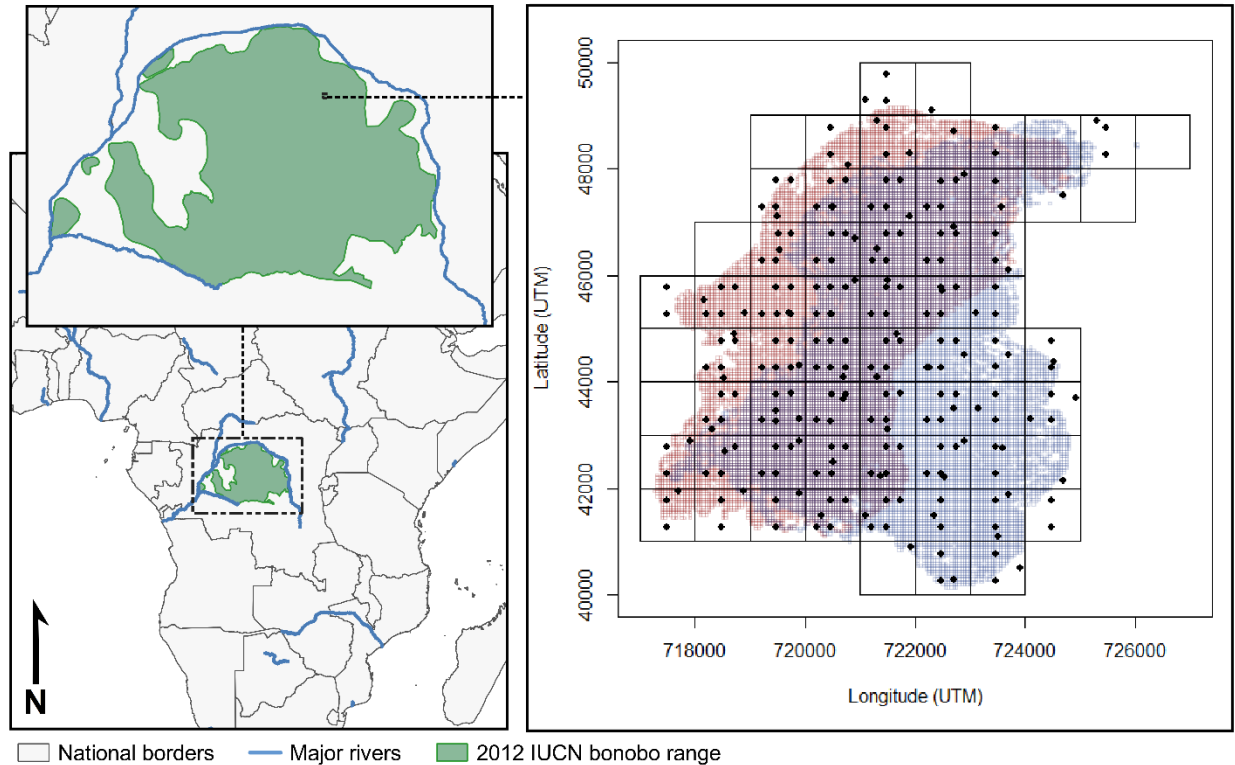
Fig. 1. (Left) Location of the study site relative to global bonobo distribution. (Right) 50 x 50m habitat plots (black dots; not to scale) within 1 km^2 grid cells (black square) overlaid upon all visited 50x50 cells within the 95% home range kernels for Ekalakala (red) and Kokoalongo (blue) bonobo groups.

2.2 Vegetation plots

We conducted vegetation plot sampling by overlaying 1x1 km grid cells over the whole ranging area and aimed to conduct plot sampling in every grid cell utilized by at least one of the groups (Fig. 1; SI 1.2). Like the observational cells, all habitat plots were 50 x 50m in size, within which data were collected on all trees meeting the minima defined for observational cells. In total, we sampled 236 plots within these grid cells, of which 214 plots fell within the 95% home range of either group, with 162 and 170 within the 95% range of EKK and KKL, respectively (Fig. 1). Plot sampling averaged 4.1 ± 1.6 (SD) plots per km^2 (range: 1 to 7) and was determined to be of sufficient sampling depth (SI 1.3).

2.3 Comparison of datasets

2.3.1 Density

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

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

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

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 Morisitia'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 34.6km^2 (KKL). This amounts to 58.6km^2 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_{mean} ±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_{mean} ±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
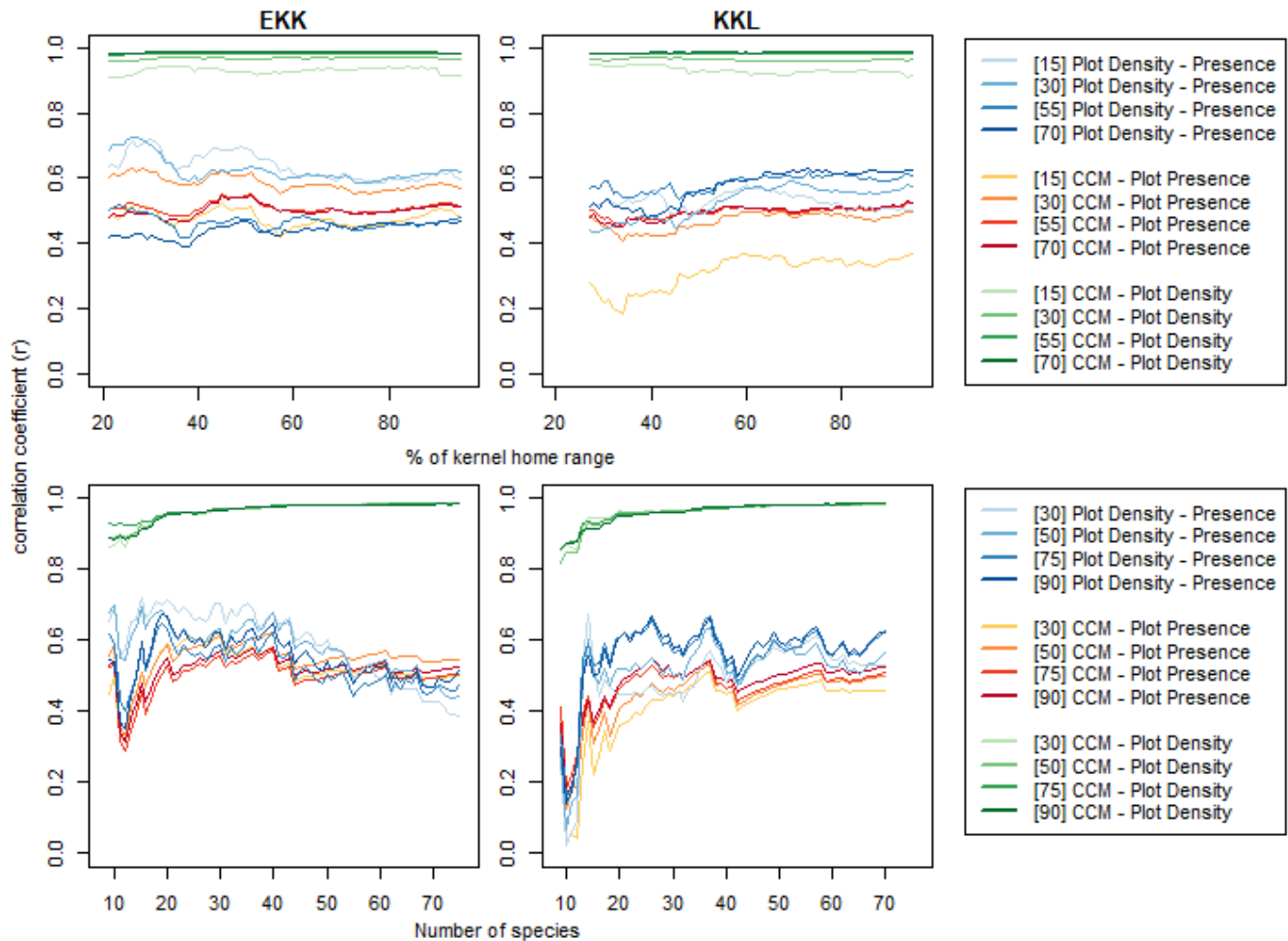
Fig. 2. *Correlation coefficients of density estimates between sampling methods (i.e., CCM and vegetation plots) for EKK (left) and KKL (right), according to home range percentage (top) and dietary inclusion (bottom). Color groups depict the three comparisons in this study (see legend), with numbers in brackets indicating number of species included (top legend) or percent home range included (bottom legend).*

Once our moving window reached the dataset minimum of 20 plots at ca. 30% kernel, the correlation coefficient of the CCM with plot estimates increased until they reached a maximum around 60% kernel home range in both groups (Fig. S6). Peripheral areas of the home range were generally lower in agreement than more central areas but did not show persistent decreases with increasing peripheralization 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).
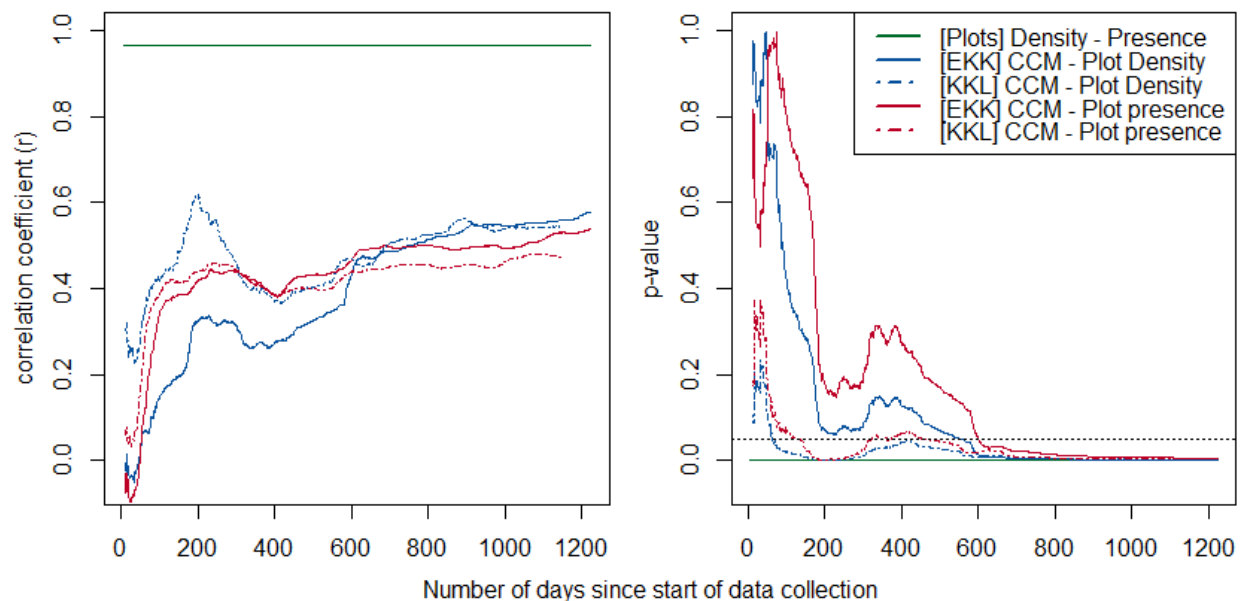
307

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% ± 16.3% (SD; range: 0 – 68.4%)

334   of the 500x500m cells and in 18.4% ± 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).
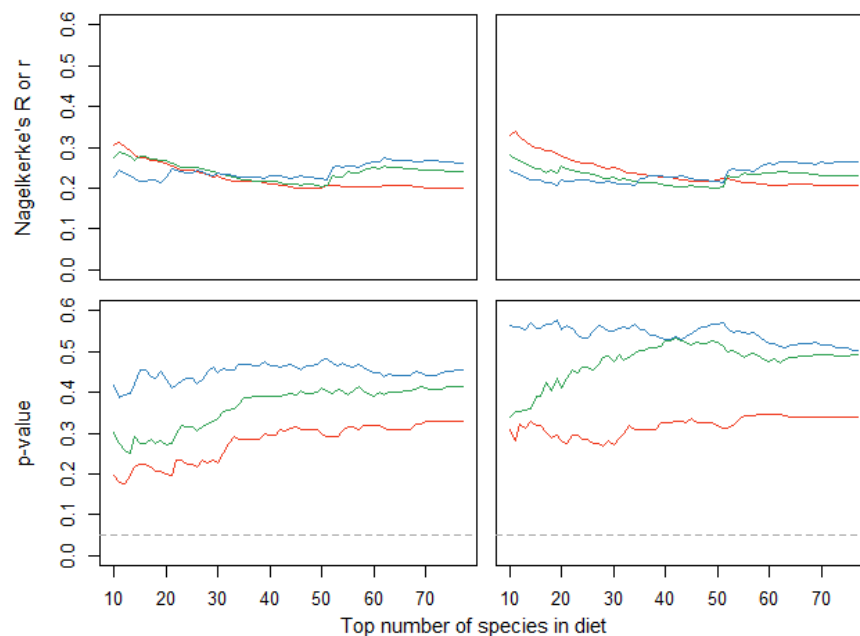
339

340   **Fig. 5.** *Averaged proportion variance explained (r) or Nagelkerne'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   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

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