

# 1 **Behavioural diversity of bonobo prey preference as a potential cultural trait**

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7

## 8 **Abstract**

9 The importance of cultural processes to behavioural diversity, especially in our closest living  
10 relatives, is central for revealing the evolutionary origins of human culture. Whereas potential  
11 cultural traits are extensively investigated in chimpanzees, our other closest living relative, the  
12 bonobo, is often overlooked as a candidate model. Further, a prominent critique to many  
13 examples of proposed animal cultures is premature exclusions of environmental confounds  
14 known to shape behavioural phenotypes. We addressed these gaps by investigating variation  
15 in prey preference expression between neighbouring bonobo groups that associate and share  
16 largely overlapping home ranges. We find specific group preference for duiker or anomalure  
17 hunting that are otherwise unexplained by variation in spatial usage of hunt locations,  
18 seasonality or sizes of hunting parties. Our findings demonstrate that group-specific  
19 behaviours emerge independently of the local ecology, indicating that hunting techniques in  
20 bonobos may be culturally transmitted. We suggest that the tolerant intergroup relations of  
21 bonobos offer an ideal context to explore drivers of behavioural phenotypes, the essential  
22 investigations for phylogenetic constructs of the evolutionary origins of culture.

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## 25 **Introduction**

26 Humans and other social animals exhibit a diversity of behavioural phenotypes attributed to  
27 genetic and/or social (i.e., culture) evolutionary processes influenced by the environment  
28 (Castro and Toro, 2004; Van Schaik et al., 2003; Whiten, 2017). While culture is identified as  
29 a pivotal selective process in human evolution (Boyd and Richerson, 1995; Castro and Toro,  
30 2004; Creanza et al., 2017), its relative contribution to shaping the behavioural diversity  
31 observed in non-human animals, including our closest living relatives, remains debated. For  
32 instance, in comparison to the other great ape species, little is known about potential cultural  
33 traits in bonobos (*Pan paniscus*) (Whiten, 2017), thereby limiting phylogenetic comparisons.

34 Culture is defined as group-specific behavioural patterns acquired through some form of  
35 social learning (Laland and Janik, 2006). There is ample evidence that some foraging  
36 techniques are socially learned (e.g., primates (Whiten and van de Waal, 2018); cetaceans  
37 (Mann et al., 2012); carnivores (Thornton and Raihani, 2008)) and therefore represent good  
38 candidates for cultural traits. However, to distinguish whether social processes contribute to  
39 the emergence of behavioural phenotypes, it is essential to quantify ecological variation and  
40 account for its influence on behaviour expression, a challenging endeavour in wild settings.

41 Our closest living relatives, bonobos and chimpanzees, hunt a variety of species across groups  
42 and populations (Gilby et al., 2015; Hobaiter et al., 2017; Hohmann and Fruth, 2008;  
43 Sakamaki et al., 2016; Samuni et al., 2018; Wakefield et al., 2019). However, it remains  
44 unclear whether this diversity is independent of large or even small-scale ecological variation  
45 in the distribution of prey species (Hobaiter et al., 2017; Sakamaki et al., 2016). Accounting  
46 for potential local ecological drivers is methodologically challenging in chimpanzees, a  
47 territorial species where each group predominantly occupies unique non-overlapping areas  
48 (Mitani et al., 2010; Samuni et al., 2017). In contrast, the tolerant intergroup relations of  
49 bonobos (Furuichi, 2020; Lucchesi et al., 2020) permit a context in which different  
50 behaviours are expressed by individuals of different groups in the same place and at the same  
51 time. Here, we investigate variation in bonobo predation patterns of two groups (Ekalakala  
52 and Kokoalongo) at the Kokolopori Bonobo Reserve. The groups share an extensive home  
53 range overlap (65% kernel and 80% maximum convex polygon overlaps; Fig. 1) and regular  
54 gene flow, thereby reducing ecological and genetic influences as an explanatory variable for  
55 inter-group differences in behavioural expressions. Specifically, we tested whether variation  
56 in prey preference between the two bonobo groups is explained by a) environmental variables,  
57 such as area usage and seasonality, and/or b) social factors, such as the number of hunters and  
58 group identity.

## 59 **Methods**

60 **(a) Study site and data collection.** We investigated behavioural diversity between two fully  
61 habituated bonobo groups (Ekalakala and Kokoalongo, habituated since 2007) at the  
62 Kokolopori Bonobo Reserve, Democratic Republic of Congo (N 0.41716°, E  
63 22.97552°; (Surbeck et al., 2017)). We conducted full day party follows of the bonobo groups  
64 (1102 and 931 observation days in Ekalakala and Kokoalongo, respectively) and  
65 documented all occurrence hunting behaviour (here defined as capture of mammalian prey).  
66 All prey types were captured across most months, and both during the dry (June-August and  
67 December-February) and wet (March-May and September-November) seasons. Hunt  
68 participants were almost exclusively adult (>10 yrs) individuals, and both sexes were  
69 observed to participate. Adult group sizes fluctuated during the study between 9-11 adult  
70 individuals in Ekalakala and 16-24 adult individuals in Kokoalongo due to several deaths and  
71 migration events.

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73 **(b) Home range utilization distribution.** We recorded data on party locations at one-minute  
74 intervals using a GPS (Garmin© 62). We constructed home range utilization distributions of  
75 the bonobo groups using kernel density estimates (Worton, 1989). The home range (95%  
76 kernel) of the two groups between August 2016 and December 2019 was: Ekalakala – 35km<sup>2</sup>,  
77 Kokoalongo – 40km<sup>2</sup>, and the overlapping area encompassed 64% and 66% of the home ranges  
78 of Ekalakala and Kokoalongo, respectively.

79 Habitat structure and spatial distribution of prey species has been used as explanations for  
80 variation in hunting behaviours (Hobaiter et al., 2017; Sakamaki et al., 2016). However, as  
81 our data originate from two groups with extensive home range overlap, the explanatory power  
82 of these drivers is minimized. Nonetheless, we can evaluate intra-range variation in local  
83 ecology by accounting for relative home range usage across the groups. To do so, we assigned  
84 each hunt with two kernel usage values, one constituting the kernel usage of the group that  
85 hunted (*hunt group*) and the other constituting the kernel usage of the group that did not hunt  
86 (*other group*). We used the values to calculate a score of ‘usage difference’ (i.e., *other group* -  
87 *hunt group*; ranging between -50 and 86; mean ± sd: 20.19 ± 26.10). Higher scores reflected  
88 an area that is more predominantly used by the group that hunted.

89  
90 **(c) Statistical analysis.** We applied a Bayesian Regression model with prey type as a  
91 categorical response and logit link function to examine the influence of environmental (area  
92 usage and seasonality) and social (group identity and presence of potential hunters) factors on  
93 prey preference expression. We fitted the model in R (version 3.6.1 (R Core Team, 2016))  
94 using the function *brm* of the R package ‘brms’ (Bürkner, 2017) and the default flat priors. As  
95 predictors, we included the following environmental factors: a) ‘usage difference’ score as  
96 described above, and b) a seasonal temporal term, by including the sine and cosine of the  
97 Julian dates of the hunts converted into a circular variable (Stolwijk et al., 1999).

98 Additionally, we included the following social factors: a) group identity and b) adult party  
99 size recorded at 30-minute intervals. We did not differentiate between the number of adult  
100 males versus adult female party members as we do not expect it to have a difference on prey  
101 acquisition (both were regular hunt participants in our study).

102 We ran 2,000 iterations over four MCMC chains, with a ‘warm-up’ period of 1,000 iterations  
103 per chain leading to 4,000 usable posterior samples (Bürkner, 2017). Visual inspection of all  
104 MCMC results revealed satisfactory Rhat values (< 1.01; (Gelman et al., 2013)), no divergent

105 transitions after warmup, and stationarity and convergence to a common target, suggesting  
106 that our results are stable. We report the estimate (mean of the posterior distribution) and the  
107 95% credible intervals (CI<sub>95%</sub>) indicating the strength of the effects. For estimate  
108 comparability and to ease model convergence, we z-transformed ‘usage difference’ and party  
109 size before fitting the models. The data reported in this paper are available as a supplementary  
110 dataset.

## 111 **Results**

112 Between August 2016 and January 2020 we observed 59 successful captures and consumption  
113 of mammals by the bonobos, including anomalure, duiker, and squirrel species (Table 1).  
114 During a six months period (Jul-Dec 2019) we also documented 11 unsuccessful hunt  
115 attempts on duiker and anomalure in both groups (duiker-  $N_{\text{Ekalakala}} = 2$ ,  $N_{\text{Kokoalongo}} = 2$ ;  
116 anomalure-  $N_{\text{Ekalakala}} = 4$ ,  $N_{\text{Kokoalongo}} = 3$ ). Overall, we observed all Ekalakala and 84% of  
117 Kokoalongo adult group members (100% if considering only individuals that were present for  
118 the entire study period) participating in hunts.

119 **Table 1.** Successful hunts in Ekalakala and Kokoalongo between August 2016- Jan 2020

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### **A. occurrence of successful hunts**

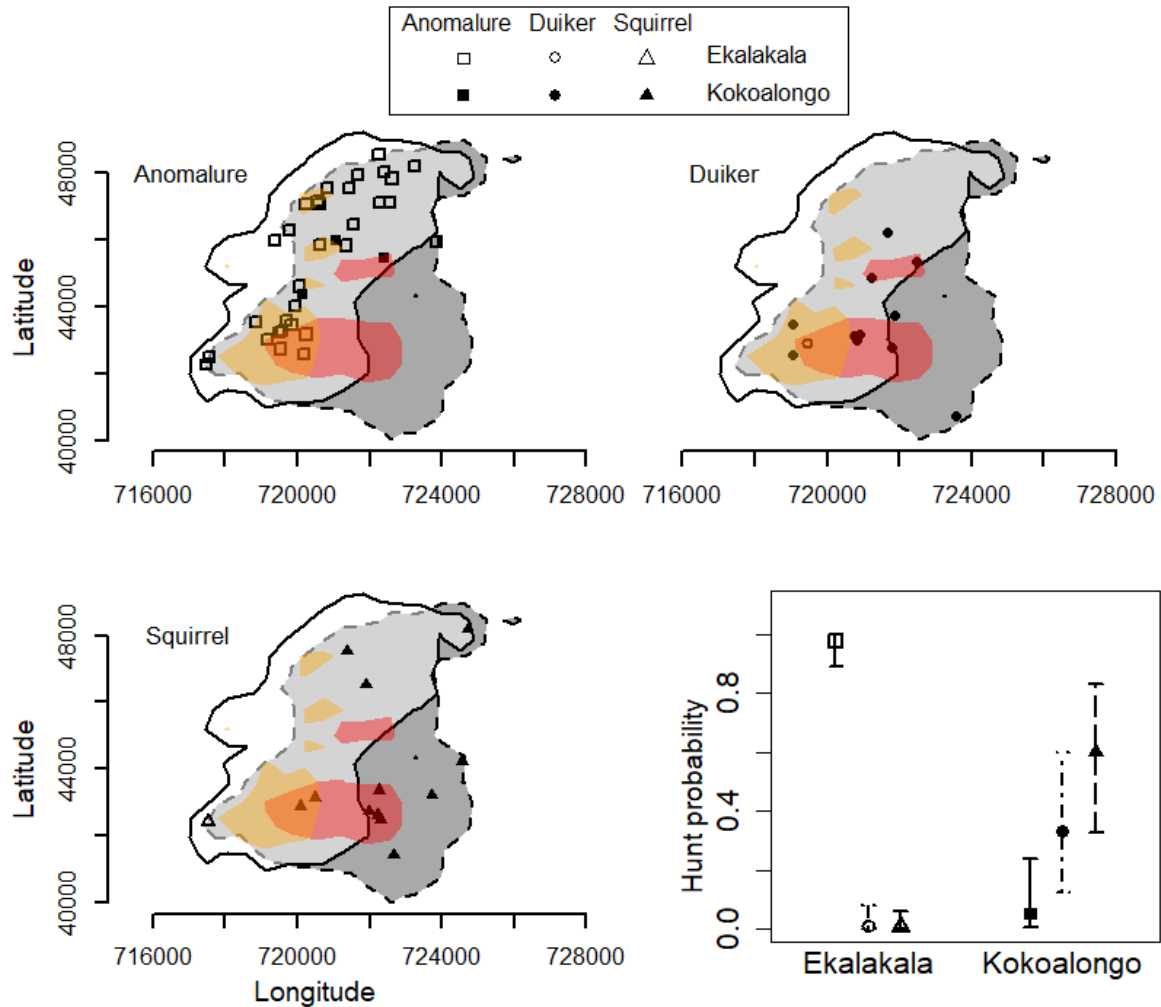
Group	Duiker species ( <i>Philantomba monticola</i> , <i>Cephalophus castaneus</i> )	Squirrel species ( <i>Funisciurus congicus</i> )	Anomalure species ( <i>Anomalurus derbianus</i> , <i>Anomalurus beecrofti</i> )
Ekalakala	1	1	31
Kokoalongo	11	12	3

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123 Group home ranges extensively overlapped and most anomalure and duiker hunts occurred  
124 within the overlapping areas (94% of anomalure and 83% of duiker hunts), as opposed to 46%  
125 of squirrel hunts (Fig. 1). The groups engaged in frequent and prolonged intergroup  
126 associations (31% of observation days), and nine of the hunts (5 duiker, 3 anomalure, 1  
127 squirrel) occurred during intergroup encounters and involved between-group meat sharing.  
128 Due to the cohesiveness of bonobo groups (Hohmann and Fruth, 2002), the conspicuous  
129 nature of anomalure and duiker hunting (e.g., distress calls of duikers), and since the  
130 acquisition of meat often attracts individuals to hunting areas (Samuni et al., 2018), we are  
131 confident that we observed most anomalure and duiker feeding events. However, as the  
132 hunting and feeding of squirrel is often quiet and solitary, we may have underestimated this  
133 type of hunting.

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**Figure 1.** Predation patterns in Kokolopori bonobos. Hunting locations of the three prey types: anomalure (square; top left), duiker (circle; top right), and squirrel (triangle; bottom left) in relation to the 95% Kernel usage area of Ekalakala (white polygon with solid border) and Kokoalongo (dark grey polygon with dashed border) and 50% Kernel usage area (Ekalakala in yellow, Kokoalongo in red). The overlapping 95% kernel area between Ekalakala and Kokoalongo is depicted in light grey. Also depicted are hunt probabilities of the different prey types between Ekalakala and Kokoalongo (bottom right) as obtained from the BR model.

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Kokoalongo bonobos were more likely to capture duiker (estimate = 7.09,  $CI_{95\%} = [3.71, 12.00]$ ; Fig. 1, Table 2) and squirrel species (estimate = 7.49,  $CI_{95\%} = [4.14, 12.17]$ ), and were less likely to capture anomalure species in comparison with Ekalakala. The same pattern persisted during intergroup encounters (once we observed anomalure captured by a Kokoalongo female after a hunt by Ekalakala individuals). We found that group-specific prey preferences were independent from potential local spatial and temporal ecological variation. Overall, more than 80% of all hunts occurred in overlapping areas (95% kernel), and neither utilization differences of specific hunt locations (reflecting varying opportunities to encounter

153 prey species) nor potential annual seasonal variation strongly affected phenotypic variation in  
 154 prey types captured (Table 2). Variation in prey preference can also arise from between-group  
 155 difference in sizes of association parties, or presence of certain specialized hunters. However,  
 156 the number of adult individuals present during hunts (i.e., available hunters; mean  $\pm$  sd:  
 157 Ekalakala -  $7.9 \pm 1.6$ ; Kokoalongo -  $8 \pm 4.3$ ; encounter -  $14.5 \pm 7.4$ ) had no strong effect on  
 158 prey outcome (Table 2). Further, we observed 16 different individuals (four males and 12  
 159 females) catching prey, encompassing 72% of Ekalakala and 40% of Kokoalongo group  
 160 members. These percentages are likely an underestimation of the overall number of  
 161 individuals who captured the prey, as their identity was recorded for less than half of all  
 162 hunts. Finally, our results are likely independent from genetic variation, as low genetic  
 163 differentiation is expected (Schubert et al., 2011) mainly due to regular gene flow attributed to  
 164 female migration between Ekalakala and Kokoalongo.

165  
 166 **Table 2.** Bayesian Regression model results of the effect of group identity, number of  
 167 available hunters and ecological variation on prey species captured (<sup>1</sup>anomalure and  
 168 <sup>2</sup>Ekalakala as reference categories).  
 169

Coded level		Estimate	SE	95% CI
Duiker <sup>1</sup>	Intercept	-4.49	1.48	-7.91, -2.26
	<b>Group (Kokoalongo<sup>2</sup>)</b>	<b>7.09</b>	<b>2.13</b>	<b>3.71, 12.00</b>
	Available hunters	0.72	0.57	-0.34, 1.95
	Usage difference	0.59	0.65	-0.59, 1.96
	Sine of Date	1.33	1.06	-0.55, 3.59
	Cosine of Date	0.45	1.15	-1.69, 2.82
Squirrel <sup>1</sup>	Intercept	-4.58	1.39	-7.76, -2.45
	<b>Group (Kokoalongo<sup>2</sup>)</b>	<b>7.49</b>	<b>2.07</b>	<b>4.14, 12.17</b>
	Available hunters	-0.07	0.63	-1.27, 1.21
	Usage difference	0.86	0.65	-0.31, 2.24
	Sine of Date	1.26	1.07	-0.64, 3.68
	Cosine of Date	1.00	1.14	-1.11, 3.37

## 170 Discussion

171 Overall, our findings demonstrate that social processes rather than local ecological variation  
 172 predicted group-specific prey acquisition in Kokolopori bonobos, providing strong indication  
 173 of cultural traits in wild bonobos. Observed differences in prey species preferences may arise  
 174 if different techniques are required to locate and capture them. Duiker and squirrel hunting are  
 175 either strictly terrestrial (duiker) or arboreal (squirrel) activities, which appear opportunistic  
 176 and commonly involved a single individual hunter (more so for squirrel hunting). Conversely,  
 177 anomalure hunting required the engagement of several group members, during which the  
 178 bonobos employed both terrestrial and arboreal positions. At this stage it is unclear which

179 forms of learning such hunting techniques in bonobos may necessitate (e.g., emulation,  
180 stimulus enhancement, or imitation). However, as successful prey acquisition can be  
181 influenced by social learning (Mann et al., 2012; Whiten and van de Waal, 2018), hunting  
182 techniques may emerge as a form of cultural transmission.

183 Another potential explanation for prey preference variation is the presence of individuals who  
184 act as social hunt catalysts (i.e., “impact hunters” (Gilby et al., 2015)). The ‘impact hunter  
185 hypothesis’ explains how joint hunt participation may emerge when hunts by single  
186 individuals are costly (e.g., risk of injury, low success probability). The hypothesis proposes  
187 that increased motivation of certain individuals to hunt (and potentially suffer initial costs)  
188 encourages others to join. For example, if certain group-members motivate social hunts (in  
189 this case anomalure), then the absence of such individuals in a group may lead to a bias  
190 towards solo hunting (in this case duiker and squirrel). Although apparent group-specific  
191 hunting behaviour may emerge as an artefact of the presence of impact hunters, patterns in  
192 our data indicate that this is unlikely to be the root of observed group differences. First, the  
193 absence of individualistic hunting (as apparent in Ekalakala) cannot be explained by the  
194 impact hunter hypothesis, as this hypothesis addresses social hunt occurrence. Second,  
195 although preliminary, similar frequencies of unsuccessful hunt attempt of anomalure in both  
196 groups, indicate that prey preference expression is likely driven by the group hunting  
197 technique efficiency rather than catalyst hunters. Additionally, as many adult group members  
198 participated in hunts and captured prey, collectively, our results indicate that we indeed  
199 document group, instead of individual, tendencies.

200 It is puzzling how such group differences would evolve and persist even when prolonged  
201 associations between Ekalakala and Kokoalongo should potentially promote intergroup social  
202 learning opportunities. Tolerance, at a degree that facilitates social learning in its various  
203 forms, is fundamental in converting innovations into transmitted traditions (Whiten and van  
204 de Waal, 2018). To improve “learning” gains, social learners should be selective in the timing  
205 of observations and their choice of “models” from whom to observe (Boyd and Richerson,  
206 1995). Although the two groups associate for extended periods their intergroup relations are  
207 complex and unpredictable, characterized by a mixture of affiliative and agonistic exchanges,  
208 frequent fission-fusions and heightened arousal (Cheng et al., under review). Unpredictability  
209 of intergroup interactions is thus expected to hamper intergroup learning opportunities of  
210 certain skills which may require extensive time and effort to acquire (e.g., hunting  
211 techniques). Following group psychology predictions of ingroup bias and favouritism

212 (Brewer, 1993), outgroup members may as well be less appealing “models” for learning.  
213 Together, inconsistent intergroup relations and in-group bias may explain how group-specific  
214 prey preferences persist despite numerous intergroup learning opportunities, indicating group  
215 bias and conformity. A by-product of divergent hunting techniques is reduced intergroup  
216 competition, which is likely adaptive, especially when groups share ranging zones. Thus,  
217 group-specific prey preferences in bonobos may have evolved as a form of microlevel niche  
218 differentiation that alleviates feeding competition.

219 Investigating the potential impact of culture on behavioural diversity in non-human animals is  
220 challenging due to the difficulties of estimating and accounting for local ecological variation  
221 as a driver of behavioural diversity. Challenges may even arise when behavioural variation  
222 appears between groups that occupy nearby but non-overlapping ranging areas. Bonobo social  
223 groups’ regular overlap in ranging area and tolerant interactions, offer fertile ground in which  
224 to explore whether variation in behavioural expressions occurs independently of spatial and  
225 temporal use of specific habitat locations. Here, by accounting and largely excluding potential  
226 local ecological variation, we provide strong indication for culturally transmitted subsistence  
227 hunting techniques in bonobos, informing on the evolution of behavioural diversity.

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232 **Acknowledgements**

233 We are grateful to the Bonobo Conservation Initiative and Vie Sauvage, especially Sally Coxe  
234 and Albert Lotana Lokasola, for their continuous support of this work. We thank the Ministry  
235 of Research of the Democratic Republic of the Congo for permitting the study, and the people  
236 of the villages of Bolamba, Yete, Yomboli and Yasalakose for granting access to their forest.  
237 We thank all the research assistants and local field assistants for their dedication and support  
238 in the field and for Erin Wessling and Catherine Hobaiter for their comments on this  
239 manuscript. This work is funded by the Max Planck Society and Harvard University.  
240 The authors declare no competing interests, and all contributed to the methodology and  
241 writing of this work.

242

243 **Ethics Statement**

244 The research presented here was non-invasive and approved by the Max Planck Society and the  
245 Ministry of Research of the Democratic Republic of the Congo. The authors declare that they  
246 have no conflict of interest.

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