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## **Functional Social Structure in Baboons:**

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## **Modelling Interactions Between Social and Environmental Structure in**

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## **Group-Level Foraging**

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17

18 **Abstract:**

19           In mobile social groups, cohesion is thought to be driven by patterns of attraction at both  
20 the individual and group level. In long-lived species with high group stability and repeated  
21 interactions, such as baboons, individual-to-individual attractions have the potential to play a  
22 large role in group cohesion and overall movement patterns. In previous work, we used GPS  
23 mapping of a group of baboons in De Hoop, Western Cape, South Africa, to demonstrate the  
24 influence of such attractions on movement patterns. We also demonstrated the existence of  
25 emergent group-level structures, which arose as a consequence of individual social influence.  
26 Specifically, we found a core-periphery structure, in which a subset of influential animals  
27 exerted an influence on each other and those animals in the periphery, while those in the  
28 periphery were influenced by the core but did not exert any influence over others. Here, we use  
29 agent-based modelling of baboon groups to investigate whether this group-level structure has any  
30 functional consequences for foraging behaviour. By varying individual level attractions, we  
31 produced baboon groups that contained influence structures that varied from more to less  
32 centralized. Our results suggest that varying centrality affects both the ability of the group to  
33 detect resource structure in the environment, as well as the ability of the group to exploit these  
34 resources. Our models predict that foraging groups with more centralized social structures will  
35 show a reduction in detection and an increase in exploitation of resources in their environment,  
36 and will produce more extreme foraging outcomes. More generally, our results highlight the link  
37 between social and environmental structure on functional outcomes for mobile social groups of  
38 animals.

39 **Keywords:** Baboons, social network, core-periphery, foraging, decision making

## 40 **Introduction**

41 Among the primates, group living is thought to have evolved as a means to reduce predation risk,  
42 and competition within and between groups is thought to influence a group's social structure  
43 (Boinski and Garber, 2000; Van Schaik, 1983, 1989). Baboons have long been used to test such  
44 socioecological theories, because they are one of the best studied of all primate taxa and occupy  
45 a wide range of ecologies (Henzi and Barrett, 2003; Henzi and Barrett, 2005). Efforts have also  
46 been made to study the internal structure of baboon groups at a more proximate level. In a now  
47 classic paper, Stuart Altmann (1974) made a series of predictions regarding the manner in which  
48 resource distribution and competition would structure the geometry of baboon groups. Thanks to  
49 advances in technology that allows individual positions to be mapped, some of Altmann's  
50 insights have now been tested, and his predictions have been shown to apply in at least one  
51 baboon population (Dostie et al., 2016). High resolution sampling of behaviour in other baboon  
52 populations has also shown how resource distribution and social interactions between animals  
53 combine to determine the geometric structure of groups (Farine et al., 2016).

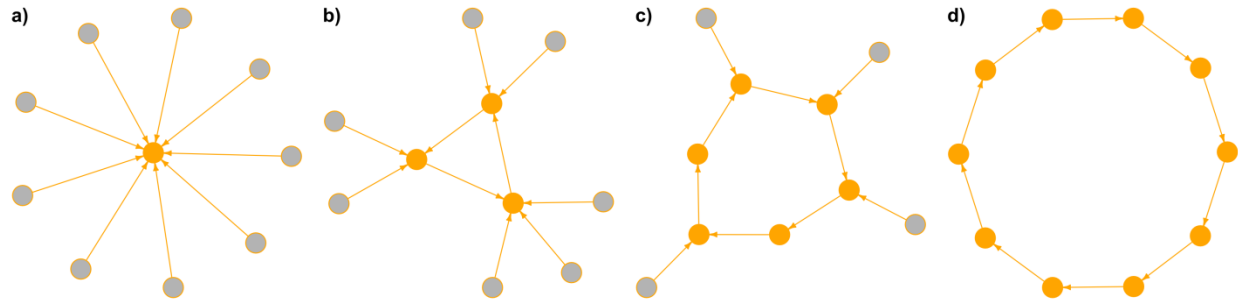
54 Using similar methods, it has also become possible to capture the “social influence”  
55 structure of groups from empirical data (Bonnell et al., 2017; Eriksson et al., 2010; Katz et al.,  
56 2011; Lukeman et al., 2010; Mann, 2011). That is, how patterns of attraction and repulsion  
57 between individuals give rise to the internal structure of groups. In our own work on baboons, we  
58 have considered how group-level structures can arise from the combination of individual  
59 influence patterns (Bonnell et al., 2017). Specifically, Bonnell et al. (2017) found evidence for a  
60 core/periphery structure at the group level, where a core of more dominant, inter-dependent  
61 individuals exerted a unidirectional influence on the movements of other, peripheral animals.

62           An obvious question that arises from such findings is whether any functional benefits  
63   accrue from particular influence structures. Research to date has shown that local influence  
64   between neighboring individuals can propagate information through collectives faster than any  
65   individual can travel (Sumpter et al., 2008). Similarly, there is evidence that such local  
66   interactions allow a few knowledgeable individuals to guide the decisions of a large number of  
67   naive individuals (Couzin et al., 2005). In these cases, the effects of influence structures are  
68   dominated by spatially-neighbouring individuals, where all individuals are treated as  
69   homogenous and have equal influence. In cases like this, group size alone may prove to be an  
70   advantage in collective decision making (referred to as the “wisdom of the crowd”: (Galton,  
71   1907). This occurs through the averaging of individual decisions, resulting in group decisions  
72   closer to optimal than any one individual. When there is internal structure to a group, however,  
73   the specific network of connections between individuals can influence group decision making  
74   (Krause et al., 2010; Rosenthal et al., 2015). It is also important to recognize that such internal  
75   structure can give rise to emergent patterns that do not necessarily confer an advantage. That is,  
76   emergent patterns can often result simply from the existence of non-linear interactions (Bradbury  
77   and Vehrencamp, 2014). Consequently, it is important to consider what, if any, advantage a  
78   particular pattern might convey, and in what contexts (Parrish and Edelman-Keshet, 1999).

79           Here, we develop testable predictions about the functional role of influence structures  
80   within mobile simulated baboon troops engaged in foraging tasks that can be applied to real-  
81   world situations. This will enable more precise predictions regarding the influence of habitat  
82   structure and composition on group shape and structure across baboon populations, as well as  
83   contributing more generally to work in movement ecology and collective behaviour.

84 To explore the functional consequences of variation in a core-periphery structure we use  
85 agent-based modelling. Specifically, we investigate how characteristics of the resource landscape  
86 interact with internal group structure to promote or impede the ability of groups to locate  
87 resource-rich areas, and subsequently take advantage of them. We expected to find that less  
88 centralized social structures (i.e., those with a larger core of influential animals) will result in (i)  
89 the group as a whole being better able to identify high value resource structures on the landscape,  
90 and (ii) will result in less within-group variance in foraging efficiency. In more centralized  
91 groups (i.e., those with a smaller core), we predicted the opposite trends.

92 To achieve this, we quantify the foraging efficiency of simulated groups by performing  
93 virtual foraging trials. In these trials, we alter the social influence structure of the group, the size  
94 of the group, and the structure present in the resource landscape. We define influence structures  
95 within these simulated groups using a core-periphery approach, where a core is defined as a set  
96 of inter-dependent individuals, and peripheral individuals are those that are influenced by the  
97 core but not each other (Fig. 1). We varied influence structures by altering the size of the core,  
98 generating influence structures ranging from a single leader (e.g., one individual is the core) to a  
99 homogenous influence structure (i.e., all individuals form part of the core) (Fig. 1). We further  
100 varied group size to alter the magnitude of scramble competition. Finally, we altered the resource  
101 landscapes in which our foraging experiments were run, creating a context where resources were  
102 distributed randomly and homogeneously, versus a context in which a single high-density  
103 resource path was present and one in which several high-density paths were present. We used a  
104 single high-density path in order to provide a clear optimum for foraging so that we could  
105 quantify the relative effects of social influence structure and group size on the ability to exploit  
106 environmental structure.



107

108 **Figure 1:** Group level influence structures in four groups of 10 individuals: a) one individual at  
109 the center ( $C_{\text{per}} = 0.1$ ), b) three individuals form a core ( $C_{\text{per}} = 0.3$ ), c) six individuals form a core  
110 ( $C_{\text{per}} = 0.6$ ), and finally d) all individuals are inter-dependent ( $C_{\text{per}} = 1.0$ ).

111

## 112 **Methods**

### 113 *Movement model*

114 The movement model used is based on correlated random walk models (Van Moorter et al.,  
115 2009). In our model, animals are simply biased towards visible sites that are close and have high  
116 resources. To calculate the resulting influence of food patches on a simulated animal, we weight  
117 each patch within a visual radius ( $R_{\text{vis}}=50\text{m}$ ) based on the distance from the focal animal and the  
118 amount of food at that patch,  $W'_p = \frac{\text{patch}_{\text{resource}}}{\text{patch}_{\text{distance}}}$ . Where patch resources vary from 0-1. We then  
119 standardize the patch weights to sum to one,  $W_p = \frac{W'_p}{\sum_{p=1}^n W'_p}$ , and calculate the average food vector  
120 based on these weights  $\vec{V}_f = \sum_{p=1}^n W_p * \vec{V}_p$ .

121 Along with this motion bias towards resources, we add a social attraction force into the  
122 model by adjusting motion based on attraction to a particular group member. We use a linear  
123 function describing an increasing attraction towards a group member beyond an attraction radius  
124 ( $d_a=10\text{m}$ ) (Couzin et al., 2002; Warburton and Lazarus, 1991):

125 
$$\vec{V}_a = \left(1 - \frac{d_a}{d(g)}\right) * \vec{V}_g$$

126 The attraction vector ( $\vec{V}_a$ ) of the focal animal describes the attraction to one other  
127 individual. The combined result of these forces are thus:

128 
$$\vec{V}_t = b_{bearing} * \vec{V}_{t-1} + b_{food} * \vec{V}_f + b_{attraction} * \vec{V}_a$$

129 Where  $\vec{V}_t$  is the resulting motion vector at time t,  $\vec{V}_{t-1}$  is the previous motion vector,  $\vec{V}_f$  is the  
130 vector towards food patches, and  $\vec{V}_a$  is the attraction vector. The parameters  $b_{bearing}$ ,  $b_{food}$ , and  
131  $b_{attraction}$  represent the relative influence of each force acting on the simulated animal. We set  
132  $b_{bearing}$  and  $b_{food}$  to a value of 1, and  $b_{attraction}$  to a value of 2. This produces a set of  
133 conditions where social forces predominate over food or movement persistence, and where  
134 movement persistence might be expected to be relatively similar to food bias, i.e., under  
135 conditions where food is of low value and widely distributed.

136 To account for variable uncertainty in motion due to conflicting forces, the final resulting  
137 motion vector is sampled from a wrapped normal distribution (Von Mises) with  $\mu = atan2(\vec{V}_t)$ ,  
138 and  $\sigma = -2 \log\left(\frac{\|\vec{V}_t\|}{\|\vec{V}_t\|_{max}}\right)$ . Where  $\|\vec{V}_t\|_{max}$  is simply the maximum length possible of the  
139 resulting influence vectors (e.g., when they all point in one direction). This results in very little  
140 uncertainty around  $\vec{V}_t$  when all the influencing factors are operating in the same direction and  
141 increased uncertainty in motion when they are all conflicting (Van Moorter et al., 2009).

142

143 *Social influence structures*

144 Each group added to a foraging trial is initialized with a fixed influence structure, where each  
145 individual is assigned one other group member to “follow.” These influence structures are  
146 defined by assigning individuals to either core or periphery status. Each group is assigned a  
147 group size ( $G_{\text{size}}$ ) and a percentage of individuals in the core ( $C_{\text{per}}$ ). By varying these parameters,  
148 we can create influence structures that are more or less despotic or democratic (Fig. 1). The  
149 larger the core size in the group, the more foraging decisions represent the outcome of many  
150 interdependent movements. Conversely, the smaller the core group, the more the group foraging  
151 decisions are “despotically” driven by one individual’s movements.

152

### 153 *Simulated foraging trails*

154 First, we investigated the influence of varying core and group size on foraging behaviour  
155 in a uniform versus heterogeneous landscape. We simulated a base landscape (2000m x 2000m)  
156 with randomly distributed food patches (0.01 patches/m<sup>2</sup>), assuming a homogenous resource  
157 landscape with opportunistic and quickly depleted patches. We compared to this to a second  
158 landscape that contained a high food density path with twice the number of randomly distributed  
159 patches (0.002 patches/m<sup>2</sup>). This path was non-linear and follows a parabolic curve, starting at  
160 the bottom-left corner of the landscape. We used a uniform random distribution to generate 1000  
161 groups with group size varying between 5 and 100 agents, and the proportion of group members  
162 constituting the core varying from 0 to 1. Each group was then run on both the path and non-path  
163 landscapes.

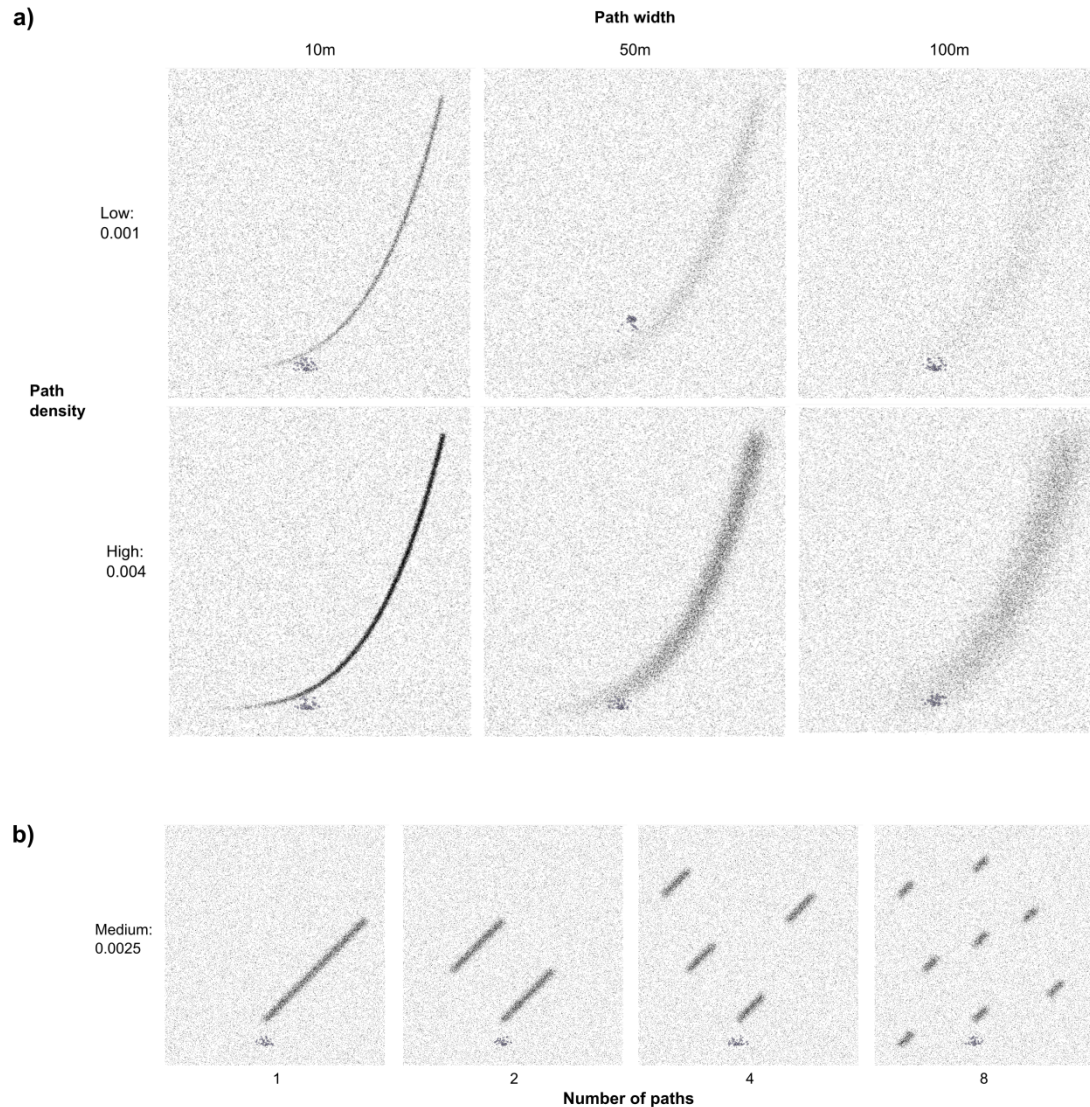
164 Each simulation starts a group at the bottom-middle of the landscape and allows the  
165 group to forage for 2 hours (7200 time steps). The 2-hour limit marks the approximate time that a



166 large group traveling along the high density path would take to reach the top of the simulated  
167 landscape, thus depleting the high resource path and rendering the resource landscape equivalent  
168 to the non-path environment. By constraining the time to 2 hours, we focus on the time period  
169 where the path and non-path environments differ the most, and subsequently where troop  
170 foraging might show the greatest differences. This experimental setup is intended to represent a  
171 baboon group starting from a fixed location, such as a sleeping site. Adding a high-density path  
172 presents the group with a clearly advantageous foraging trajectory. We measure each  
173 individual's intake of food over the simulation, as well as the distance from the high-density path  
174 to the center of the group.

175         We then set up a set of second foraging trials, where we fixed the group size and social  
176 structure and varied environmental structure. Two groups of 50 agents, one with a core of 45  
177 agents and a second with a core of 5 agents, were made to forage on (i) landscapes in which the  
178 width and amount of food on the path were varied (Fig 2a), and (ii) landscapes in which the  
179 number and length of the paths were varied (Fig. 2b). For (i) we used a uniform random  
180 distribution to specify landscape structure, with path width varying between 10 and 100m, and  
181 amount of food in the path varying between 0.001 and 0.004 patches/m<sup>2</sup>. For (ii) we again used a  
182 uniform random distribution to specify landscape structure, varying the number of paths from 1  
183 to 8, where the length of the paths were made smaller as the number of paths went up (e.g., the  
184 landscape with 2 paths had 2 paths each 1/2 the size of the one path landscape, 4 paths each 1/4<sup>th</sup>  
185 the size of the one path landscape, ... etc). For both sets of trials that varied an aspect of  
186 environmental structure, we generated 500 foraging landscapes and simulated foraging for small  
187 and large core groups, resulting in 1000 runs for each trial.

188



189

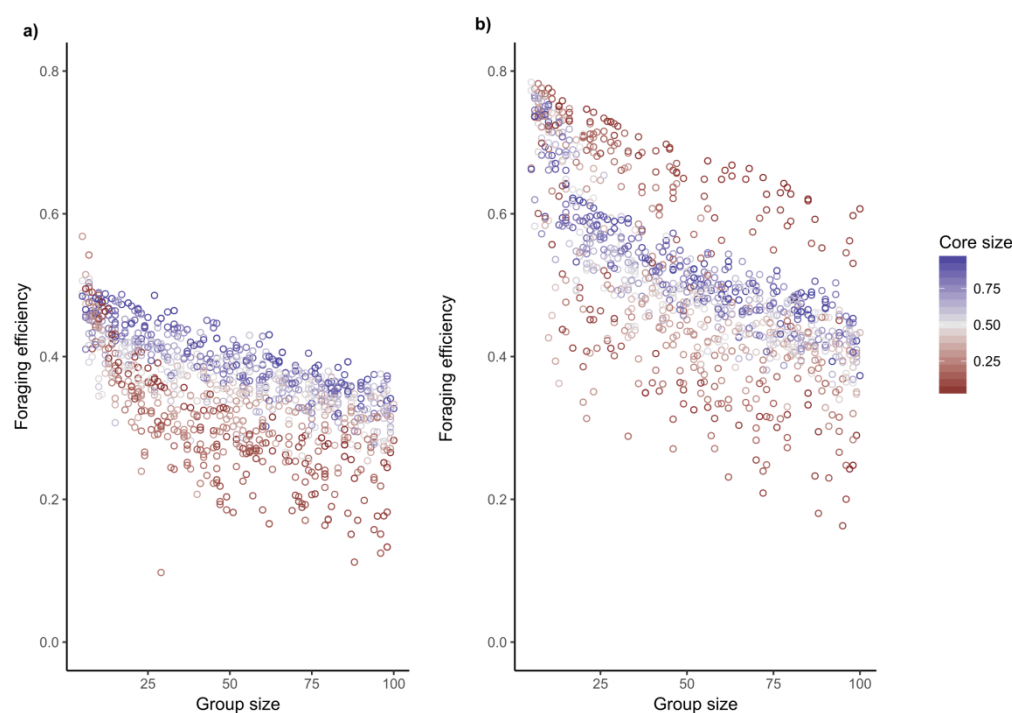
190 **Figure 2:** Range of resource landscapes used in the foraging trails. The high-density paths were  
191 added to a background of randomly distributed food patches by a) varying the width and density  
192 of food patches within a preset path, and b) varying the number and size of the paths in the  
193 landscape. The simulated group started each foraging trail located at the bottom middle of the  
194 landscape.

195

## 196 Results

197 *Foraging efficiency: which group structures do better and under what conditions?*

198 In a uniform habitat, groups with larger cores outperformed those with small cores, showing  
199 consistently higher food intake across the entire range of group sizes (Fig. 3a). When foraging in  
200 a landscape with a high-density path, however, we found that groups with smaller cores could  
201 sometimes outperform groups those larger cores across the range of group sizes, although they  
202 could also do much worse (Fig. 3b). Overall, foraging efficiency was higher under conditions in  
203 which a high-density path was present (Fig. 3).



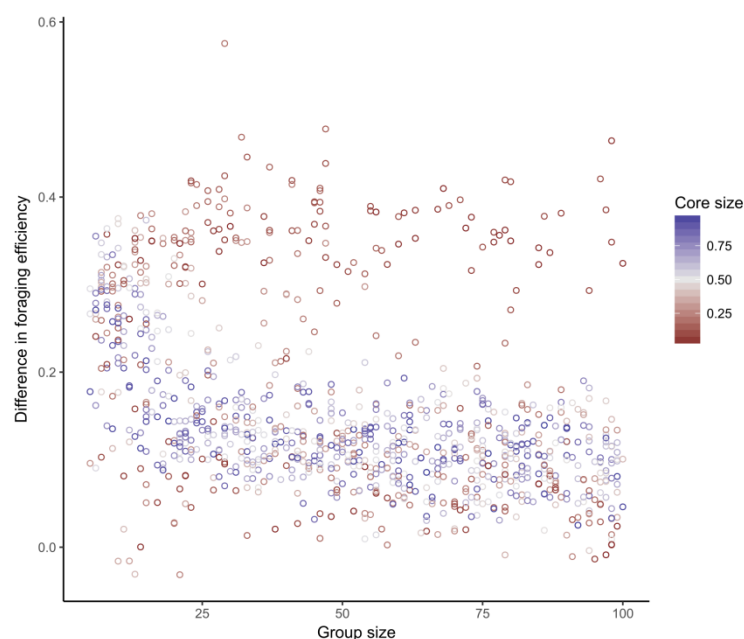
204

205 Figure 3: Rate of foraging intake under alternative influence structures, group size and landscape  
206 settings: a) uniform landscape, and b) high-density path on the landscape. Foraging intake is the  
207 percentage of total possible intake. The color of the points represents the percentage of the group  
208 that is part of the core, the remaining individuals are assigned to the periphery and follow a  
209 randomly specified core member.

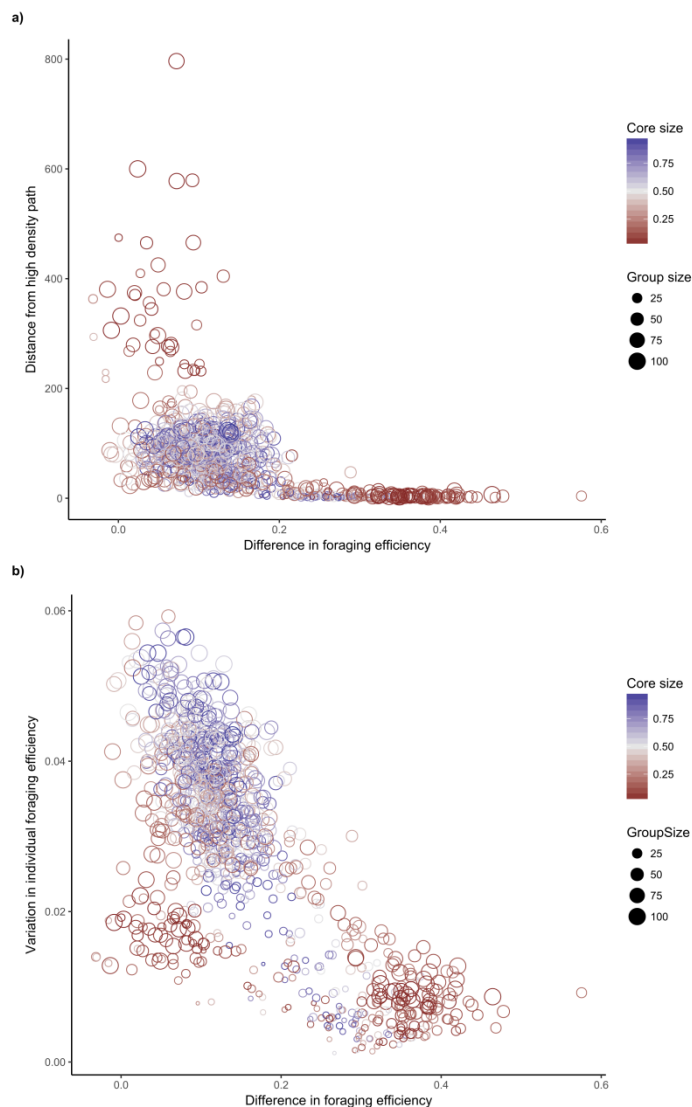
210

211 As a further check on this, we compared the difference in foraging efficiency of groups of a  
212 given size and composition in the structured versus unstructured environment. This revealed that  
213 almost all combinations of group size and structure performed better in the environment with the

214 high-density path. Nevertheless, groups with smaller cores apparently were able to benefit more  
215 from the presence of a high-density path than large core groups, and the strength of this effect  
216 increased with group sizes above 25 producing a bifurcation (Fig. 4).



217  
218 Figure 4: Difference in foraging efficiency across environments with and without the high-  
219 density path for a given group size and core-periphery structure.  
220  
221 This bifurcation can be explained by examining the groups' distance from the high-density path  
222 Fig 5a). Small core groups that showed large positive differences in foraging efficiency (the  
223 upper part of the bifurcation) were also the ones that maintained close proximity to the high-  
224 density path (Fig. 5a). Although groups with large cores maintained looser proximity to the high-  
225 density path, groups of all sizes consistently remained within 200m of it. Larger groups with  
226 small cores often wandered very far from the high-density path resulting in reduced efficiency  
227 (Fig. 5a).



228

229 **Figure 5:** Resulting foraging patterns when group size and social structure are varied. The ability  
230 of groups to (a) maintain close proximity to the high-density path, and (b) the level of individual  
231 variation in foraging efficiency are compared to the ability of groups to take advantage of  
232 resource structure in the environment. The ability of groups to take advantage of resource  
233 structure is measured as the difference in foraging efficiency for each group between the high-  
234 density path and non-path environments (i.e., control). Point size represents the size of the group,  
235 and the color represents the size of the core within the group.

236

237 *Variability in foraging efficiency: do peripheral individuals benefit?*

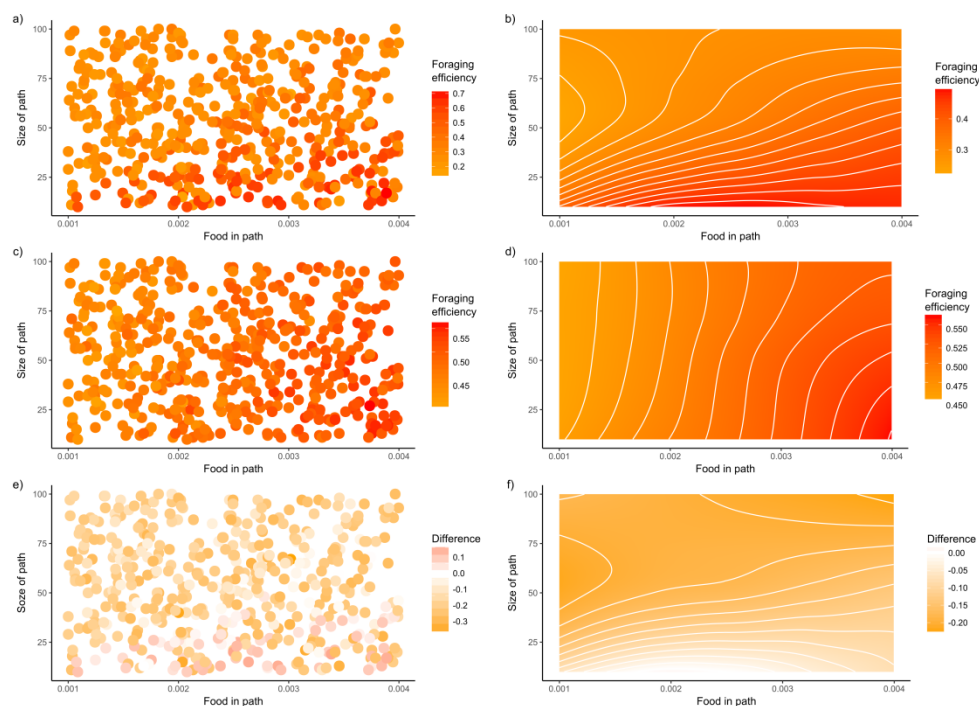
238 When we compared variability in individual level foraging efficiency, we found that large groups  
239 with large cores showed the highest intra-group variability in performance (Fig. 5b). As group  
240 size decreased, groups with large cores tended to show reduced individual variability along with  
241 increased foraging efficiency in the structured environment. For groups with small cores, there  
242 were two outcomes, that did not seem depend on group size (Fig. 5b). One outcome  
243 corresponded to small core groups that performed much better in the structured (high-density  
244 path) environment, while the other corresponded to small core groups that performed only  
245 marginally better in the structured environment. In both cases, there was lower intragroup  
246 variability compared to groups with large cores

247

248 *Varying environmental structures: what can groups with different structures exploit?*

249 We then investigated how groups of a fixed size but different core-periphery structures  
250 responded to variation in environmental structure. We found that groups with small cores  
251 responded to both the size of the high-density path and amount of food it contained (Fig. 6ab,  
252 Table 1), whereas groups with large cores largely responded only to the amount of food (Fig.  
253 6cd, Table 1). When overall foraging efficiency was compared, we found that groups with large  
254 cores tended to do better under most conditions (Fig. 6ef).





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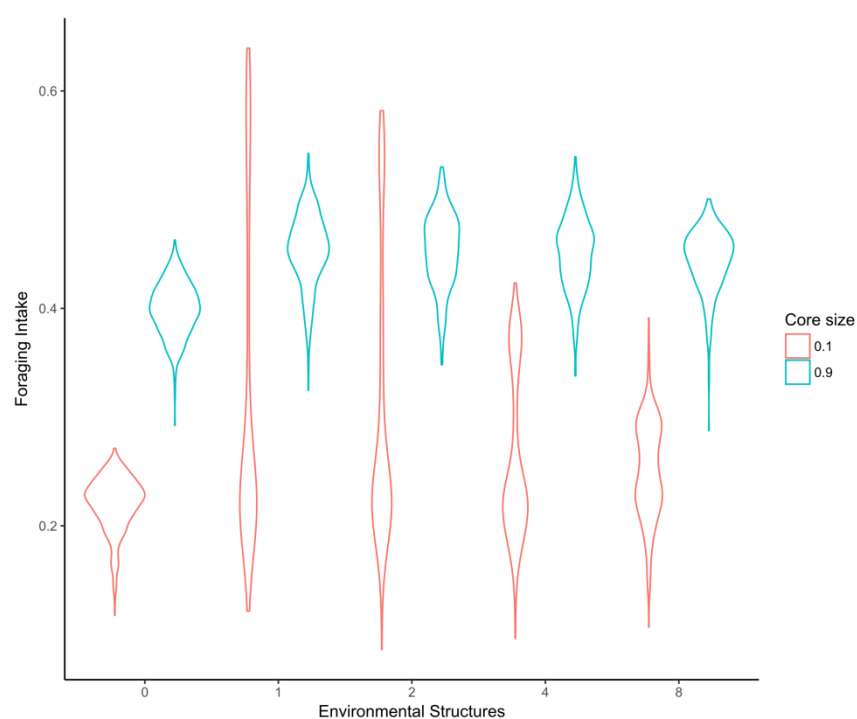
256 **Figure 6:** Foraging outcomes in resource environments with varying structure. Environmental  
 257 structure was varied by adding a high-density resource path and altering the width and amount of  
 258 food in the path. Two groups were made to forage in each resource environment: (a) a group of  
 259 50 individuals with 5 core members, with (b) modeled trend (loess), and (c) a group of 50  
 260 individuals with 45 core members, with (d) modeled trend (loess). The difference between the  
 261 two groups under the same environmental conditions (e) and modeled trend (f) are presented.

262

263 **Table 1:** Linear model comparing the effect size of the amount and size of high density paths on  
 264 foraging outcomes.

| Group                   | Standardized estimate (sd) |
|-------------------------|----------------------------|
| <b>Large core group</b> |                            |
| Size of path            | -0.15 (0.03)               |
| Food in path            | 0.76 (0.03)                |
| Adj R <sup>2</sup>      | 0.60                       |
| <b>Small core group</b> |                            |
| Size of path            | -0.41 (0.04)               |
| Food in path            | 0.27 (0.04)                |
| Adj R <sup>2</sup>      | 0.25                       |

265           When we varied the number and size of high density paths, creating a gradient from one  
266 long structure to many small structures, we found that groups with small cores had the ability to  
267 outperform groups with large cores only when there were a few large structures in the  
268 environment (Fig. 7, Fig. 2b). Otherwise groups with large cores consistently outperformed those  
269 with small cores.



270  
271 **Figure 7:** Foraging intake for large core and small core groups with varying the environmental  
272 structure. Environmental structure varied from no additional structure (0 = uniform distribution),  
273 to the addition of one long high-density resource path, to an increasing number of smaller and  
274 more numerous high density paths (e.g., 8 = 8 paths 1/8<sup>th</sup> the size of the initial path). The  
275 distribution of foraging outcomes are represented by violin plots, where the width indicates the  
276 density of outcomes at a particular value of foraging intake.

277  
278 **Discussion**

279 Our results show that the structure of the resource environment can have a large impact on the  
280 functional outcomes of social influence structures, and accounting for environmental structure is



281 thus an important consideration when attempting to understand the drivers of social influence  
282 patterns within baboon groups. More specifically, our simulations make the prediction that the  
283 development of homogenous influence structures (i.e., decentralized groups with large cores)  
284 will be favored in homogenous resource environments. For more structured resource  
285 environments, however, our simulations suggest something more nuanced as the outcomes are  
286 likely to depend on both the degree to which centralized structures hurt the group when it fails to  
287 locate resources in the environment (i.e., the costs of reduced detection), and the exact nature of  
288 environmental structure. When our simulated baboon group was presented with a generally  
289 homogenous environment with a single structured component (i.e., our high-density path), the  
290 failure to detect the path, as a consequence of possessing a small core of influential animals,  
291 incurred a high cost (Fig. 3a). When groups with small cores were presented with a more heavily  
292 structured landscape (i.e., several small high-density paths), the costs of missing one structural  
293 component (i.e., the difference between high performing and low performing small core groups)  
294 was reduced (Fig. 7). In the case of groups with larger cores, foraging benefits remained similar  
295 across all resource structures. Path width also interacted with group structure: in landscapes  
296 where the path width of the resource was relatively narrow, the added persistence of small core  
297 groups in maintaining proximity to such structures allowed such groups to forage more  
298 efficiently (Fig. 5a). Thus, small cores may be most effective under conditions when habitats are  
299 heterogeneous, with a few areas of high-density resources that are heavily restricted spatially.

300 Interestingly, and contrary to our original intuitions, we found that groups with smaller  
301 cores displayed lower variation in individual foraging intakes compared to groups with large  
302 cores, and this occurred regardless of whether groups with small cores detected the high-density  
303 path. More specifically, when groups with small cores found the high-density path, this resulted

304 in both increased group-level foraging intake and decreased individual variability, suggesting  
305 that peripheral individuals benefited from the group's closer proximity to the high-density path.  
306 When groups with small cores failed to find the high-density path, group-level foraging intake  
307 dropped, accompanied by a slight increase in individual variation, although this remained lower  
308 than for groups with large cores. One possible explanation here is that this reflects variation in  
309 travel speed: groups with smaller cores move faster across the landscape than those with larger  
310 cores, as the latter have a greater tendency to meander. As a result, peripheral individuals in  
311 groups with smaller cores may encounter new food sources more rapidly than peripheral  
312 individuals in slower, more meandering groups, and hence ensure inter-individual variation in  
313 foraging intake remains relatively low. For groups with large cores, we found that variation in  
314 individual foraging intakes decreased with decreasing group sizes, and was accompanied by an  
315 increase in group foraging intake. Overall, this suggests that smaller groups and lower inter-  
316 individual variation in foraging intake are both associated with shorter distances from the high-  
317 density path. This, in turn, suggests that smaller groups with larger cores are better able to take  
318 advantage of this form of highly concentrated environmental structure (Fig. 5ab).

319 More generally, our results conform to predictions that more centralized social groups,  
320 with influence structures tied to very few individuals, produce more extreme outcomes (Conradt  
321 and Roper, 2005). That is, groups with small cores either find and exploit the structure of the  
322 environment highly effectively, or they miss the high-density path completely and so fail to  
323 exploit it at all. Groups with larger cores, on the other hand, are highly effective at finding these  
324 kinds of environmental structure but are not as effective at exploiting it when they do so. Thus,  
325 variation in core size can be seen as a trade-off between the benefits of exploitation versus  
326 exploration (Fig. 5a).

327           In our simple model, there are no other mechanisms by which groups with smaller cores  
328 can increase their ability to detect environmental structure, nor for groups with larger cores to  
329 increase their effectiveness at exploiting of environmental structure (i.e., they have no means of  
330 maintaining tighter proximity to the path). As such, we have presented a form of null model,  
331 where our predictions are based solely on individuals that are foraging for local resources with a  
332 social bias in movement. Empirical data that deviates from these predictions can therefore help  
333 identify novel mechanisms by which baboon groups (and indeed groups of other species)  
334 increase their ability to detect and/or exploit environmental structure, and this in turn may be  
335 dependent on whether they possess a centralized (small core) or decentralized (large core)  
336 influence structure. Similarly, observational studies might also point to alternative social  
337 influence structures that have enhanced functional outcomes, i.e., those not neatly categorized as  
338 centralized or decentralized. Longitudinal studies might be most useful here, as the development  
339 of particular social influence structures could then be observed and enable the quantification of  
340 the relationship between environmental contexts (e.g., seasons) and social structures (e.g.,  
341 movement bias) in baboon troops. Cross-sectional studies could also highlight differences  
342 between different groups within a population under differing environmental conditions, as well  
343 as cross-species comparisons (Reyna-Hurtado et al., 2017).

344           The *Papio* baboons offer great potential in this respect, as they are found throughout  
345 many differing environments, their evolutionary history is extremely well studied, and the  
346 different allotaxa show a variety of social structures that lend themselves to empirical tests of the  
347 kind suggested here (Barton et al., 1996; Henzi et al., 2009; Jolly, 2001; Patzelt et al., 2011;  
348 Schreier and Swedell, 2009; Snyder-Mackler et al., 2012; Weyher et al., 2014). Building on our

349 simulated results, we may therefore be able to acquire an even better grasp on how social  
350 structure enables baboons to make the best use of space, time and energy.

351

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359 **Competing interests:** We declare we have no competing interests

360

361

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436 **Supplementary material**

437 Simulation Model:

438 Full model code is available from: [github.com/tbonne/Functional-Influence-Structures](https://github.com/tbonne/Functional-Influence-Structures)

439

440 Clustering analysis:

441 To aid in the interpretation of the simulated foraging outcomes a clustering approach was used.

442 Foraging outcomes for each simulated group was measured by: 1) the difference in foraging

443 efficiency of this group when foraging on landscapes with and without a high density path, 2)

444 variation in individual foraging within the group, and 3) the distance between the high density

445 path and the group. The function NbClust (Charrad et al., 2014) was used to determine the

446 optimal number of clusters, using canberra distance, the Ward D2 method (Murtagh and

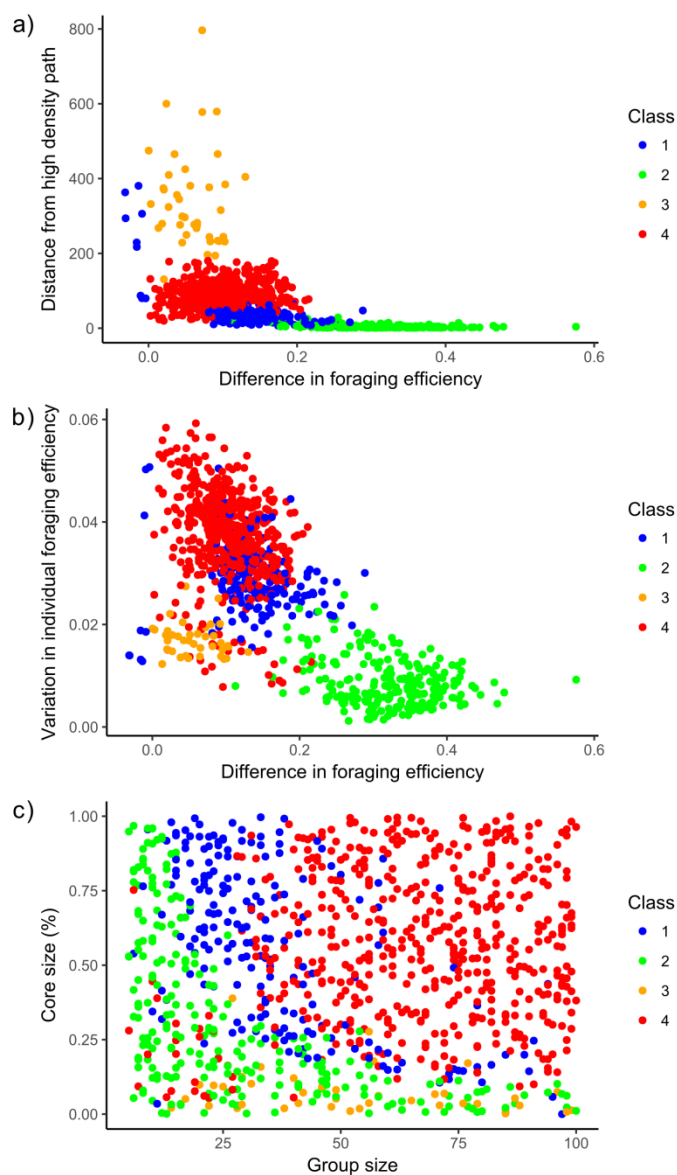
447 Legendre, 2014), and 26 indices to test the validity of the choice of clustering (choosing the

448 number of clusters selected by the majority of the indices). The optimal number of clusters in

449 foraging outcomes was 4, and can be visualized in figure S1-ab. The degree to which these

450 outcomes correspond to group size and core size within the groups can be seen in figure S1 c.

451



452

453 Figure S1: Clustering of foraging outcomes: a-b) identified classification of outcomes based on  
454 foraging efficiency, variation within group foraging, and distance maintained from the high  
455 density resource path. Plot c) displays how the categories of outcomes compare with the group  
456 size and core size measures.

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