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Functional social structure in baboons: Modeling interactions between social and environmental structure in group-level foraging

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ABSTRACT

In mobile social groups, cohesion is thought to be driven by patterns of attraction at both the individual and group level. In long-lived species with high group stability and repeated interactions, such as baboons, individual-to-individual attractions have the potential to play a large role in group cohesion and overall movement patterns. In previous work, we found that the patterning of inter-individual attraction gave rise to an emergent group-level structure, whereby a core of more influential, inter-dependent individuals exerted a unidirectional influence on the movements of peripheral animals. Here, we use agent-based modeling of baboon groups to investigate whether this core–periphery structure has any functional consequences for foraging behavior. By varying individual level attractions, we produced baboon groups that contained influence structures that varied from more to less centralized. Our results suggest that varying centrality affects both the ability of the group to detect resource structure in the environment, as well as the ability of the group to exploit these resources. Our models predict that foraging groups with more centralized social structures will show a reduction in detection and an increase in exploitation of resources in their environment, and will produce more extreme foraging outcomes. More generally, our results highlight how a group's internal social structure can result in mobile social animals being able to more (or less) effectively exploit environmental structure, and capitalize on the distribution of resources. In addition, our agent-based model can be used to generate testable predictions that can be tested among the extant baboon allotaxa. This will add value to the existing body of work on responses to local ecology, as well as providing a means to test hypotheses relating to the phylogeography of the baboons and, by analogy, shed light on patterns of hominin evolution in time and space.

1. Introduction

When it comes to understanding patterns of human evolution, baboons have long been used as both “analogs and avatars” (Jolly, 2009: 190). With respect to the former, Cliff Jolly's classic “seed eater” model was one of the first to use baboons as analogs for the patterns seen in human evolution (Jolly, 1970). Here, Jolly argued that the patterns of dental modification seen in gelada (*Theropithecus* spp.) stood in the same relation to the *Papio* baboons as *Australopithecus* did to *Pan*, allowing us to get a grip on the question of what adaptive shifts were required to “convert an ape into an australopithecine” (Jolly, 2009: 190). As Jolly (2009: 190) himself points out, this form of analogical reasoning was mistaken by critics for the use of gelada as an avatar: “a living form that has been selected as a model for an extinct form because it is believed to resemble it most closely in all respects.” Why critics leapt to such a conclusion, when the analogical nature of Jolly's reasoning is so clear, perhaps stems from the fact that, early on, baboons were seen as potentially relevant avatars for extinct hominins (e.g., DeVore and Washburn, 1963), resulting in an enormous research effort to understand baboon behavior (see Henzi and Barrett, 2003 for review); like the hominins, the *Papio* baboons' arrival on the evolutionary scene is linked to the emergence of the African savanna biome, and they faced the same selection pressures (including those that result from the adoption of a more terrestrial lifestyle, the need to cope with more widely dispersed and seasonal resources, and increased predation risk). It is also obvious, however, that the baboons have solved the problem of savannah living in a

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very different way, and their use as avatars for hominins can only be applied in the most superficial manner.

Although the use of baboons as avatars was misplaced, the intense research effort placed into baboons as a consequence has generated a singularly rich, detailed database of their ecology and behavior. This, in combination with advances in genetics, means we now have the means to consider the phylogenetic and biogeographical history of baboons as a genus (Jolly, 2001, 2009; Barrett, 2009). Such consideration reveals complex patterns of introgression, hybridization, reticulation, population isolation and differentiation across space and time: a braided stream not a simple branching tree (e.g., Zinner et al., 2011). The suggestion that the recent evolution of *Homo sapiens* may have occurred in populations with a complex internal structure similar to that seen in the baboons, and probably did so across many regions of Africa (Scerri et al., 2018), means that, while they cannot be taken as avatars, it is becoming increasingly apparent that the baboons can serve as highly informative analogs for our own lineage with respect to evolutionary processes occurring across both time and space.

A full understanding of baboon phylogeography, however, requires an equally full understanding of how social structure varies (or does not) in response to ecology, given that behavior can shape the genetic structure of populations (Kopp et al., 2014). Although we have a much better understanding of baboon behavioral ecology than many other primate species, there remain gaps in our knowledge (e.g., we still know much less about Guinea baboons and Kinda baboons, for example, than the other allotaxa: see other papers in this special issue), and there is still much to learn about the scope and limits of baboons' ability to respond to ecological variation. More detailed, cross-population studies on behavioral variation both within and between the baboon allotaxa will enables us to generate better hypotheses about the likely evolutionary scenarios and selective histories needed to account for the present day patterns of their genetic architecture (e.g., Henzi and Barrett, 2003, 2005).

One of the earliest attempts to place baboon ecology and behavior in this kind of evolutionary framework was Altmann's (1974) now classic paper “Baboons, space, time and energy”. Here, Altmann proposed a set of principles and hypotheses aimed at identifying the adaptive significance of group processes, which could then be tested using both observational and experimental data. In so doing, Altmann (1974) was attempting to move away from the correlational approach of the earliest socioecological models that simply mapped species' traits onto habitat characteristics and then supplied a post hoc explanation for the patterns shown. Altmann wished to establish if there was any necessary link between a species' social structure and the habitat it occupied. In this way, he reasoned, we would be able to understand the ways that selection might act to generate functional group processes, and so explain, and not simply predict, why social organization took the form it did.

A number of Altmann's principles dealt with the manner in which resource distribution and competition would structure the geometry of baboon groups, and he thus anticipated many of the developments in movement ecology and collective behavior that are now shaping current research in the behavioral ecology of primates and other taxa (Westley et al., 2018). Many of these developments reflect advances in technology that allow individual spatial positions to be mapped accurately; indeed, some of Altmann's predictions have now been tested and shown to apply in at least one baboon population (Dostie et al., 2016). High resolution sampling of behavior in other baboon populations has also shown how resource distribution and social interactions between animals combine to determine the geometric structure of groups (Farine et al., 2016).

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

An obvious question that arises from such findings is whether any functional benefits accrue from particular influence structures. Research to date has shown that local influence between neighboring individuals can propagate information through collectives faster than any individual can travel (Sumpter et al., 2008). Similarly, there is evidence that such local interactions allow a few knowledgeable individuals to guide the decisions of a large number of naive individuals (Couzin et al., 2005). In these cases, the effects of influence structures are dominated by spatially-neighboring individuals, where all individuals are treated as homogenous and have equal influence. In cases like this, group size alone may prove to be an advantage in collective decision making (referred to as the “wisdom of the crowd”: Galton [1907]). This occurs through the averaging of individual decisions, resulting in group decisions closer to optimal than any one individual.

When there is internal structure to a group, however, the specific network of connections between individuals can influence group decision-making in ways that may be adaptively advantageous (Krause et al., 2010; Rosenthal et al., 2015). It is also important to recognize that emergent patterns do not necessarily confer an advantage. That is, emergent patterns can often result simply from the existence of non-linear interactions (Bradbury and Vehrencamp, 2014). Consequently, it is important to consider what, if any, advantage a particular pattern might convey, and in what contexts (Parrish and Edelstein-Keshet, 1999). Understanding how internal social structure is generated and maintained (e.g., whether it is an emergent property of local interactions, or whether it represents the efforts of particular animals to sustain particular spatial positions with respect to others) also offers a guide to discovery with respect to evolutionarily relevant questions concerning the genetic and physiological mechanisms that underpin certain behaviors, and how and when these might have evolved (see, for example, Bergey et al., 2016).

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

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

We quantified the foraging efficiency of simulated groups by performing virtual foraging trials. In these trials, we altered the social influence structure of the group, the size of the group, and the structure present in the resource landscape. We defined influence structures within these simulated groups using a core–periphery approach, where a core is defined as a set of interdependent individuals, and peripheral individuals are those that are influenced by the core but not by each other (Fig. 1). We varied influence structures by altering the size of the core, generating influence structures ranging from a single leader (e.g., one individual is the core) to a homogenous influence structure (i.e., all individuals form part of the core; Fig. 1). We further varied group size to alter the magnitude of scramble competition. Finally, we altered the resource landscapes in which our foraging experiments were run, creating contexts where (i) resources were distributed randomly and homogenously, (ii) a single high-density resource path was present, and (iii) several high-density paths were present. We used the single high-density path to provide a clear optimum for foraging so that we could quantify the relative effects of social influence structure and group size on the ability to exploit environmental structure.

2. Methods

A simulation model was constructed in Java, using repast symphony 1.2 libraries (North et al., 2013). Full model code is available from: github.com/tbonne/Functional-Influence-Structures. The simulation contained a movement model and a social model. The movement model described how individuals move through the landscape, influenced by both resources and social factors. Where the social model described who individuals respond to in their group. We made use of this simulation to run foraging trials consisting of one group in alternative resource distributions. By altering the underlying distribution of resources in the environment, as well as the social structure of the group, we generated simulated data that can be used to better understand the interaction between social and environmental structures.

2.1. Movement model

Our movement model was based on correlated random walk models (Van Moorter et al., 2009). In the model, animals were biased simply towards visible sites that are close and have high resources. To calculate the resulting influence of food patches on a simulated animal, we weighted each patch within a visual radius ($R_{\text{vis}} = 50$ m) based on the distance from the focal animal and the amount of food at that patch, $W'_p = \text{patch}_{\text{resource}}/\text{patch}_{\text{distance}}$, where patch resources varied from 0 to 1. We then standardized the patch weights to sum to one, $W_p = W'_p / \sum_{p=1}^{n} W'_p$, and calculated the average food vector based on these weights $\vec{V}_f = \sum_{p=1}^{n} W_p * \vec{V}_p$.

Along with this motion-bias towards resources, we added a social attraction force into the model by adjusting motion based on attraction to a particular group member. We used a linear function describing an increasing attraction towards a group member beyond an attraction radius ($d_a = 10$ m) (Warburton and Lazarus, 1991; Couzin et al., 2002):

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

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

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

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 vector towards food patches, and $\vec{V}_a$ is the attraction vector. The parameters b_{bearing}, b_{food}, and $b_{\text{attraction}}$ represent the relative influence of each force acting on the simulated animal. We set b_{bearing} and b_{food} to a value of 1, and $b_{\text{attraction}}$ to a value of 2. This produced a set of conditions where social forces predominated over food or movement persistence, and where movement persistence might be expected to be relatively similar to food bias, i.e., under conditions where food is of low value and widely distributed.

To account for variable uncertainty in motion due to conflicting forces, the final resulting motion vector was sampled from a wrapped normal distribution (Von Mises) with $\mu = a\tan2(\vec{V}_t)$, and $\sigma = -2\log(\|\vec{V}_t\| / \|\vec{V}_t\|_{\max})$, where $\|\vec{V}_t\|_{\max}$ is simply the maximum length possible of the resulting influence vectors (e.g., when they all point in one direction). This resulted in very little uncertainty around $\vec{V}_t$ when all the influencing factors are operating in the same direction and increased uncertainty in motion when they are all conflicting (Van Moorter et al., 2009).

2.2. Social influence structures

The group in a foraging trial was initialized with a fixed influence structure, where each individual was assigned one other group member to "follow." These influence structures were defined by assigning individuals to either core or periphery status. Each group was assigned a group size (G_{size}) and a percentage of individuals in the core (C_{per}). By varying these parameters, we created influence structures that were more or less despotic and democratic (Fig. 1). The larger the core size in the group, the more foraging decisions represent the outcome of many interdependent movements. Conversely, the smaller the core group, the more the group foraging decisions are "despotically" driven by one individual's movements.

2.3. Simulated foraging trails

First, we investigated the influence of varying core and group size on foraging behavior in a uniform versus heterogeneous

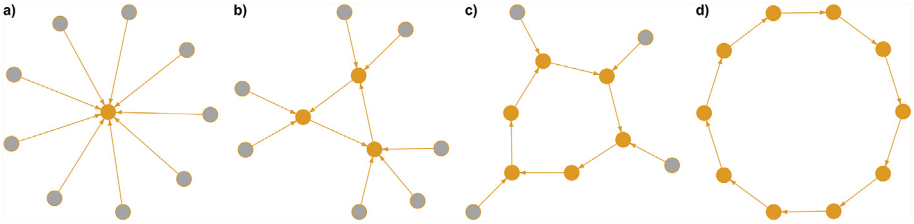

Figure 1. Group level influence structures in four groups of 10 individuals: a) one individual at the center ($C_{\text{per}} = 0.1$), b) three individuals form a core ($C_{\text{per}} = 0.3$), c) six individuals form a core ($C_{\text{per}} = 0.6$), and finally d) all individuals are inter-dependent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

landscape. We simulated a base landscape (2000 m × 2000 m) with randomly distributed food patches (0.01 patches/m^2), assuming a homogenous resource landscape with opportunistic and quickly depleted patches. Each patch was randomly assigned a resource value based on a uniform distribution between 0 and 1 units, and foragers depleted the patch at a rate of 0.01 units/s. We compared this to a second landscape that contained extra patches placed along a preset path. Patches were added along this path ($N = 8000$ representing 20% of all patches in the landscape), using a normal distribution with a standard deviation of 100 m. The path itself was non-linear and followed a parabolic curve, starting at the bottom-left corner of the landscape. We used a uniform random distribution to generate 1000 groups with group size varying between 5 and 100 agents, and the proportion of group members constituting the core varying from 0 to 1. Each group was then run on both the path and non-path landscapes.

Each simulation started with a group positioned at the bottom-middle of the landscape and we allowed the group to forage for 2 h (7200 time steps). During each time step (representing 1 s in the model), all agents first calculated their next direction of travel, based on their previous direction of travel, distance and amount of resources of all patches within visual range (50 m), as well as a social attraction towards one other individual in the group (Eq. (1)). Each agent then performed an action: if situated in a non-depleted food patch, the individual foraged in the patch, otherwise the individual moved according to their desired direction of travel by 1 m. This process was then repeated. The 2-h limit marks the approximate time that a large group traveling along the high density path would take to reach the top of the simulated landscape, thus depleting the high resource path and rendering the resource landscape equivalent to the non-path environment. By constraining the time to 2 h, we were able to focus on the time period where the path and non-path environments differed the most, and subsequently where troop foraging might show the greatest difference. This experimental setup is intended to represent a baboon group starting from a fixed location, such as a sleeping site. Adding a high-density path presented the group with a clearly advantageous foraging trajectory. We measured each individual's intake of food over the simulation, as well as the distance from the high-density path to the center of the group.

To aid in the interpretation of the simulated data a clustering approach was used to determine if groups showed distinct foraging outcomes. Foraging outcomes for each simulated group was measured by: 1) the difference in foraging efficiency in landscapes with and without a high density path, 2) the variation in individual foraging efficiency within the group, and 3) the distance between the high density path and the group. The function NbClust (Charrad et al., 2014) was used to determine the optimal number of clusters, using canberra distance, the Ward D2 method (Murtagh and Legendre, 2014), and 26 indices to test the validity of the choice of clustering. We choose the number of clusters selected by the majority of the indices.

We then set up a second set of foraging trials, where we fixed the group size and social structure and varied environmental structure. Two groups of 50 agents, one with a core of 45 agents and a second with a core of 5 agents, were made to forage on (i) landscapes in which the width and amount of food on the path were varied (Fig. 2a), and (ii) landscapes in which the number and length of the paths were varied (Fig. 2b). For (i) we used a uniform random distribution to specify landscape structure, with path width varying between 10 and 100 m, and amount of food in the path varying between 4000 and 16,000 patches. For (ii) we again used a uniform random distribution to specify landscape structure, varying the number of paths from 1 to 8, where the length of the paths was made smaller as the number of paths went up (e.g., the landscape with 2 paths was allocated 2 paths that were each half the size of the one path landscape, where we used 4 paths, they were each 1/4 the size of the one path landscape, and so on). For both sets of trials that varied an aspect of environmental structure, we generated 500 foraging landscapes and simulated foraging for small and large core groups, resulting in 1000 runs for each trial.

3. Results

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

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

As a further check on this, we compared the difference in foraging efficiency of groups of a given size and composition in the structured versus unstructured environment. This revealed that almost all combinations of group size and structure performed better in the environment with the high-density path. Nevertheless, groups with smaller cores apparently were able to benefit more from the presence of a high-density path than large core groups, and the strength of this effect increased with group sizes above 25, producing a bifurcation (Fig. 4).

This bifurcation can be explained by examining the groups' distance from the high-density path (Fig. 5a). Small core groups that showed large positive differences in foraging efficiency (the upper part of the bifurcation) were also the ones that maintained close proximity to the high-density path (Fig. 5a). Although groups with large cores maintained less proximity to the high-density path, groups of all sizes consistently remained within 200 m of it. Larger groups with small cores, however, often wandered very far from the high-density path resulting in reduced efficiency (Fig. 5a).

3.2. *Variability in foraging efficiency: do peripheral individuals benefit?*

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

3.3. *Are there distinct foraging outcomes?*

Our clustering analysis suggested that there were 4 distinct foraging outcomes (Fig. 6a,b). These clusters mapped well onto the particular social structure and group size characteristics of groups (Fig. 6c).

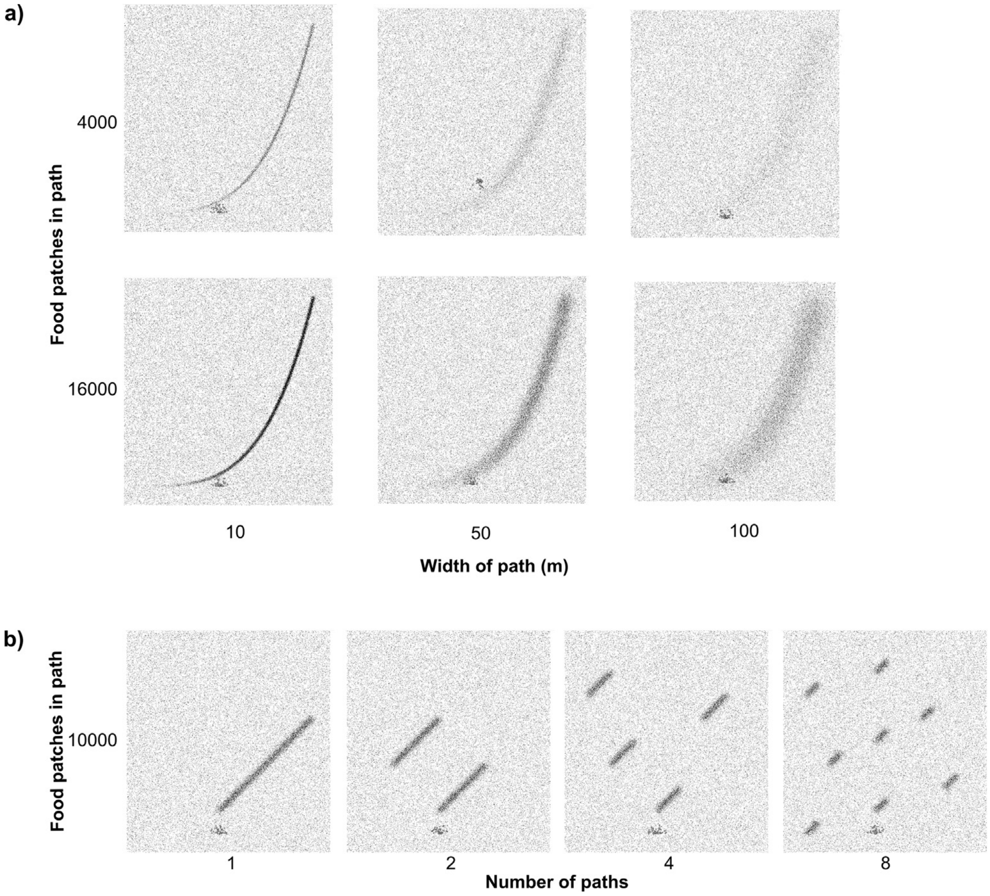

Figure 2. Range of resource landscapes used in the foraging trails. The high-density paths were added to a background of randomly distributed food patches by a) varying the width and number of food patches within a preset path, and b) varying the number and size of the paths in the landscape. To facilitate comparisons between groups, all groups started at the same location (the small cluster of points seen at the bottom-middle of the landscape in the figure) and the landscape remained fixed for all simulated trials.

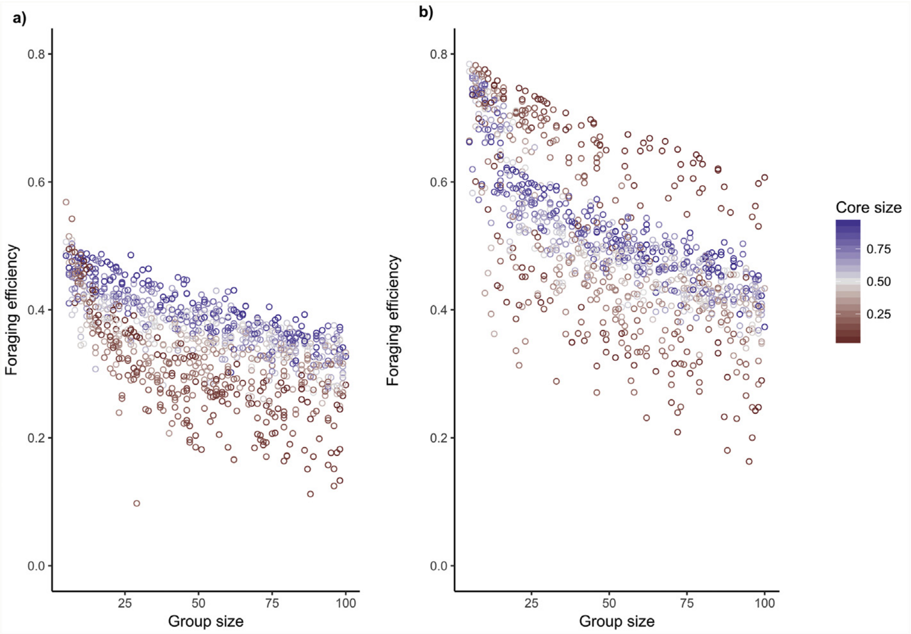

Figure 3. Rate of foraging intake under alternative influence structures, group size (number of individuals) and landscape settings: a) uniform landscape, and b) high-density path on the landscape. Foraging intake is the percentage of total possible intake. The color of the points represents the percentage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

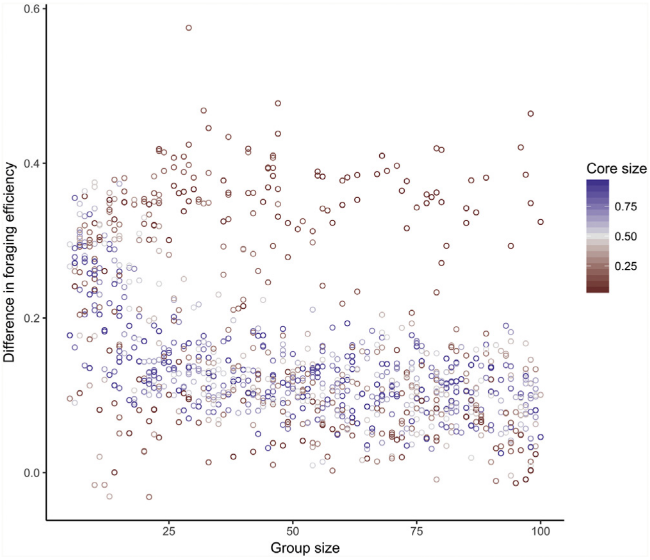

Figure 4. Difference in foraging efficiency across environments with and without the high-density path for a given group size and core–periphery structure.

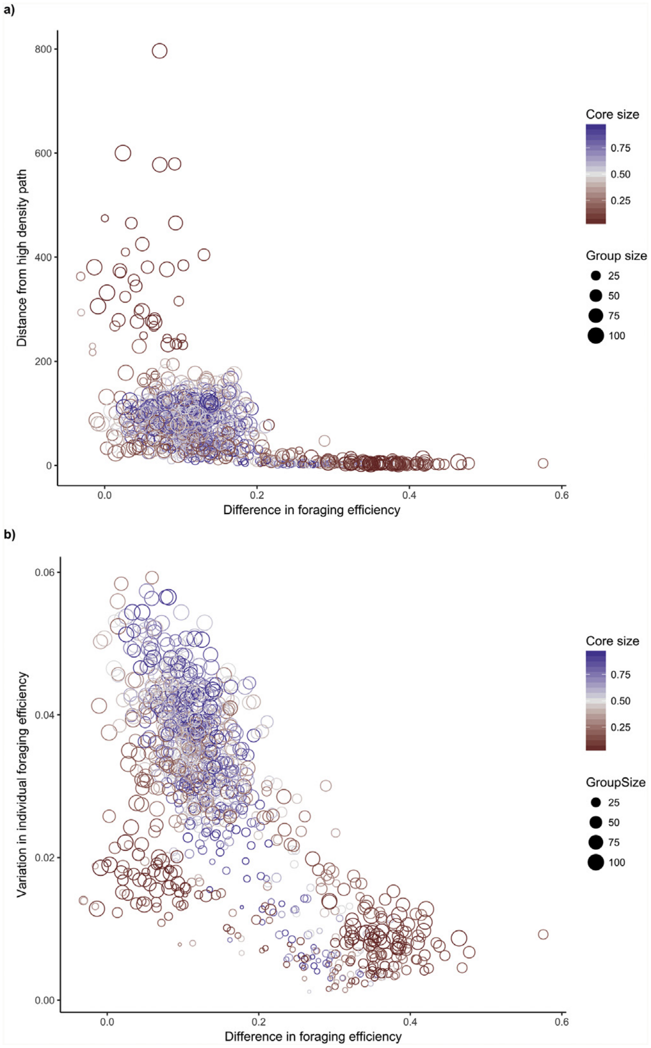

Figure 5. Resulting foraging patterns when group size and social structure are varied. The ability of groups to (a) maintain close proximity to the high-density path, and (b) the level of individual variation in foraging efficiency are compared to the ability of groups to take advantage of resource structure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

3.4. *Varying environmental structures: what can groups with different social structures exploit?*

We investigated how groups of a fixed size but different core–periphery structures responded to variation in environmental structure. We found that groups with small cores responded to both the size of the high-density path and amount of food it contained (Fig. 7a, Table 1), whereas groups with large cores largely responded to the amount of food (Fig. 7b, Table 1). When overall foraging efficiency was compared, we found that groups with large cores tended to do better under most conditions (Fig. 7c).

When we varied the number and size of high density paths, creating a gradient from one long structure to many small structures, we found that groups with small cores had the ability to outperform groups with large cores only when there were a few large structures in the environment (Figs. 8 and 2b). Otherwise, groups with large cores consistently outperformed those with small cores.

4. Discussion

Our results show that the structure of the resource environment can have a large impact on the functional outcomes of social influence structures. Accounting for environmental structure is thus an important consideration when attempting to understand the drivers of social influence patterns within baboon groups. More specifically, our simulations make the prediction that the development of homogenous influence structures (i.e., decentralized groups with large cores) will be favored in homogenous resource environments. For more structured resource environments, however, our simulations suggest something more nuanced as the outcomes are likely to depend on both the degree to which centralized structures hurt the group when it fails to locate resources in the environment (i.e., the costs of reduced detection), and the exact nature of environmental structure.

When our simulated baboon groups were presented with a generally homogenous environment with a single structured component (i.e., our high-density path), the failure to detect the path, as a consequence of possessing a small core of influential animals, incurred a high cost (Fig. 3a). When groups with small cores were presented with a more heavily structured landscape (i.e., several small high-density paths), the costs of missing one structural component (i.e., the difference between high performing and low performing small core groups) was reduced (Fig. 7). In the case of groups with larger cores, foraging benefits remained similar across all resource structures. Path width also interacted with group structure: in landscapes where the path width of the resource was relatively narrow, the added persistence of small core groups in maintaining proximity to such structures allowed such groups to forage more efficiently (Fig. 5a). Thus, small cores may be most effective under conditions when habitats are heterogeneous, with a few areas of high-density resources that are heavily restricted spatially.

Contrary to our original expectations, we found that groups with smaller cores displayed lower variation in individual foraging intakes compared to groups with large cores, and this occurred regardless of whether groups with small cores detected the high-density path. More specifically, when groups with small cores

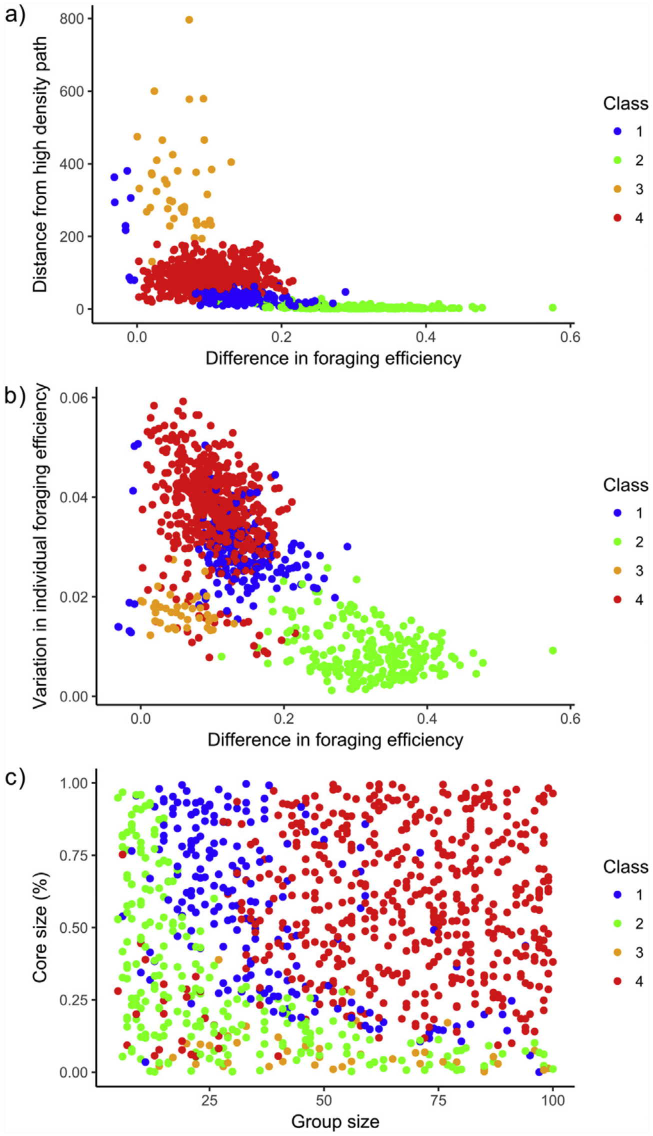

Figure 6. Clustering of foraging outcomes: a–b) identified classification of outcomes based on foraging efficiency, variation within group foraging, and distance maintained from the high density resource path. Plot c) displays how the categories of outcomes compare with the group size and core size measures.

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

More generally, our results conform to predictions that more centralized social groups, with influence structures tied to very few individuals, produce more extreme outcomes (Conradt and Roper, 2005). That is, groups with small cores either find and exploit the structure of the environment highly effectively, or they miss the high-density path completely and so fail to exploit it at all. Groups with larger cores, on the other hand, are highly effective at finding these kinds of environmental structure but are not as effective at exploiting them when they do so. Thus, variation in core size can be seen as a trade-off between the benefits of exploitation versus exploration (Fig. 5a). How the different group-level foraging abilities shown in our simulated trials would affect foraging performance in more naturalistic set-ups is the logical next step required here. Most foraging landscapes encountered by baboons are not likely to be as strongly structured as we used in our simulations; rather, most baboon foraging landscapes tend to vary between relatively uniform landscapes with abundant low quality foods to more patchy landscapes with variable quality foods (e.g., Barton et al., 1992). In addition, baboon foraging strategies are influenced by predation risk (Cowlishaw, 1997), something that can also be expected to influence the internal structure of groups.

In our simple model, there are no other mechanisms by which groups with smaller cores can increase their ability to detect environmental structure, nor for groups with larger cores to increase their effectiveness at exploiting of environmental structure (i.e., they have no means of maintaining tighter proximity to the path). As such, our model represents a starting point for further theoretical and empirical work. Building a deeper empirical understanding of how social network structures interact with group foraging would require expanding on the simple structures and parameters tested here (Bode et al., 2011). For example, incorporating more than one individual to follow, allowing for other social processes (such as contest competition), the inclusion of predation risk, or varying simulations across more realistic environmental structures, e.g., mapping environments with satellite remote sensing. The ability to incorporate additional social and ecological factors into the model would allow for a more nuanced interrogation how these factors interact.

Exploring a wide range of parameterizations and contexts will thus build a more nuanced theoretical understanding between group-level social structures and collective movement. Similarly, collecting observational data from multiple baboon troops in different environments, and collecting data within the same troops across time, will allow for comparisons between theoretical predictions and observations, i.e., does core size vary predictably as environments vary between uniform and more structured? The model we have presented should thus be seen as a null model, where our predictions are based solely on individuals that are foraging for local resources with a social bias in movement. Empirical data that deviate from these predictions can therefore help identify novel mechanisms by which baboon groups (and indeed groups of other species) increase their ability to detect and/or exploit environmental structure, and this in turn may depend on whether they possess a centralized (small core) or decentralized (large core) influence structure. Observational studies might also point to alternative social influence structures that have enhanced functional outcomes, i.e., those not neatly categorized as centralized or decentralized. Longitudinal studies might be most useful here, as the development of particular social influence structures could then be observed and enable the quantification of the

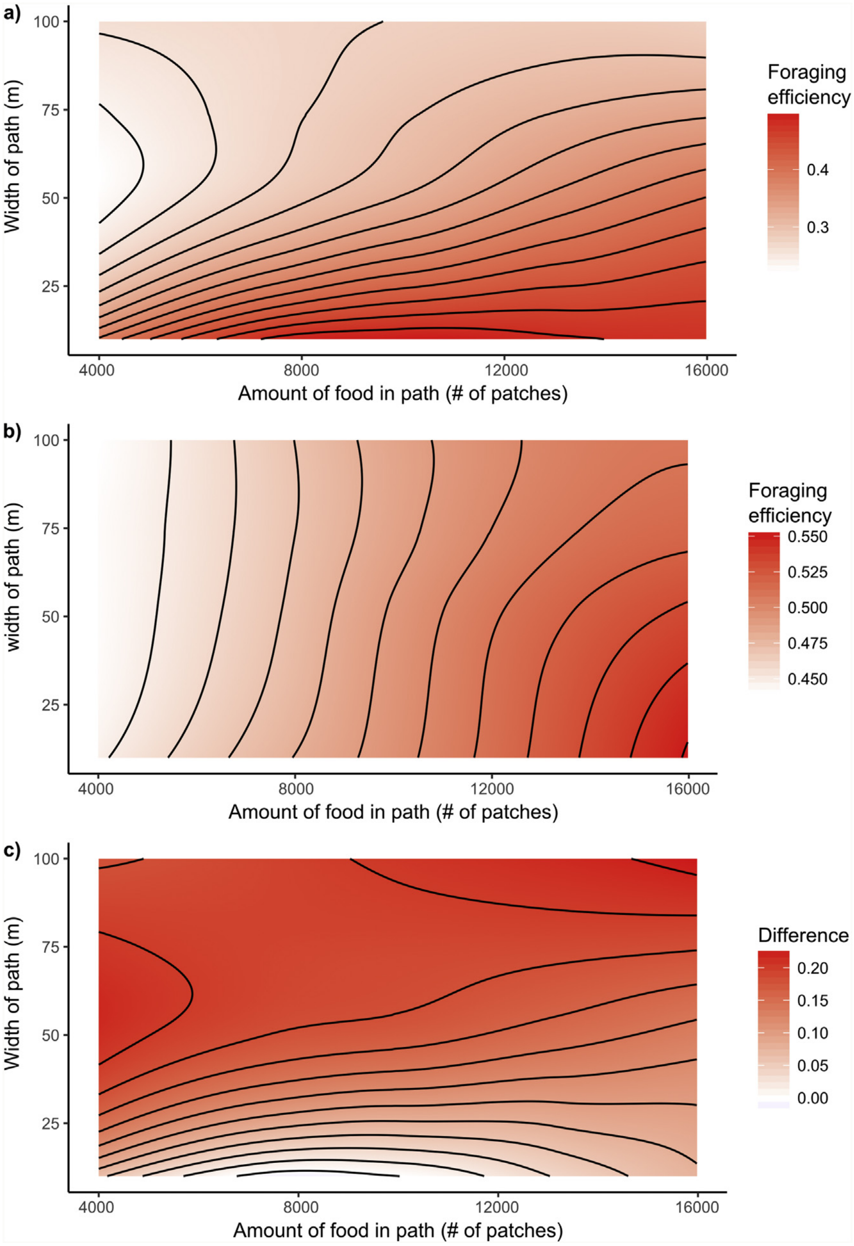

Figure 7. Mean foraging outcomes in resource environments with varying structure. Environmental structure was varied by altering the width and amount of food in the high-density resource path. Foraging outcomes for two groups are presented: a) a group of 50 individuals with 5 core members, b) a group of 50 individuals with 45 core members, and c) the difference in foraging efficiency between the two groups (large core group − small core group).

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

Group	Standardized estimate (standard deviation)
Large core group	
Size of path	−0.15 (0.03)
Food in path	0.76 (0.03)
Adjusted R^2	0.60
Small core group	
Size of path	−0.41 (0.04)
Food in path	0.27 (0.04)
Adjusted R^2	0.25

relationship between environmental contexts (e.g., seasons) and social structures (e.g., movement bias) in baboon troops. Cross-sectional studies could also highlight differences between different groups within a population under differing environmental conditions, as well as cross-species comparisons (Reyna-Hurtado et al., 2017).

The *Papio* baboons offer great potential for understanding the interplay between social and environmental structuring, given their wide geographical distribution and variation in social structures across the different allotaxa (Barton et al., 1996; Jolly, 2001; Henzi et al., 2009; Schreier and Swedell, 2009; Patzelt et al., 2011; Snyder-Mackler et al., 2012; Weyher et al., 2014). Determining whether and how often baboon groups adopt the optimal configuration needed to exploit environmental resources is another means of investigating variation in the scope and limits of ecological plasticity across various allotaxa, helping to refine phylogeographic models, and enabling us to generate an understanding of baboon evolution that incorporates the complexities of history. For example, we can determine whether the internal influence structure of troops is responsive to variation in

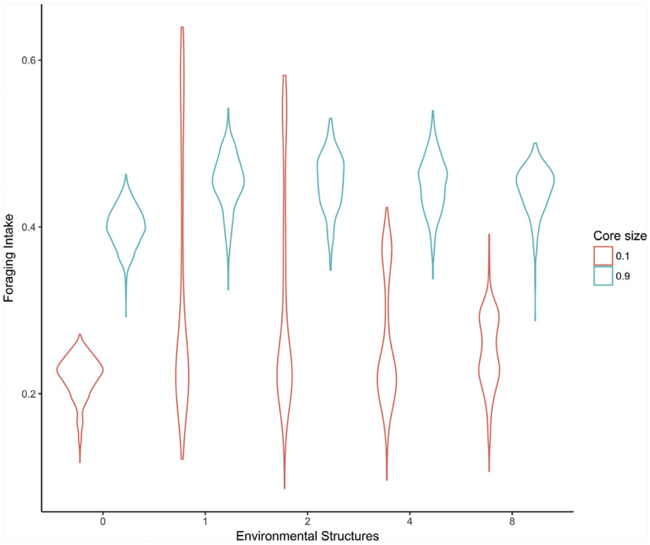

Figure 8. Foraging intake for large core and small core groups when varying environmental structure. Environmental structure varied from no additional structure (0 = uniform distribution), to the addition of one long high-density resource path, to an increasing number of smaller and more numerous high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

environmental structure within a single group, or whether a given group's influence structure is dictated solely by social factors and cannot adjust to environmental variation, such that certain internal structures represents a cost in terms of foraging efficiency. This, in turn, can give some insight into the variation on which selection has acted (and can continue to act, potentially). In the first example, if group-level structures are responsive to ecological variation it suggests that animals are capable of altering their behavior to produce different internal structures, and hence selection may have acted on individual behavioral flexibility. In the second example, where structures are more fixed and incur foraging costs, then aspects of the structure itself (and the individual attributes that underlie them) may have come under selection, such that particular kinds of traits are favored in particular habitat types and ecotypes. In the latter case, the costs in terms of flexibility in the foraging realm may be balanced against benefits in other domains, such as mating and other aspect of male–female relationships, including adjusting to the risk of infanticide. Building on our simulated results, we may therefore be able to acquire an even better grasp on how social structure enables baboons to make the best use of space, time and energy on an ecological time-scale. Combining this approach with the rich empirical database on baboon behavior, ecology, and phylogeographic patterns, will also allow us to develop models of baboon behavior on an evolutionary time-scale, further enhancing the value of baboons as analogs for hominin evolution.

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Conflicts of interest

We declare we have no competing interests.

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Supplementary Online Material

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