A Social Networks Approach to Sheep Movement and Leadership

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Networks of interactions based on social associations and movement offer insights into group organization and dynamics, and provide unique tools for biologists[1-5]. An important topic in animal social behavior is how individual differences drive group behaviors and shape collective decisions[6]. The identity of influential individuals may vary by behavioral context – one individual may lead group movements, while another influences group consolidation when subgroups disperse. Therefore, identifying influential individuals and determining how they exert influence is not a trivial task. Social network analysis helps biologists understand group structure, movement, and the spread of information.

We used dynamic and static networks to determine the role of leadership and subgroup associations on movement patterns and group organization. Over seven days, we collected behavioral and spatial data on 19 individually-identifiable domestic sheep at Mpala Conservancy, Kenya. To identify the movement and association preferences of each sheep, we recorded at fixed intervals how frequently individuals were observed in front of the herd or alone, and whether they influenced group movement. Group movement was initiated when a sheep in front of the herd either led the group (pulling) or was displaced by another individual (pushing).

Using Principle Components Analysis (PCA), we reduced 13 behavioral measures into two independent components, which explained 71% of the variance. The first component was based on spatial position - the frequency of being observed in the front, back, periphery and/or center of the herd. The second component focused on the influence of others in group movement, and was based on individual's ratio of pushing to pulling, number of initiated pulls that were followed, and ratio of pushing to being pushed. By plotting these two scores against each other, we grouped sheep into five categories. We identified five groups based on the two PCA loadings – positive loadings on both, negative loadings on both, two combinations of positive and negative loadings, and scores near zero for both components. Although not all individuals fell into these five categories, these represented most sheep and showed that sheep had distinct 'personalities' (PCA score combinations).

The PCA results helped guide our social network analysis. Since one component was based on pulling and pushing, we generated networks for these behaviors. Each time we observed a pull, we recorded the identity of both the puller and the followers. Based on how frequently an individual pulled and who followed, we constructed directed weighted networks. We repeated this for the push data, and produced a second directed weighted network. These two networks showed some striking results. Although there was a high level of individual variation, a few sheep were clearly influential in leading movements. Consistent with the PCA scores, some individuals tended to be primarily pullers while others tended to be followers or displacees rather than taking an active leadership role. The pull network also showed that a single sheep had high degree and was responsible for a disproportionately high number of pulls; observations also confirmed that she was a 'leader'. On the other end of the spectrum was a 'loner' sheep; she was occasionally seen pulling, but had low betweenness scores and never pushed or was pushed by others.

In addition to the movement data, we looked at social associations between individuals by recording individuals in distinct subgroups. A subgroup was defined as a group clustered at least five meters away from the nearest sheep. Inter-individual distances within the subgroup were less than five meters, generally 1-2 meters. We also recorded relative spatial position (center vs periphery, front/middle/back of the herd).

Since all sheep moved between subgroups, the static network based on subgroup associations resulted in one large clique and was therefore uninformative; all sheep had similar degree, clustering coefficient and betweenness scores. As a result, we decided to retain the temporal fission/fusion pattern, and generate a dynamic network that identified communities by minimizing the costs of changing groups or associations[7]. We computed dynamic metrics[8, 9] equivalent to those derived from static networks and showed that even though diameter was same in both networks, density and clustering coefficient decreased in the dynamic network. This suggests that the dynamic networks revealed less frequent interactions that were not seen in the static networks. Based on PC1 scores, sheep with high probability of being in the center of the herd had high values of average degree, dynamic degree, and cluster coefficient. PC2 scores based on pushing and pulling revealed no correlations with any network measures.

Examination of the actual community switches showed, however, that personality scores based on pushing and pulling were important and negatively correlated with number of times an individual switched groups. Sheep switching groups had higher dynamic degree scores, possibly due to the increased number of associates in different groups. Since sheep with high PC2 scores switched their groups less often, it is possible that their group-level influence was based on the increased number of interactions resulting from their community loyalty.

Overall, our study demonstrates the value of using dynamic networks in situations where static networks are uninformative about the biological determinants underlying associations. By addressing many aspects of an individual's behavior and reducing these behaviors to two variables, which we then correlate with social network metrics, we can identify a few key individuals with a disproportionate influence on others. This influence is shown either by the way they initiate group movement or by the centrality of their physical presence in social interactions.

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