

Behavioral Ecology: Social Organization in Fission–Fusion Societies

Scaling from individual movement and decision-making to population structure is central to ecology; recent studies of African elephant populations which have taken this approach have shed new light on how complex, multi-level social systems are organized.

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In many group-living species, integrated movement decisions made by individuals scale up to group motion. Groups merge (fusion) or split (fission) as they move through the environment, making group composition a dynamic property. If individuals can modify the persistence of associations with certain others, complex higher-order social structure can result. African elephant societies represent one of the most sophisticated ‘fission–fusion’ systems, unusual in their flexibility and potential for multiple scales of organization; social groups can divide into small parties with one or two individuals, or parties and social groups can fuse with other groups to form aggregations of hundreds of animals. Recent studies by Wittemeyer *et al.* [1] and Archie *et al.* [2] have investigated association structures in wild elephant populations; by revealing the importance of both ecological and genetic factors they have provided answers to long-held hypotheses about the organization of elephant societies.

Animal population substructure has profound implications for the transmission of disease and socially transferable information, and is a prerequisite for the evolution of reciprocally altruistic behaviors. How, and why, associations form and persist in animal populations is still poorly understood however, even in relatively simple systems. Small freshwater fish, for example, exhibit fission–fusion dynamics with non-random associations,

individuals forming a community structure with ‘social cliques’ [3]. Initially it may seem surprising that organisms as simple as small fish have the capacity for inter-individual discrimination, especially when considering the huge number of potential pairwise interactions in natural populations [4]. Theoretical studies, however, have shown that non-random assortment of individuals within a population can occur without any individual recognition capabilities at all; if individuals differ with respect to behavioral or motivational properties, they can spontaneously form persistent, and closer, associations with others that are similar to themselves (‘self-sorting’) [5].

In addition to ‘passive’ self-sorting, individuals in groups often exhibit ‘active’ preferences,

such as associating more strongly with familiar individuals. Even subtle environmental cues can have a strong influence on the associations that develop. In certain species of fish, individuals exhibit strong preferences for associating with others that have experienced the same diet or habitat conditioning as themselves [4,6], yet direct experience of others may not be used in making such decisions (perhaps being difficult or costly to encode cognitively [4]). Thus, even without complex recognition capabilities, individuals within populations can influence their probability of being associated with certain types of individual, and even specific individuals, over time.

The challenge remains, however, to ascertain how, and why, social attraction scales to within-group and population-level structures. There are processes of importance that occur over a range of timescales, from the short-term modification of direction in response to other group members, to processes such as familiarity which may be built up over hours, days or even weeks, to those that are relevant over the reproductive lifetime of individuals. Similarly, processes of



Figure 1. Elephants on the move.

African elephants live in a society in which fission and fusion of mobile groups creates hierarchical structures over a range of scales. (Photo by Tom Morrison.)

evolutionary significance often occur over a broad range of scales [7]. Evading a predator may require regular vigilance and rapid reactions, whereas locating appropriate habitat in an unpredictable environment may occur over a much longer time and spatial scale.

Relating the scales of organization that underlie fission–fusion behavior is particularly challenging when the organisms involved, and corresponding social systems, are even more complicated. Long-lived and cognitively complex organisms such as dolphins, chimpanzees and elephants all live in flexible fission–fusion societies where intricate social interactions and decision-making scale to organisational complexity at higher levels. As is common in many collective systems, local actions and interactions create higher-order properties, which may in turn modify individual behavior; creating a recursive relationship — one involving feedback among levels of organization — making cross-scale studies crucial [5,7]. A further aspect of social systems that is very important to consider is relatedness among members of a population and the ability for individuals to associate with close kin. Associating with relatives can strongly influence the evolution of social behavior through kin selection and therefore may be an important determinant of who tends to associate with whom, and for how long.

Two recent studies [1,2] have advanced our understanding of the importance of scale, and of relatedness among individuals, in separate wild populations of the African elephant *Loxodonta africana* (Figure 1), demonstrating that such complex social systems can indeed be tractable. Wittemeyer *et al.* [1] quantitatively identified distinct ‘tiers’ of social organization, and investigated both how multi-level structures emerge in populations and how relationships among them are affected by ecological properties such as seasonal

changes in resource availability. Archie *et al.* [2] combined observational association data and genetic information to investigate the importance of kin associations in determining structure at different hierarchical levels within elephant populations.

Both of these studies focused on associations among female breeding elephants with calves (calves were always found close to their mother). The lowest social unit in these studies is therefore that of *mother–calf*. Wittemeyer *et al.* [1] used cluster analysis techniques to search for higher-level structuring in an elephant population. Confirming previous qualitative work [8], they found that mother–calf units combine together to form higher-level *core groups*, which, although stable, do have the capacity to undergo fission. Core groups themselves were found to have non-random associations with one another, forming what are termed *bond groups*. These tended to be more ephemeral than core groups (exhibiting a higher probability of fission), particularly during the dry season when competition for food may increase, outweighing aggregation benefits such as protection from predators or alloparental care of young [1]. At a higher level still, further non-random associations were found among the bond groups. Understanding the functional significance of such high-order structure is difficult however, and, as the authors point out, it is possible that this highest order structuring may emerge from social processes but have little, if any, adaptive significance.

Archie *et al.* [2] also investigated the multi-level social structure of African elephants, specifically addressing the question of whether relatedness among individuals determines observed fission–fusion dynamics within and between the core groups (strongly cohesive groups of mother–calf units). Analyzing both mitochondrial and nuclear DNA from individually recognizable elephants within known core groups, they

confirmed that individuals do tend to be highly related — they are sometimes termed ‘family groups’ — and that, if core groups undergo fission temporarily, adult females are more likely to remain with first-order maternal relatives (mothers, daughters and maternal sisters). When considering the relationship between relatedness and fission–fusion at the higher bond group level, however, they found that, with the exception of core group matriarchs (the oldest female), members of bond groups were found not to be closely related. These results indicate that evolved cooperative social behaviors will enhance inclusive fitness only through their effects on core group members.

These new studies [1,2] have elucidated important roles of both ecological processes and relatedness in complex multi-level societies of the African elephant. Many questions still remain about the functional complexity of fission–fusion social systems and recent technological advances in automated tracking of individuals [9] and mathematical modelling are likely to provide particularly valuable new information. As many species with complex social lives (such as chimpanzees, cetaceans and elephants) are threatened by human influence, understanding the social behavior of these species, and how anthropogenic modifications of the environment impact social organizations, may prove critical for future conservation efforts.

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Time Perception: Space–Time in the Brain

Accurate timing over the sub-second scale is essential for a range of human perceptual and motor activities, but the mechanisms for encoding this time scale are poorly understood. Recent work is suggesting that timing does not involve a centralised clock, but patterning within a distributed network.

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Time perception over fine scales is fundamental to many aspects of our lives, including speech recognition and production, motion perception, sound localisation and fine motor coordination. Many of these tasks do not require explicit encoding of time: perception of visual motion, for example, relies on the output of spatio-temporally tuned neurons rather than on independent estimates of space and time. However, the conscious awareness of the passage of time and judgement of duration do require an explicit representation of time. Although we now have a quite firm understanding of the mechanisms of many processes that involve temporal encoding – such as binaural sound localisation and motion perception – the mechanisms that allow us to estimate the duration of events are far more elusive.

The prevailing model for event timing has involved a centralised internal clock or pacemaker feeding into an accumulator (for example, see [1,2]). More recent models, however, consider distributed timing networks, with different mechanisms timing different interval lengths [3,4]. While there is good evidence for different clocks for different interval lengths, most evidence to

date suggests that clocks transcend sensory modalities. For example, performance in rhythmic tapping is well correlated with the ability to judge the length of auditory intervals of similar periodicity [5], implying a common mechanism. Similarly, training in somatosensory interval discrimination – which can cause a 2-fold improvement in performance – generalises across skin locations and also across modalities to improve auditory discrimination of similar intervals [6], and learning a visual discrimination of stimuli presented to the left visual hemifield transfers completely to stimuli in the right hemifield [7].

A new study, reported in this issue of *Current Biology*, questions the notion of centralised cross-modal clocks. Johnston *et al.* [8] have shown

Figure 1. The main experiment of Johnston *et al.* [8].

Subjects fixated at centre while observing a spatially localised grating move rapidly, alternately leftwards and rightwards, for 15 s. After a brief pause a 'standard' grating was presented for 600 ms on the unadapted side (brown symbols) followed (or preceded) by a probe of variable duration on the adapted side (grey symbols), and subjects asked to judge which appeared longer (in the actual experiment they were sequential, not simultaneous). In order to appear the same duration as the standard (brown bar), the probe presented to the adapted retina had to be about 100 ms (17%) shorter (grey bar).

that adaptation to a fast-moving (20 Hz) spatially localised grating decreases the apparent duration of subsequently presented gratings by about 17% (Figure 1). The adaptation does not affect the apparent duration of auditory tones, nor of visual stimuli displayed to spatially different positions, whether in the same or different hemifield. Various control experiments excluded the possibility that apparent temporal frequency, reduced via adaptation, was responsible for the diminution in apparent duration. Interestingly, the adaptation did not affect the perceived onset or offset of the visual stimuli (measured by auditory matching), only the apparent duration between them.

The results suggest that the timing of visual events is more complicated than counting the pulses of a centralised pacemaker: not only were auditory events unaltered, but the adaptation was spatially specific. Johnston *et al.* [8] argue that their results show that duration is governed by a spatially localised temporal rate signal that is subject to adaptation; this would be consistent with classical and recent work showing that moving

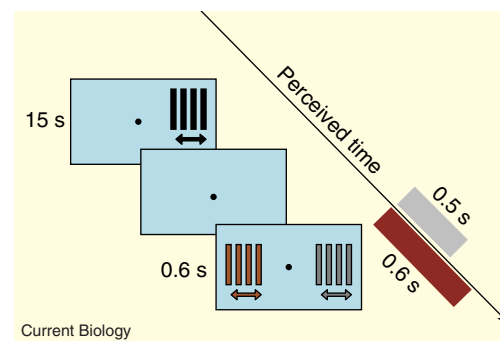


Figure 1. The main experiment of Johnston *et al.* [8]. Subjects fixated at centre while observing a spatially localised grating move rapidly, alternately leftwards and rightwards, for 15 s. After a brief pause a 'standard' grating was presented for 600 ms on the unadapted side (brown symbols) followed (or preceded) by a probe of variable duration on the adapted side (grey symbols), and subjects asked to judge which appeared longer (in the actual experiment they were sequential, not simultaneous). In order to appear the same duration as the standard (brown bar), the probe presented to the adapted retina had to be about 100 ms (17%) shorter (grey bar).