AUTHOR DRAFT VERSION

The long reach of family ties

In hyena societies, social networks are inherited with wide-ranging implications for social behaviour.

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In social species, the social structure of the population shapes many aspects of individuals' lives. Network analysis allows the quantification of social structure, detailing how individuals are tied to one another through associations within a 'social network'(*1*). While the importance of social networks for behavior and ecology is becoming well established, the processes that govern the underlying structure, and individuals' social positions relative to others, are less well known(*2*). On p. 348 of this issue, Ilany et al.(*3*) apply social network analysis to 73767 social associations observed between 482 wild hyenas during a 27-year study that spanned multiple hyena generations. They provide empirical support for a proposed model(*2*) that inheritance of social network ties - specifically that offsprings' social bonds are derived from their mothers' social affiliates - plays a key role in shaping social structure across generations. Ilany et al show how the dominance rank of the mother and the strength of her bond to her offspring affects the extent to which her social associations are passed onto them, and even that the offspring's inheritance of their mother's social ties may be linked to survival, thus providing a potential selective force promoting the evolution of the inheritance of social networks.

Generally, the emergent properties of animal societies can be thought of as resulting from individual-level variation in behaviour, and individuals' interactions with others(*1*). Since these behaviours might have quite simple bases, but nevertheless lead to complex social network structures(*4*), it is reasonable to suggest that social network properties of individuals might have reasonable heritable components. Indeed, evidence from a range of organisms, from humans to fruit flies(*5*) supports this. However, what Ilany et al. demonstrate is an altogether richer phenomenom. Through combining detailed observations with social network analysis (Figure 1), they demonstrate that the specific social relationships of hyenas resemble those of their mothers, that this resemblance persists for many years, even after parent-offspring social relationships weaken, that offspring of higher-ranking mothers and with closer bonds to their mothers inherit their social networks to a greater degree, and even that this greater degree of social network inheritance predicts increased survival of the offspring and of the mother. Hence, rather than the social tendencies of offspring resembling their parents, it is the specific social networks that are inherited (Figure 2A).

Ilany et al. provide new insights into the generation of variation in social structure and into how inheritance and sociality interact, but their results also have wider implications that currently hold unrecognised importance. The consequences of network structure have been well demonstrated for the interacting individuals within generations(*1*). However, if specific interactions carry over into subsequent generations, this trans-generational legacy in social interactions between similar genotypes (albeit different individuals) from year-to-year has

implications for our understanding of processes that co-evolve with social behaviour. Social inheritance of association networks causes a strong covariance between the many consequences of social structure and inherited genetic variation over generations (Figure 2B). Below, we outline conceptual examples of the important consequences that social inheritance may have for social transmission (focussing on contagious pathogens or other socially-transmittable microbiota, and on socially-learn behaviours), and for social interactions (focussing on the emergence and maintenance of cooperation, and on competitive interactions).

A prominent example of social transmission relates to the transmission of pathogens, or other microbiota, and much research focusses on disease-causing organisms(*1, 6*). When social structure persists across generations through inheritance, and susceptibility or immunity is also inherited, it creates a link between these, and could either increase vulnerability to disease (through disease persisting in susceptible groups across generations) or decrease risk (through immunity or reduced susceptibility within clusters). For instance, imagine a pathogen whose transmission probability is determined by specific gene-for-gene matching with hosts; under this model of social inheritance, parents and offspring are much more likely to be exposed to the same specific lineages of parasites, and vice versa, and coevolutionary interactions between host and pathogen genomes may be accelerated. Aside from contagious pathogens, there is mounting evidence that helpful bacteria are also spread socially for many species, particularly in terms of skin and gut microbiome(*7*), and that transmission occurs both vertically (from parent-to-offspring) and horizontally (between peers). As such, inheritance of social interactions across generations, whereby individuals inherit social associations from a parent, should contribute to stablising the composition of these communities through promoting persistence of particular socially-spread microbiota and reducing mixing across generations.

In almost all social systems, diverse types of information are also socially transmitted between individuals. Information can spread on social networks just like a disease can, as individuals gain the new information, adopt the behaviour, and then subsequently transmit this to others(*6, 8*). Unlike infectious diseases, however, these 'behavioural contagions' frequently depend on much more than exposure to contagious individuals. Individual decisions surrounding whether to adopt a socially-informed behaviour may, for instance, depend on if they conform with the majority of the population, or which of their specific associates are performing the behaviour, even in relatively simple animal systems(*9*). These 'social learning strategies'(*10*) can cause behaviours to spread more efficiently on heavily clustered social networks, rather than diffusely connected networks that often facilitate disease transmission(*8*). Therefore, as the inheritance of social ties that Ilany et al demonstrates forces social networks into clustered structures which persist across generations(*3*), this may promote the spread and establishment of socially-informed behaviours within groups compared to systems without social inheritance. Furthermore, social inheritance and the resulting cross-generational clustered networks of this kind may support the development of behavioural traditions or animal 'cultures', which require the initial social spread of behaviours and the maintainence of these particular behaviours over time as individuals learn these from their group members(*11*) both between- and within-generations.

Aside from social transmission, many other aspects of life depend on social behaviour. Social interactions themselves take many forms, but can often be classified as affiliative and cooperative interactions or, alternatively, antagonistic and competitive interactions. There is a rich theoretical literature that stresses the importance of social network structure for the evolution of cooperation(*12*). The type of social inheritance demonstrated by Ilany et al implies that interactions between specific genotypes persist across generations, and hence greatly increases the persistence of such interactions, as well as the chance for reciprocation of cooperative actions. The trans-generational carry-over of social structure also implies that competition will be occurring between the same interacting genotypes more than by chance, and this thereby presents the opportunity for reduced competition through prior familiarity - sometimes termed the 'dear enemy effect' to occur across generations.

The novel finding presented by Ilany et al. are in the context of a highly social species, with matrilineal social structure and inheritance, but this mechanism may have wider applicability. While the work here, and prior modelling(*2*), has focussed on social inheritance through kin-structuring, an open question is whether the same process could operate in non-kin structured systems too. For example, any animal (or plant) population for which offspring show limited dispersal might result in an increased tendency for offspring to interact socially with the same individuals that their parents interacted with, or even with the offspring of those individuals that their parents interacted with. As such, the existence of social inheritance provides a general potential for the social choices of the parents to directly influence the social setting of their offspring. Future work should seek to examine how widely specific social relationships are inherited in range of population structures, and what implications this has for the rate of evolution of the many proceses that depend on social network structure.

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Figure 1 and Figure 2: Transgenerational social network inheritance:
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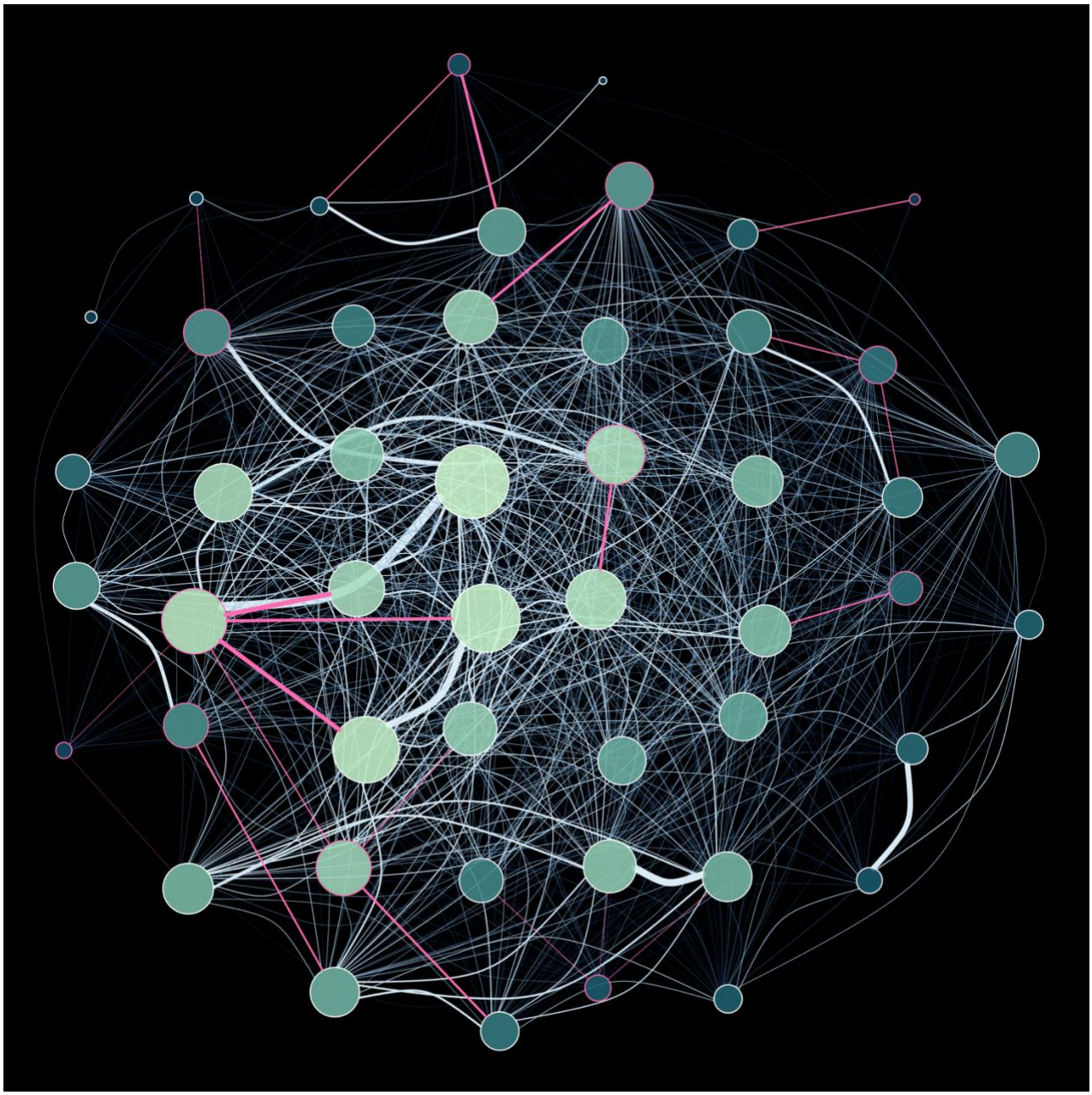

Figure 1 Hyena network showing the empricial social data (from year 2004) illustrating the intricacies and complexities of the society. Points show individuals with size and colour denoting their social centrality (larger and lighter = more social), and lines show social associations, with thickness and shading denoting the strength of the bond (thicker and brighter = stronger). Pink lines highlight the mother-offspring social bonds and pink circle outlines show the mothers.

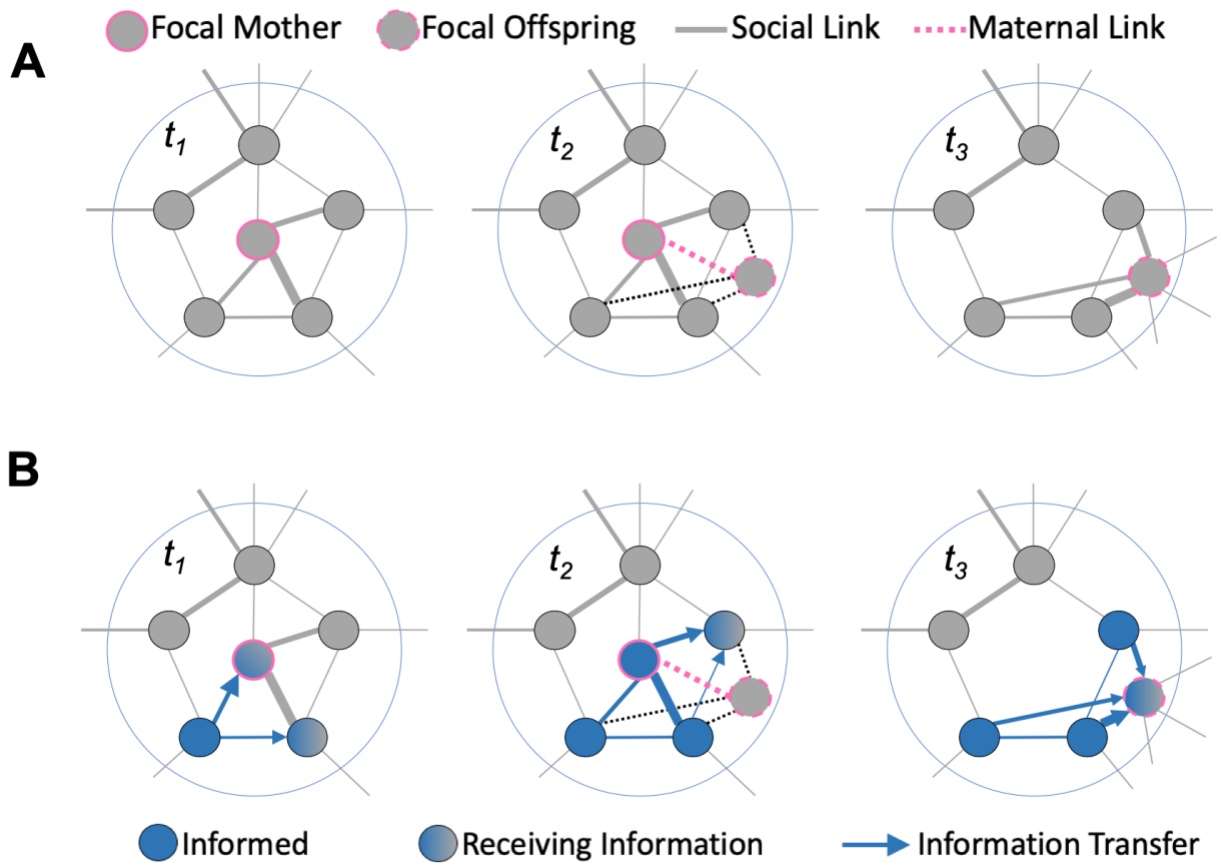

Figure 2. A) Toy networks demonstrating a social network inheritance process over three simple stages. Stage t_1: Focal mother (outlined pink) holds different strength social bonds to its associates, Stage t_2: Focal mother produces offspring (dotted pink) who is socially bonded to their mother (pink line) and inherits their strongest social bonds (dotted dark lines), and Stage t_3: Focal offspring maintains the social bonds it inherits from its mother even after it loses its maternal bond and as it gains new bonds. B) Demonstration of social inheritance influencing social processes using information spread as an example. Stage t_1: An informed individual (blue) passes a new behaviour (blue arrow) to its associates (the focal mother and another), Stage t_2: Newly informed individuals also pass on this behaviour and the mother's offspring who thus inherits social bonds to informed individuals, Stage t_3: Focal offspring is exposed the same information as its mother and also adopts the behaviour.