Shark Social and Spatial Networks

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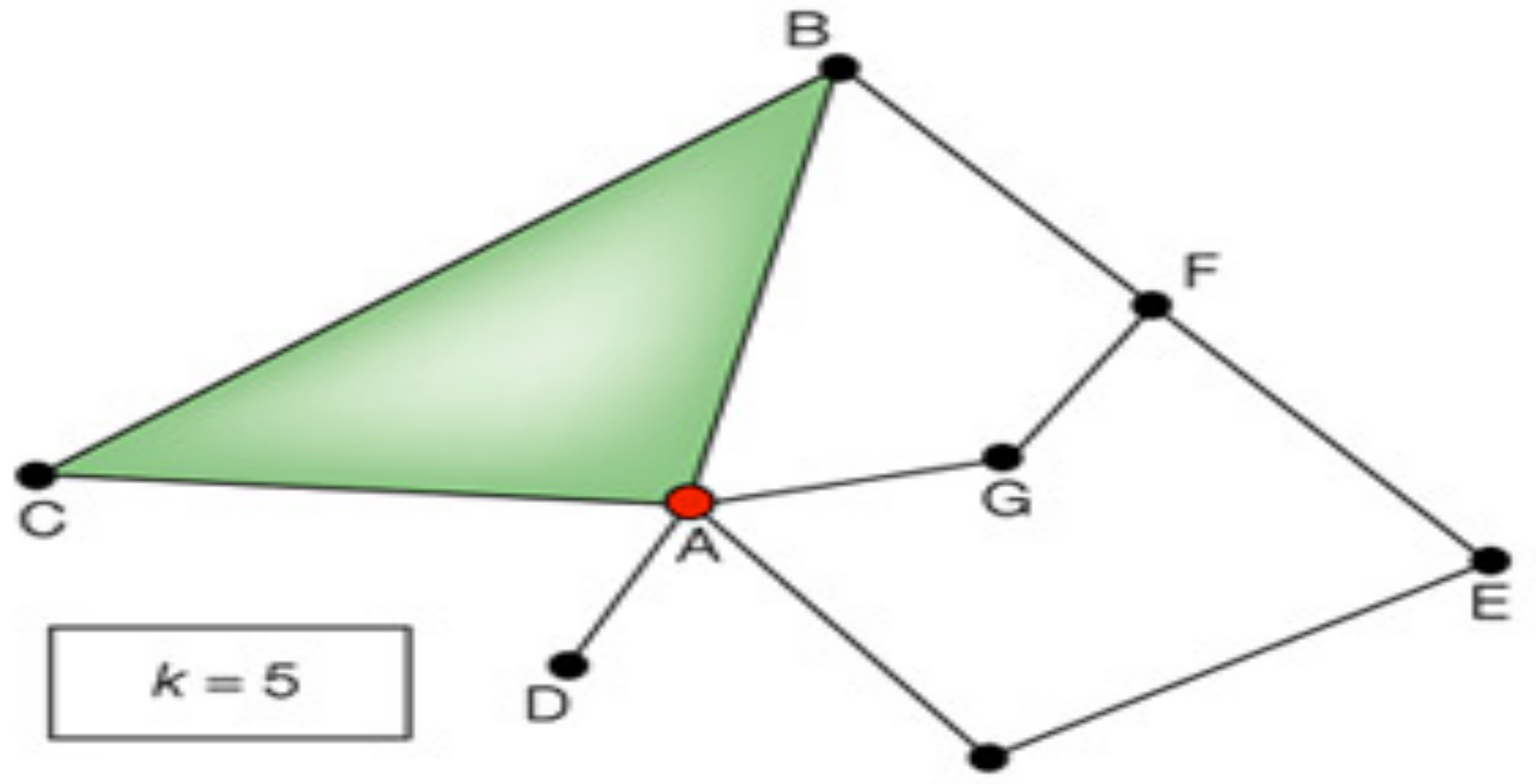
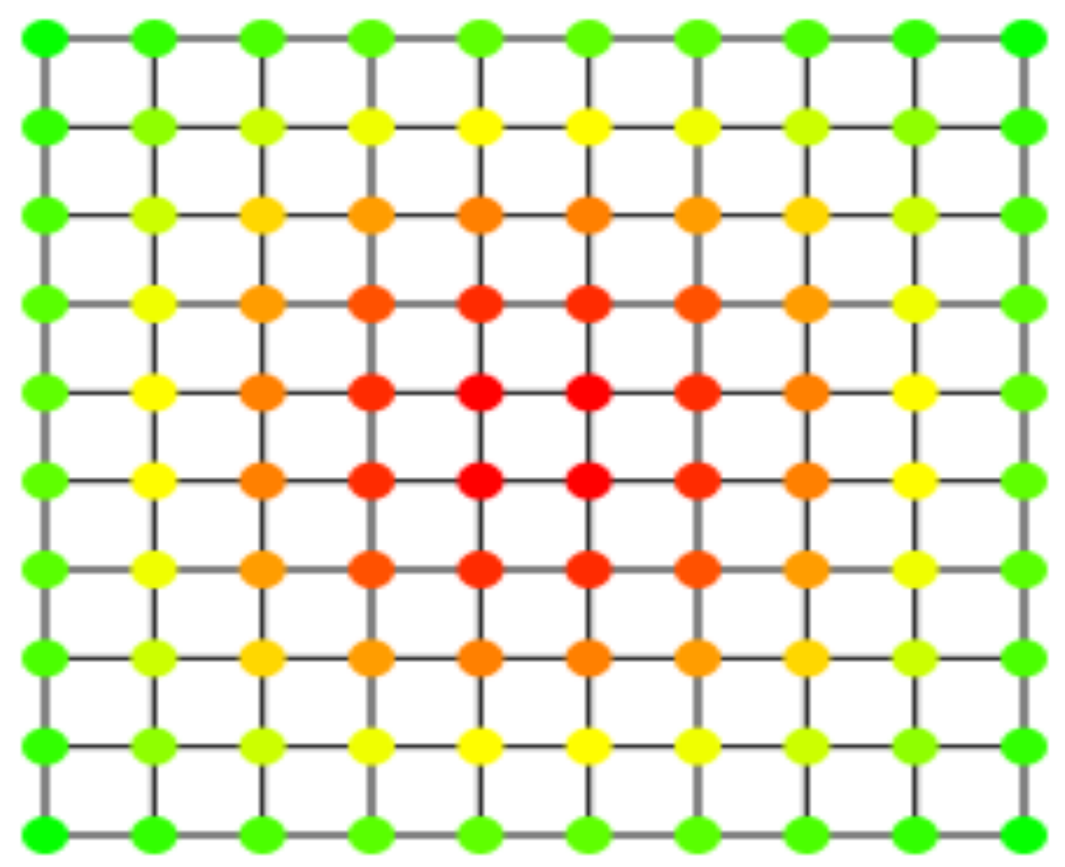
Introduction

The study of animal behaviour is complex and multifaceted and is difficult to study using conventional approaches. One aspect of behaviour, which is particularly informative from an industrial and conservational point of view is is the spatial distribution of an individual in relation to its environment. This aspect is governed by a number of factors including predation and availability of food, but perhaps the most complex of drivers is social interaction. The shark as a top predator is an important species ecologically and to the fisheries industry, moreover, sharks have a high brain to body mass ratio and acute vision, suggesting the likelihood of a physiology suited to complex social dynamics.

The modelling of complex phenomena is often made manageable by the employment of networks, which provide versatile graphical representations of interacting systems. In these networks nodes represent interacting components (such as individuals or spatial locations) and edges connect nodes known to interact, and can be weighted with a relative strength. Recent developments in network analysis have matured the field so that it is ripe for application to ecology. Of these network metric constitute an important subset and have proven useful in characterising a range of network properties. The simplest property of a node is its degree which is the number of other nodes it is connected to. The weighted analogue of the degree of a node is the sum of the weights of its connected edges. A further useful characterisation of a network node is its betweenness. This measure quantifies the number of shortest paths between any two nodes in the network that pass through the node and thus is a measure of the centrality of the node, which can have a number of different interpretations depending upon the context.



A simple network displaying the concept of degree, the degree of node A is 5.

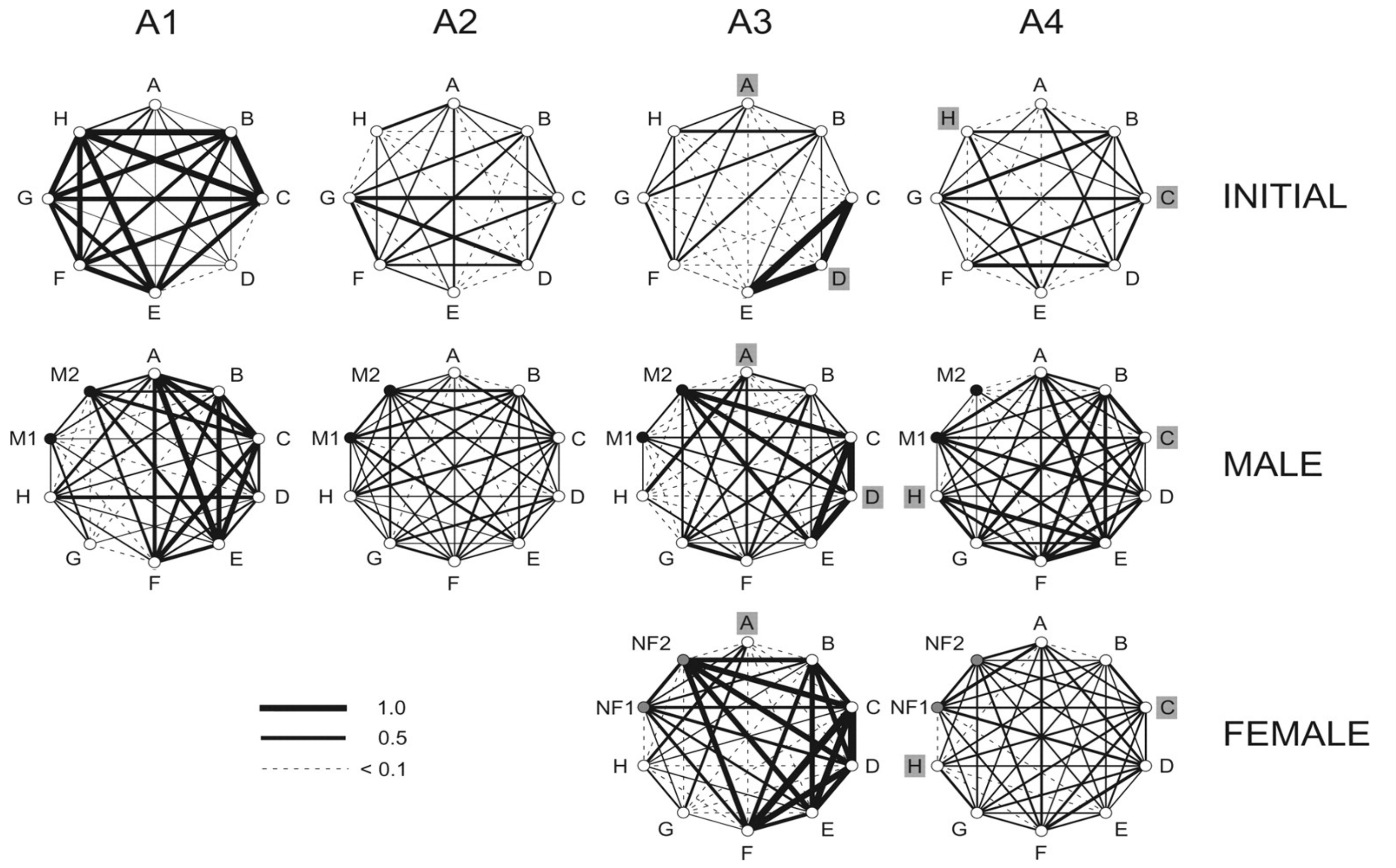


A network displaying the concept of betwenennss centrality. Red nodes have a high betweenness and green nodes have a low betweenness.

Sexual Social Network Structure in *S. canicula*

Sexual segregation has been observed across a large variety of animal societies and is generally attributed to differences in energetic investment in progeny across the sexes leading to dichotomous behavior. Such segregation is observed frequently in the small spotted catshark *S. canicula*. Females of the species generally co-aggregate in shallow warmer coastal waters and display a limited range of migration, while males occupy deeper offshore waters, displaying a large range of migration. Thus intersexual interactions in this species may display differences relative to intersexual interactions.

This hypothesis has been explored in detail in [1], where the social dynamics of independent groups of 8 female catsharks was analysed before and after the introduction of 2 new males and (independently) 2 new females. The results are summarized in the following figure:

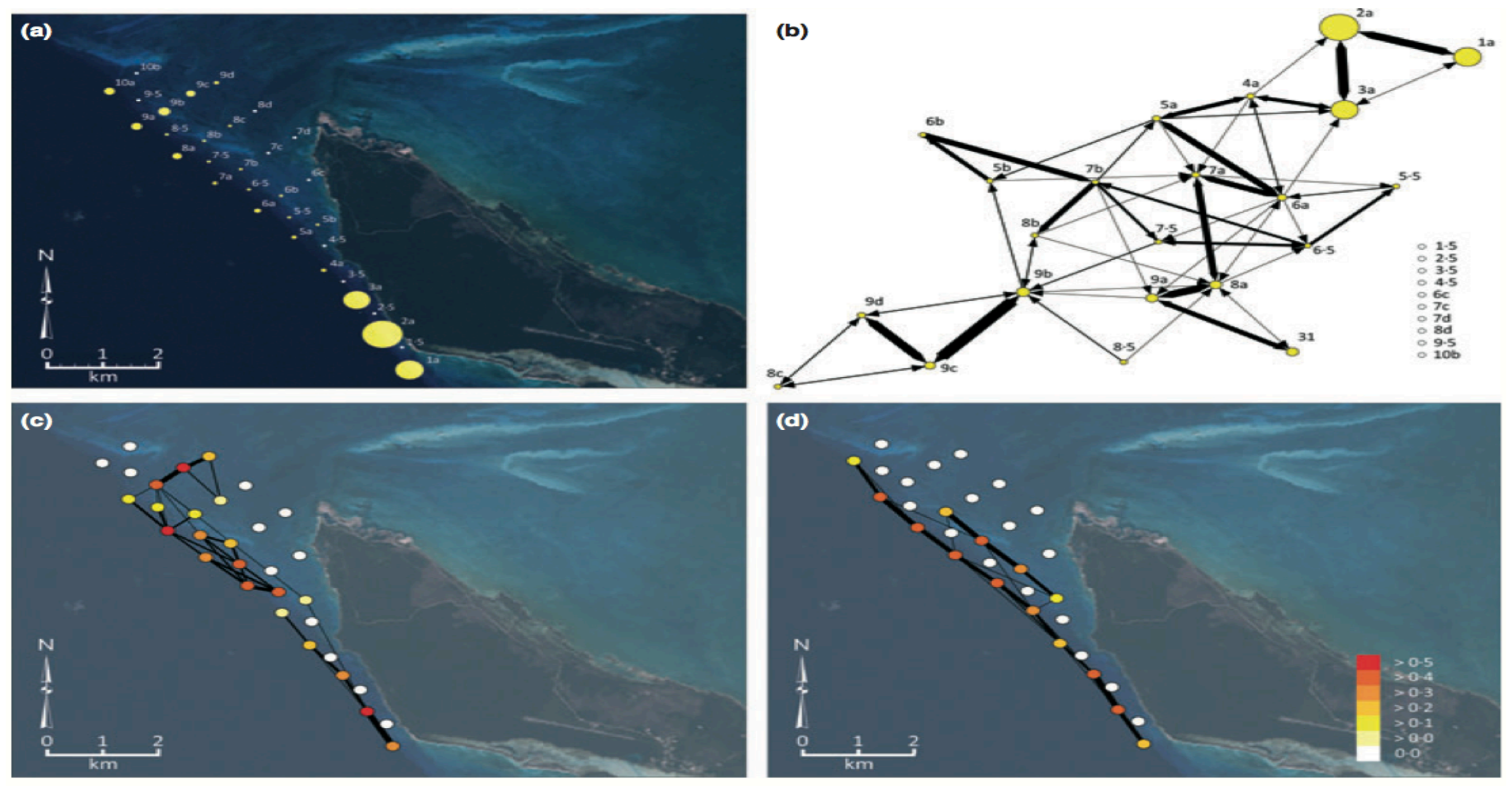


Social networks of the 4 independent shark societies (A1-4) analysed in [1], before introduction of new sharks (INITIAL), after introduction of new male sharks (MALE) and after introduction of new female sharks (FEMALE). White nodes represent resident female catsharks, black nodes represent introduced male sharks and grey nodes represent introduced females. Edges width is proportional to the relative frequency of resting contact observed between the connected pair of sharks (a measure of social preference).

S. canicula has been posited from observation and physiology to display a complex social lifestyle, with a large degree of behavioral diversity across individuals. This is verified in the analysis in [1] where initial social structure in the four groups are found to be significantly different from what is to be expected from chance. Two distinct social set-ups emerge, a heterogeneous structure (A1 and A3) where the majority of social interaction is attributable to 3 or 4 key catsharks which display preferential interactions, and a homogenous structure (A2 and A4) where all sharks display a similar degree of interaction and no clear preference. The heterogeneous structure is interpreted as representing strong ties between a small number of sharks whereas the homogeneous structure is interpreted as a loose, weak social structure.
The two social structures respond differently to the introduction of new males. In the heterogeneous structures male interactions were kept minimal in general, however peripheral females with a low weighted degree prior to introduction, i.e. not involved in a tight social clique, displayed a rise in association with other group members, which persisted and grew after acclimatization. Overall the mean association levels dropped on the introduction of males. The weaker social structure permitted the integration of the new males into the group but displayed a similar increase in association for peripheral females, in one case to the point that the peripheral females become dominant after acclimatization. Overall the mean association in this group rose.
The introduction of new female catsharks into the two social groups intriguingly instigated the opposite trends in overall mean associativity to male introduction. Associativity increased on average in the heterogeneous group and fell in the homogeneous group.

Spatial Dynamics in *C. perezi*

The movements of animals in natural environments can be tracked by tagging the animal and subsequently detecting the tag using acoustic receivers. Receivers are fixed in an array in the animal's natural environment as shown in figure a) and are represented as nodes in the network. An edge then represents a recorded movement between the two nodes and can be weighted by the observed relative frequency with which the movement is made.



Classic approaches focus simply on the frequency at which each node is visited, represented in figure a) by the node size. This, however, gives a rather static picture of the behaviour. By using the time ordering of observations to infer edges, more recent analysis hopes to extract a more dynamic picture of the behaviour.[2].

Figures c) and d) show the network created via data from a male Caribbean reef shark in separate seven month intervals. The degree of the nodes is represented by the node colour and edge weight is represented by line thickness. This visualisation shows a clear change in behaviour between the two periods - the movement becomes more oriented towards the coastal shelf as the sharks ages. Nodes with a high degree are returned to often from a range of different locations and can thus be interpreted as part of the home range of an animal. Figures c) and d) show a clear change in the home range of the shark between the two time periods.

Figure b) shows an alternative representation of the network. Instead of placing the node by geographical location, spring embedding and node repulsion are used to place nodes based on centrality measures which gives a different perspective.

Another question which can be addressed using network analysis is to what extent is the behaviour of an animal changed by the destruction of part of its habitat. This is obviously an important question due to the increased impact that human activities are having on animal habitats. The destruction of part of the habitat can be modelled by removing a node from the network and calculating the effect this has on various network metrics. An example of the analysis is summarised in the table below. It can be seen that connectedness, as measured by betweenness, is severely reduced by the removal of a targeted, highly central node but less so by a randomly chosen, less central node. Interestingly, the nodes chosen had a similar total number of detections but a very different impact when removed. This shows the limitation of classical frequency based approaches.

Network	Node removed	E	$E–E_{\text{sim}}$	Detections (n)	P*
Full	—	**1·207**	**0·000**	—	—
Random	9a	1·129	0·079	462	0·210
Targeted	9b	0·754	0·454	550	0·044

[1] D.M.P. Jacoby et al, Sex and social networking: the influence of male presence on social structure of female shark groups, *Behavioral Ecology*, 2010.
[2] D.M.P. Jacoby et al, Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analysis, *Methods in Ecology and Evolution*, 2012