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Social Networks in Wild Asses: Comparing Patterns and Processes among Populations

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Social Networks in Wild Asses: Comparing Patterns and Processes among Populations

D.I. Rubenstein, S. Sundaresan, I. Fischhoff & D. Saltz

Abstract

Asiatic wild asses inhabit some of the most arid environments in the world. All live in fission-fusion societies, but demography varies and the deserts in which they live often differ in subtle ways. Characterizing details of social structure of wild ass populations has been a challenge and has made it difficult to determine causes and consequences of any differences that might exist. We use network theory to compare the social structures of two populations of Asiatic asses/onagers inhabiting the Negev desert, Israel and khur of the Little Rann of Kuch, India and show that populations differ in important structural ways that represent adaptive responses to variations in ecological demographic and phenotypic circumstances. Our analyses show that onagers inhabiting more variable environments than khur also live in larger, more cohesive groups than khur. Presumably networks with this structure facilitate the spread of information and foster cooperation. We also show that demography matters since social fragmentation increases as populations grow. Increases in the number of components in populations, reductions in the number of associates and diminished cliquishness within components, appear to be adaptive responses to integrating increasing numbers of individuals into social networks. We also find some support for the idea that social connectedness varies with phenotype. In our larger populations, non-lactating females who are most challenged in finding sparse feeding sites, are more selective than lactating females in their choice of strong associates. Presumably networks with this structure enhance foraging success by increasing information flow among like-minded individuals. As our study demonstrates, network analysis facilitates testing predictions about the cause of social structure and its impact on transmission processes.

Keywords: Asiatic wild ass, social structure, population, network theory, Israel, India

Introduction

Animal societies vary in structure. Some are characterized by the maintenance of long-term associations among individuals, whereas in others bonds are much weaker and associations change often. This variation is clearly seen in equids. The seven extant species are members of the genus *Equus* and are thus evolutionarily closely related. Whereas horses along with plains and mountain zebra live in closed membership family groups, Grevy's zebras, wild asses and kiang live in open membership groups that fuse and fission frequently (KLINGEL 1977, MOEHLMAN 1979, 2002; RUBENSTEIN 1986, 1994). Broad differences among species with respect to physiological capabilities and features of the landscapes they inhabit account for the distinctions between these two major types of sociality (Rubenstein 1994). When all females in a group follow the same drinking and foraging schedules, they bond to a male and derive substantial material rewards; when they cannot, then fission-fusion societies form and males establish territories to intercept females as they move to and from water (RUBENSTEIN 1986, GINSBERG 1989).

Although the species can be partitioned into two broad classes of sociality, it remains unclear as to how similar the social structures are of equid species and populations that are grouped into 'open' or 'closed' membership societies. Ultimately the structure of societies emerges from rela-

tionships that develop among individuals. Yet the structure itself can shape the nature of relationships that form and the types of interactions that are exhibited. For examples, do broadly similar societies converge on similar patterns of dominance and despotism? Do structurally similar societies show similar patterns of cooperation and altruism? Do the bonds that form show biases that are associated with phenotype and are the bonds the same within broad social categories? And for broadly similar societies, to what degree are the bonds that emerge shaped by particular environmental circumstances? These are just a few questions illustrating that form and function are coupled in social systems. But until patterns of association can be characterized quantitatively so that the processes shaping them can be measured, it will be difficult to understand how ecology influences social behaviour (RUBENSTEIN & WRANGHAM 1986), how social structure feeds back on shaping social relationships and how relationships influence the transmission of ideas, pathogens and genes.

Network theory offers a powerful way of characterizing social structure and analyzing its consequences (CROFT et al. 2004, LUSSEAU 2003, NEWMAN 2003, WASSERMAN & FAUST 1994). Social systems can be depicted and modelled as networks in which, individuals become 'vertices' and their associations, or the behavioural interactions linking them, are defined as 'edges'. Depending on the process of interest, behavioural interactions can be characterized by measures as coarse-grained as joint membership in a group to more fine-grained ones involving physical proximity to neighbours, agonism, affiliation or sexual contact. Even by only using information on associations within groups, important insights about social structure are emerging. In dolphins, for example, LUSSEAU & NEWMAN (2004) have shown that particular individuals become key players in maintaining the social structure of populations and those phenotypic features such as size and sex shape these social preferences. By using more fine-grained interaction measurements, network theory has even generated predictions about the course of disease and innovation spread (KEELING & EANES 2005, MOORE & NEWMAN 2000, SUNDARESAN et al. 2006)

In our study we use network theory and associated metrics based on simple measures of association to examine the social structures of two Asiatic wild ass populations (*Equus hemionus*), the onager of Israel's Negev desert, and the khur of India's Little Rann of Kutch. Our overarching aim is to determine the degree to which broadly similar fission-fusion societies exhibit similar social structures. To the extent that they differ we want to identify the causes and potential consequences of these differences.

Issues and predictions

Although our populations of onagers and khur are of similar size and inhabit deserts, the ecology of each locale differs in important ways (table 1). The sites are similar in terms of rainfall amount, predation pressure and vegetative ground cover. They differ with respect to rainfall seasonality, habitat openness and the availability of drinking points (RUBENSTEIN & SUNDARESAN pers. obs.). In addition to these environmental differences, population size as well as age and sex composition change markedly from one year to the next in the onager population. Theory suggests that the structure of populations should change as individuals respond to different distributions of critical resources or changing demography (RUBENSTEIN & WRANGHAM 1986). Thus we make 3 predictions about how networks characterizing social structures should change as populations or individuals adapt to changing circumstances. First, we predict that in habitats in which resources become scarce and are harder to detect, populations should form more cohesive societies with more interconnected associations. Such networks by facilitating reciprocity and other forms of cooperation should increase the spread of critical information. Since rainfall is more unpredictable and watering points are more limited in Israel, we predict that onagers have a greater need to cooperate and thus will exhibit more cohesive and structured societies than khur.

Table 1: Ecological characteristics of the two wild ass populations

Ecological characteristics	Onager	Khur
rainfall	200 mm “aseasonal”	300 mm seasonal
predators	wolves and leopards (rare)	wolves (rare)
vegetation - visibility	open	open with bushy patches
vegetation - ground cover	low	low
waterholes	few	Many (artificial)

Second, since individuals of different phenotypes in open membership societies often have different ecological requirements (RUBENSTEIN 1986, 1994), we also predict that individuals seeking the most unpredictable and scarce resources should form more cohesive groupings than those with requirements that are easier to obtain. They should also be more selective, associating with like-minded individuals. Since high quality food patches are more ephemeral than watering points and since non-lactating females are freer to seek forage than lactating females (RUBENSTEIN 1994), we predict that non-lactating females should form more strong friendships than lactating females. And third, as populations grow, their composition often changes. Integrating new individuals into an expanding population should alter social relationships and structure. Thus we predict that larger and more complex societies -1990 onagers and khur- should be highly fragmented and cohesion within groups should be low.

Study populations and methods

Onager data were gathered in the Maktesh Roman in the Israeli Negev desert while the khur data were collected in the Little Rann of Kutch, an arid desert in Gujarat, India. The core study sites of both populations covered approximately 100 km² or less and included populations of similar size (16 adult and sub-adult onagers in 1989, increasing to 24 in 1990; 29 adult and sub-adult khur in 2003).

Movements and associations of wild asses were collected by driving fixed routes and recording the identity and location of every individual sighted. Data on onagers were collected during the 1989 and 1990 dry seasons; on khur data were recorded during a dry season from January – May 2003. In both study sites, searches took place every day. For each group encountered, individuals were identified by natural field marks and classified by age, sex and reproductive status (adult versus juvenile; bachelor versus territorial stallion for males; and lactating versus non-lactating for females). In this study nursing offspring were excluded from all analyses since it was assumed that their mothers determined their association choices.

For every pair of individuals in each population, the strength of association was quantified by the ‘half weight’ index of association (AI). It was computed by recording the number of times a pair of individuals was seen together (C) in relation to the total number of times each individual was sighted (A and B respectively) using the formula: $2C/(A + B)$. If a pair was never seen together $C = 0$ and $AI = 0$; if they were never seen apart then $C = A + B$ and $AI = 1$. A series of networks was constructed for different AI thresholds. To examine spreading processes that involve minimum, or even one-time, contact, ‘non-zero’ networks were created. These consisted of pairs of individuals that were sighted at least once. To examine processes that require repeated contact, hence stronger associations, ‘strong association’ networks were created by using high AI thresholds, often those in the region of $AI = .3$ to $.5$. As AI thresholds increased, the definition of a ‘friend’ became more stringent. Although the figures that follow display network outputs for the full range of AI thresholds from 0-1, critical thresholds at $AI = .3$ and $.5$ are highlighted to compare network patterns resulting from strong associations across species and contexts.

individuals connected by a continuous path. In fig. 1 there are two connected components since there are two separate clusters of vertices. Both the number of connected components and the size of the largest connected component provide information on the sub-structuring of the population. The second metric is *vertex degree*, a count of the number of individuals connected to a particular vertex. In fig. 1, for example, khur males show differences in vertex degree ranging from 0 for male 03-005, to 2 for male 03-033 to 6 for male 03-013. Examining the distribution of vertex degrees among individuals within populations, or computing the coefficient of variation of vertex degree, can reveal how phenotypic or environmental characteristics shape the nature and diversity of relationships that form within populations.

The third metric is the *cluster coefficient*. It is the probability that any two associates of one individual are themselves associates averaged over all individuals in the population. This metric is often called the 'friends of friends index'. It reveals integration of individuals into local neighbourhoods or 'cliques' (WATTS & STROGATZ 1998). Typically it is only computed for individuals having at least two associates. The last metric is *path length*. It measures the length of the 'shortest path' connecting each pair of individuals within a component. The average shortest path length for each component is known as the 'characteristic path length' or 'network diameter' (WATTS & STROGATZ 1998) and it depicts the degree to which individuals tend to associate concurrently with others in their component. Together with cluster coefficient, average path length indicates the potential for rapid spread of information or disease (CROFT et al. 2004, WATTS & STROGATZ 1998). For example, fig. 2 shows the network of the Israeli onagers during 1989. Since every individual is connected to every other individual both the shortest path and the cluster coefficient are 1. This is markedly different from the pattern for khur shown in fig. 1.

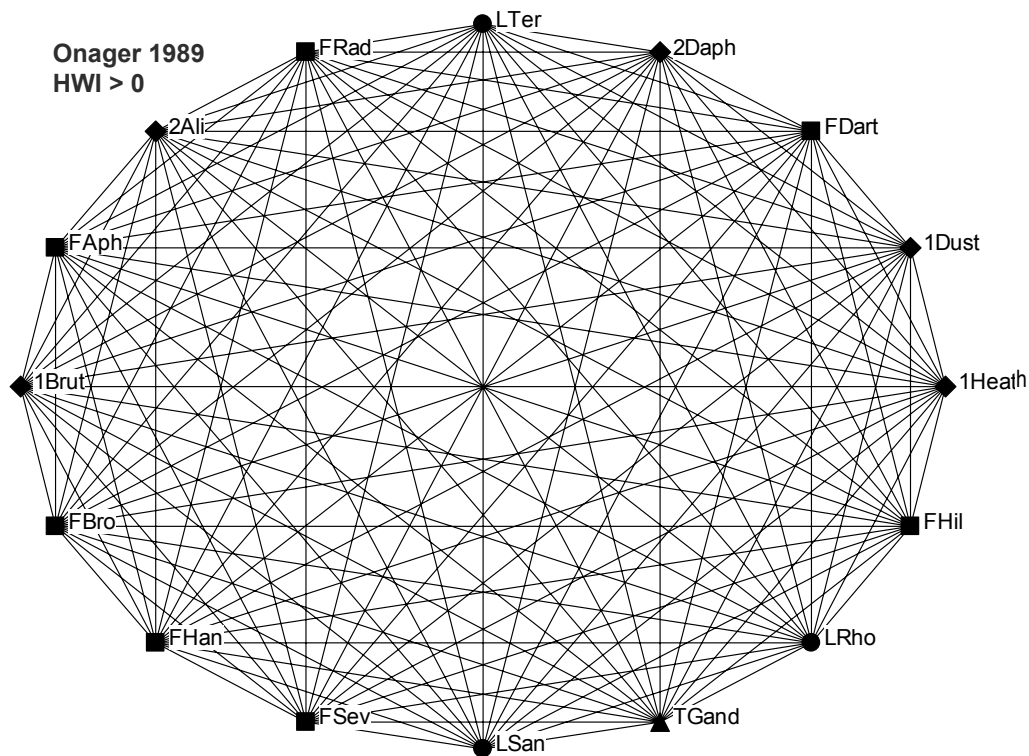


Fig. 2: Network depicting connections among 1989 onagers. Individuals are vertices with their reproductive states indicated by symbols: ▲ = males; ■ = females; ● = lactating females; and ◆ = juveniles. The network depicts associations among all pairs that were seen at least once.

Results

Distribution of Associations

Two out of three of our Asiatic wild ass populations exhibit similar patterns of association strengths (fig. 3). For khur and onagers of the 1990 cohort, only a few individuals form strong bonds with other individuals (fig. 3a & c respectively). Most pairs are only weakly connected, or not connected at all. But as the different cohorts of Israeli onagers show, association patterns can change quickly over time as a population grows and matures (fig. 3b). In 1989 when the population was relatively small, the distribution of AI values is approximately normally distributed indicating that strong bonds among pairs are common. By 1990, however, the situation is very different. As the population increases in size, strong bonds become rare and most bonds are weak.

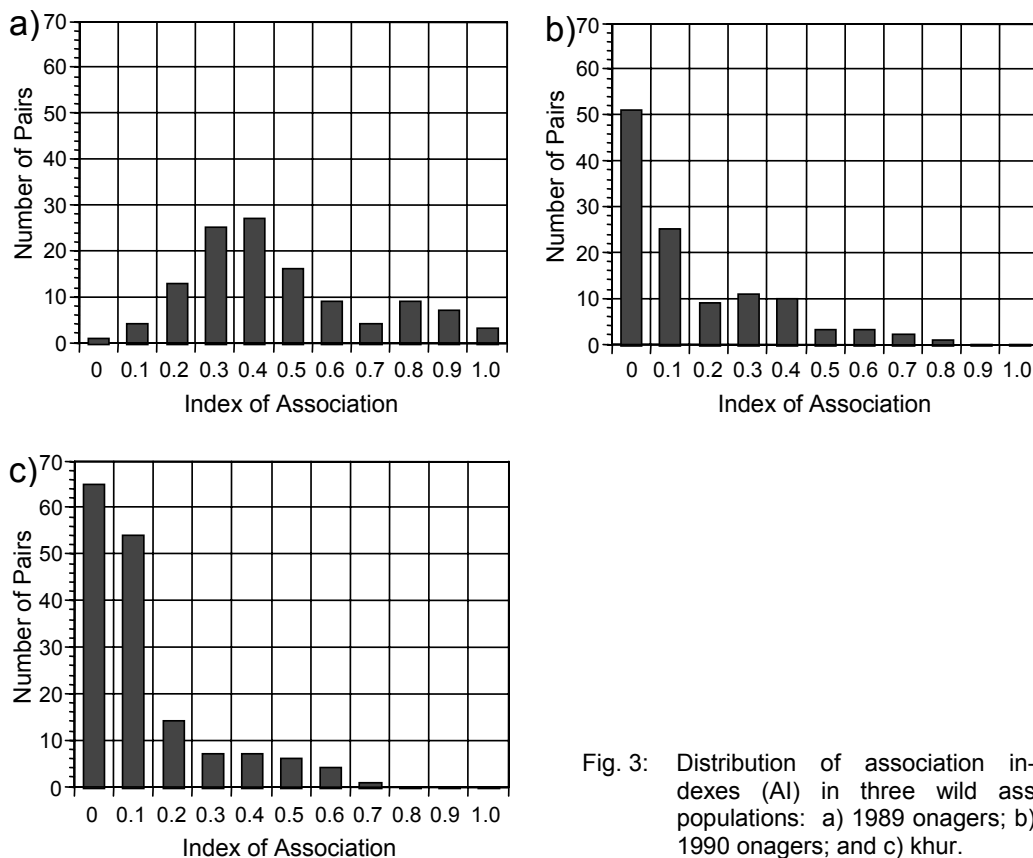


Fig. 3: Distribution of association indexes (AI) in three wild ass populations: a) 1989 onagers; b) 1990 onagers; and c) khur.

Network graphs and general patterns

Non-zero networks ($AI > 0$) of khur and the 1989 onagers are illustrated in figures 1 and 2 respectively. For the small onager population, all individuals are connected to all other individuals. For khur, however, even the lowest possible threshold of association ($AI > 0$) shows substructuring. Not only are there two connected components (one large and one composed of a singleton), within the largest component, the number of connections among individuals varies.

Networks built upon stronger associations for 1989 onagers (fig. 4 & 5), 1990 onagers (fig. 6 & 7) and khur (fig. 8) reveal for all populations that as the threshold for defining friendship increases, differences in population social structure persist. When being a close associate requires a high association threshold of $AI = .3$, all the individuals in the population of 1989 onagers remain connected in one component (fig. 4). In this strong associate network, the territorial male Gandolf is connected to the most individuals - 11 in all, 9 of 11 females, including all 3 lactating females. Females also exhibit strong associations. One lactating female, Teresa, associates with 6 females - the other 2 lactating females and 4 of 8 non-lactating females. Another, Hannah, a non-lactating female, associates with 8 females - all 3 lactating females and 6 of 8 non-lactating females. Only when the threshold for friendship becomes very stringent ($AI = .5$) does the population fragment into multiple connected components (fig. 5). At this threshold, territorial males are no longer connected to any members of the population, two females are only connected to their juveniles, and Hannah and Teresa, our representative non-lactating and lactating females, lose connections to some females, mostly those of phenotypes differing from their own.

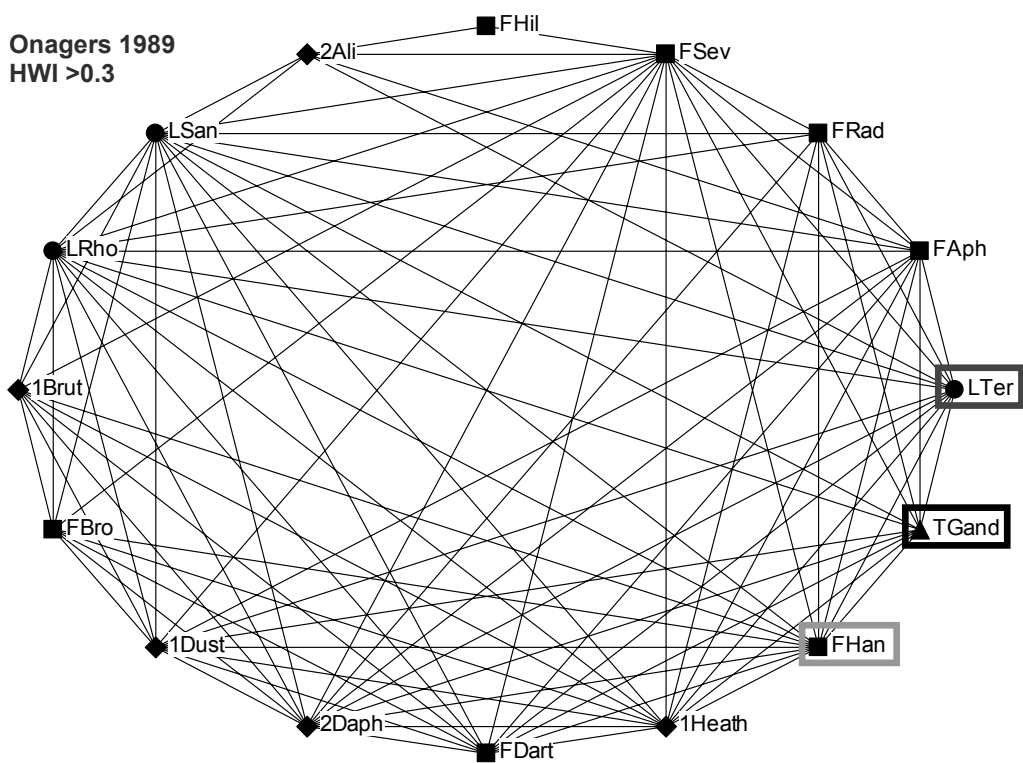


Fig. 4: Network depicting connections among 1989 onagers in which associations must exceed $AI > .15$. Individuals are vertices with their reproductive states indicated by symbols: \blacktriangle = males; \blacksquare = females; \bullet = lactating females; and \blacklozenge = juveniles. The territorial male, Gandolf, is identified by a dark box, those of a representative non-lactating female, Hannah, are identified by a box with light grey lines, while those of a representative lactating female, Teresa, is boxed in dark grey.

By 1990 the onager population is larger and many aspects of its networks have changed. Although the population consists of one connected component containing 11 adults for a moderately strong association threshold $AI > .15$ (fig. 6), there are two territorial males in the population (Gandolf and Napoleon), each only associating with a subset of the females. As for Teresa and Hannah, our representative lactating and non-lactating females, their strong associations with

other females are limited to females of similar phenotype. Networks based on even stronger association thresholds ($AI > .5$) show that most onagers maintain few strong adult associations (fig. 7). Only one male, Gandolf, bonds tightly to one female and only three non-lactating females show strong associations with more than one female, with Hannah bonding closely to 2.

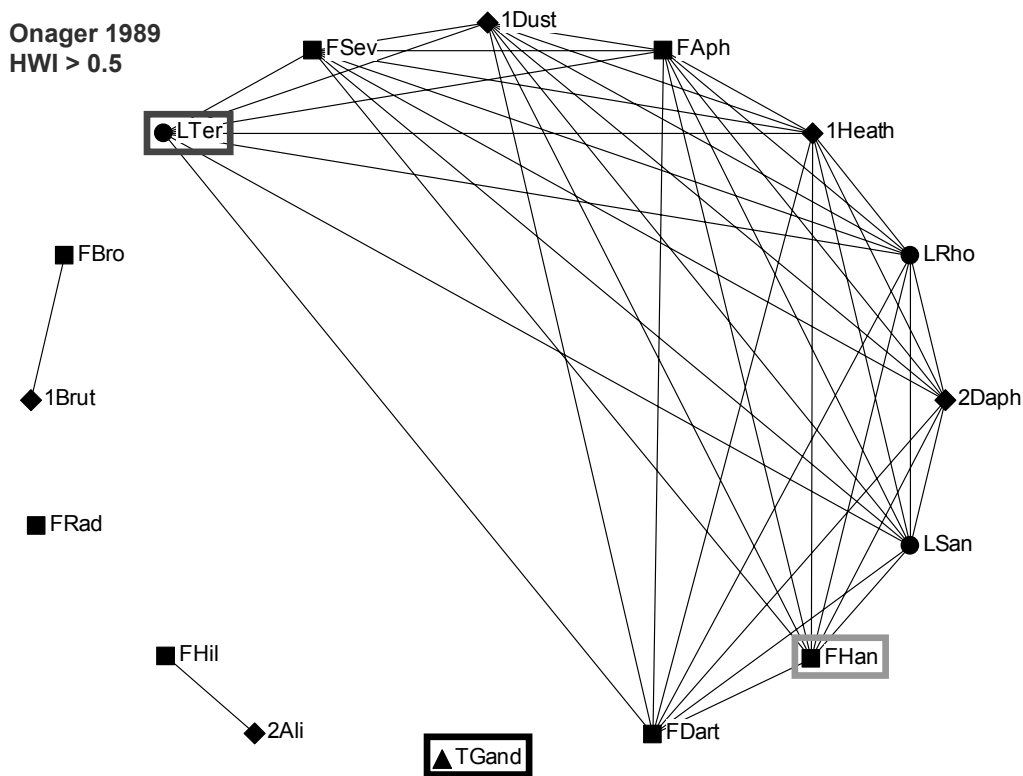


Fig. 5: Network depicting connections among 1989 onagers in which associations are strong and must exceed $AI > .5$. Individuals are vertices with their reproductive states indicated by symbols: \blacktriangle = males; \blacksquare = females; \bullet = lactating females; and \blacklozenge = juveniles. Representative individuals are depicted as in fig. 4.

For khur, the overall structure of their networks is similar to those of onagers. While most khur bond to many others when the association threshold is low ($AI > 0$; fig. 1), a large fraction of the population reveals no strong connections when the threshold is high ($AI > .5$). Connections among females become few and those that are maintained are generally among females of similar phenotype (fig. 8). As with onagers, especially the 1989 cohort, males have no strong associations with females. And for the few females that exhibit any close associations, their 'friends' tend to be of phenotypes similar to their own.

Network metrics and analyses

As described above, qualitative assessments of network graphs can illustrate overall patterns. But only quantitative comparisons of metrics derived from real and hypothetical networks can reveal details about structure, the degree to which associations represent individual preferences and the potential ways in which structure can shape transmission dynamics. Below we examine each metric in relation to ecological, demographic and phenotypic differences among populations or individuals to evaluate the hypotheses proposed above.

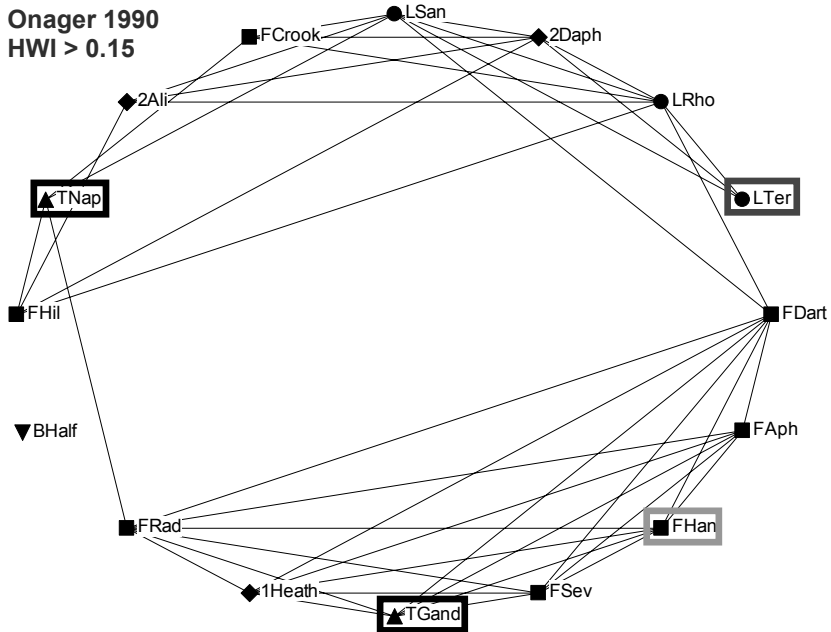


Fig. 6: Network depicting connections among 1990 onagers in which associations are moderately strong exceeding $AI > .3$. Individuals are vertices with their reproductive states indicated by symbols: ▲ = males; ■ = females; ● = lactating females; and ◆ = juveniles. The bonds of the two territorial males, Gandolf (upper triangle) and Napoleon (lower triangle), are in boxes with dark lines, and the representative females are depicted as in fig. 4.

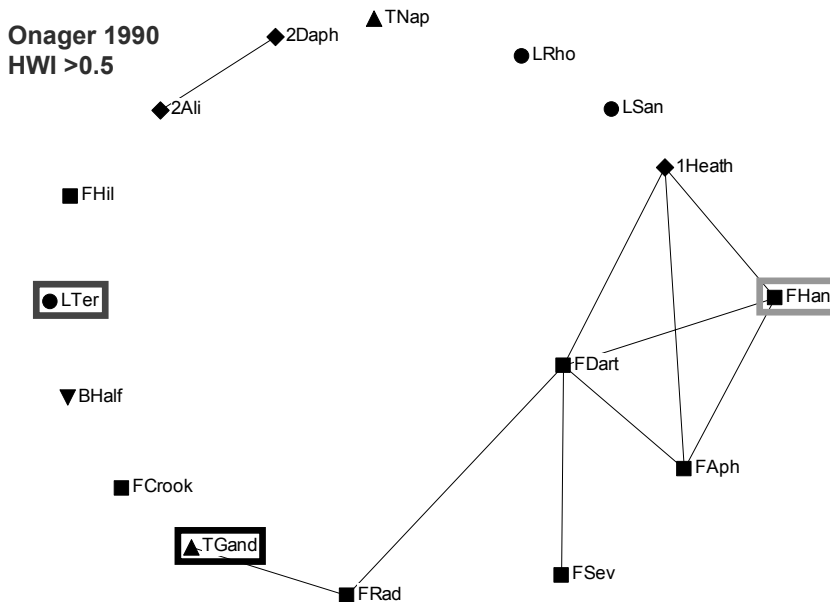


Fig 7: Network depicting connections among 1990 onagers in which associations are strong exceeding $AI > .5$. Individuals are vertices with their reproductive states indicated by symbols: ▲ = males; ■ = females; ● = lactating females; and ◆ = juveniles. Representative individuals are depicted as in fig. 4. No associations for any lactating females are strong enough to appear in this network.

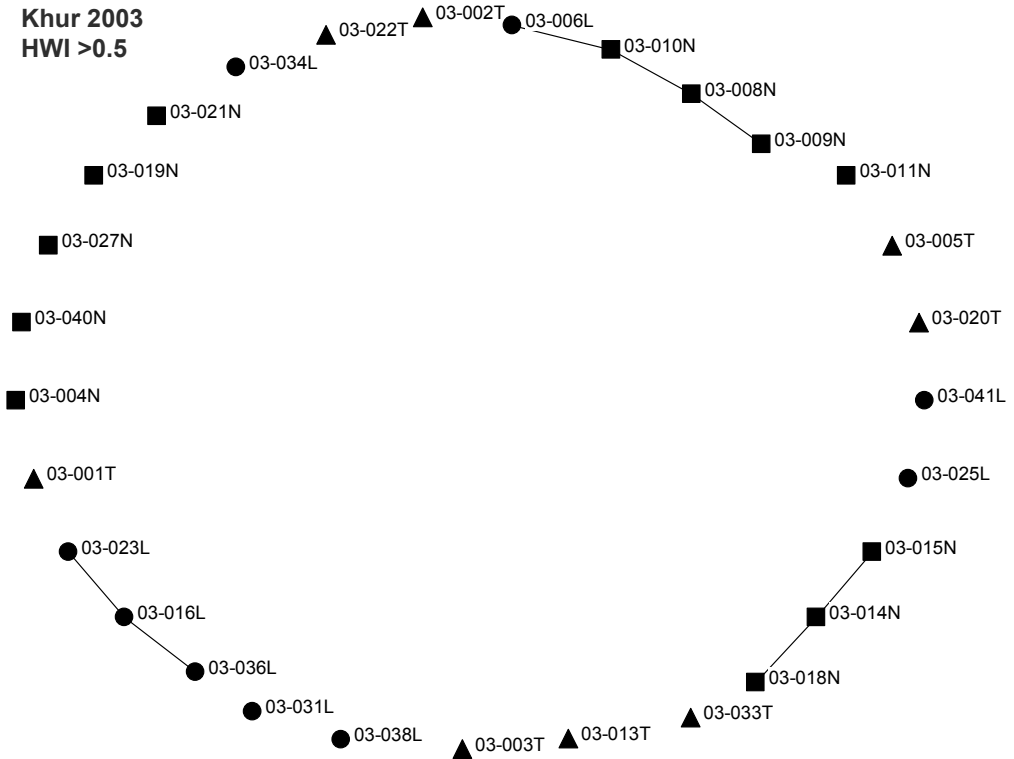


Fig. 8: Network depicting strong connections among 2003 khur in which associations must exceed $AI > .5$. Individuals are vertices with their reproductive states indicated by symbols: \blacktriangle = males; \blacksquare = females; \bullet = lactating females. Representative individuals are depicted as in fig. 4. No bonds of territorial males are strong enough to appear in this network.

Connected Components

Onagers live in more cohesive social structures than khur. Fig. 9 shows how the number of connected components changes for onagers in 1989 and 1990 as association thresholds changes from 0 to 1. In general, as the threshold for defining an association becomes more stringent, the number of separate connected components in the population increases. In addition to association strength, cohort size and composition also have an influence on network connectedness. In the 1989 onager cohort, the population remains as one cohesive unit even as the criterion for association increases to .3, whereas in the 1990 cohort, the population fragments into 4 components at this threshold. Thus with increases in size, segregation into cohesive units rises for equivalent AI thresholds. That this subdividing of the population is the result of active sorting by individuals is supported by the fact the number of connected components derived from the actual data exceeds that derived from hypothetical networks for a wide range of non-zero association thresholds.

For khur, the relationship between the number of connected components and AI thresholds is similar to that of the 1990 onager population (fig. 10). In the khur population, however, fragmentation occurs at even lower AI values than for onagers. At an AI threshold of .3 the 1990 cohort of onagers is divided into 4 components while the khur population is divided into 16. At even higher association thresholds ($AI > .7$), the khur population becomes a collection of singletons. Overall, subdivision of khur populations suggests they are more selective in choosing strong associates than onagers.

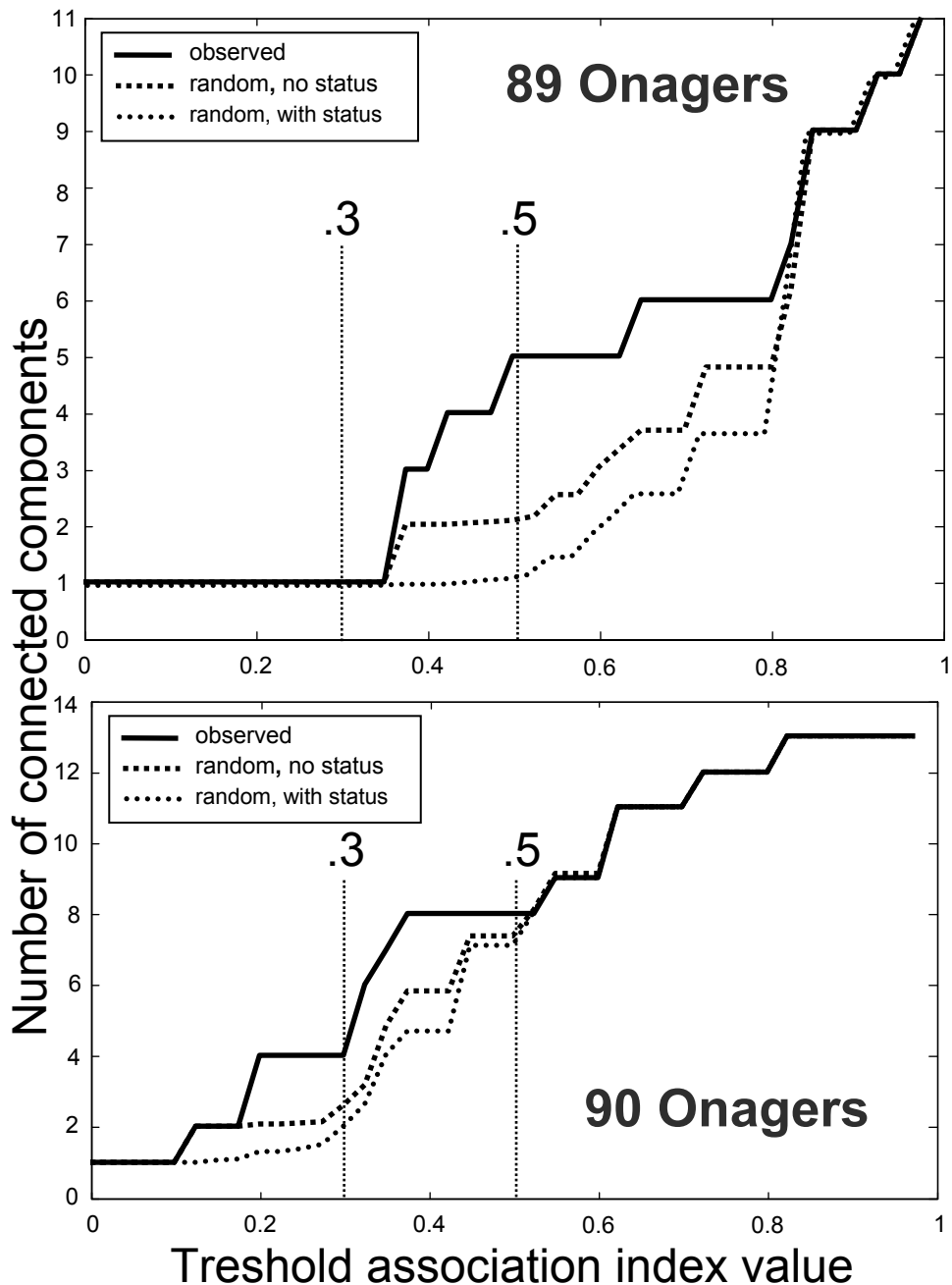


Fig. 9: Relationship between the number of connected components and increasing AI thresholds for onagers: a) 1989 cohort; b) 1990 cohort. The solid line depicts values from the observed network, whereas the two different dotted lines show values for the two 'null models'. The dashed line indicates average tendency for a range of AI thresholds. The number of connected components increases as AI threshold increase. For a wide range of intermediate AI values non-random behaviour is exhibited.

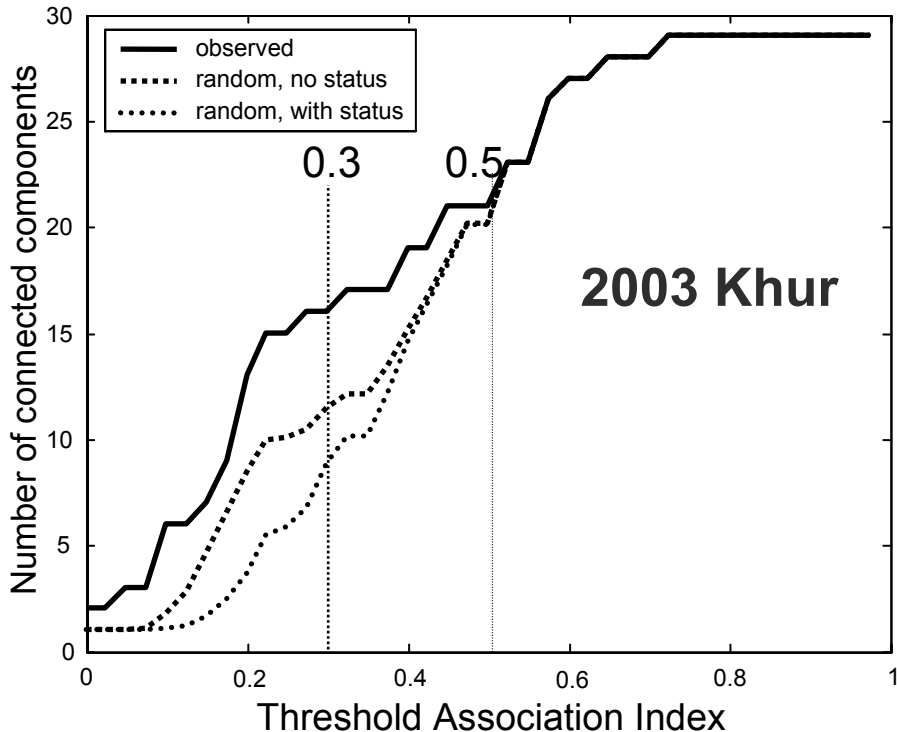


Fig. 10: Relationship between the number of connected components and increasing AI thresholds for khur. The solid line depicts values from the observed network, whereas the two different dotted lines show values for the two 'null models'. The dashed line indicates average tendency for a range of AI thresholds. The number of connected components increases as AI threshold increase. For a wide range of intermediate AI values, non-random behaviour is exhibited.

Vertex degree

Fig. 11 shows the average number individuals with whom each wild ass in non-zero networks bonds in each population and in each year. In 1989, individual onagers are connected to almost 6 other wild asses which is significantly higher than onagers in 1990 or khur in 2003. This suggests that onagers in the 1989 cohort are not particularly selective in their choice of associates, bonding at least once with a large number of individuals. Although the standardized variation in the number of bonds exhibited in the 1989 cohort is higher than the 1990 cohort or the 2003 khur population, these differences between years or locales are relatively small.

Association decisions appear to be only weakly affected by reproductive state. Inspection of networks based on strong associations ($AI = .5$; fig. 5, 7 & 8) reveals that vertex degree is similar for lactating (5.5) and non-lactating (5.0) females in the 1989 cohort. In 1990 differences in vertex degree among female reproductive classes emerge -0 for lactating females and 1.4 for non-lactating females - but the absolute levels of these values are lower than for the 1989 cohort. This suggests that non-lactating females focus their attention on a few close associates, whereas lactating females do not. For khur, the values are smaller still, but as in the larger onager population, vertex degree for lactating females is lower (.55) than that of non-lactating females (.67). Overall, it appears that in the larger wild ass populations there is a tendency for non-lactating females to be somewhat more selective with whom they form strong associations than lactating females.

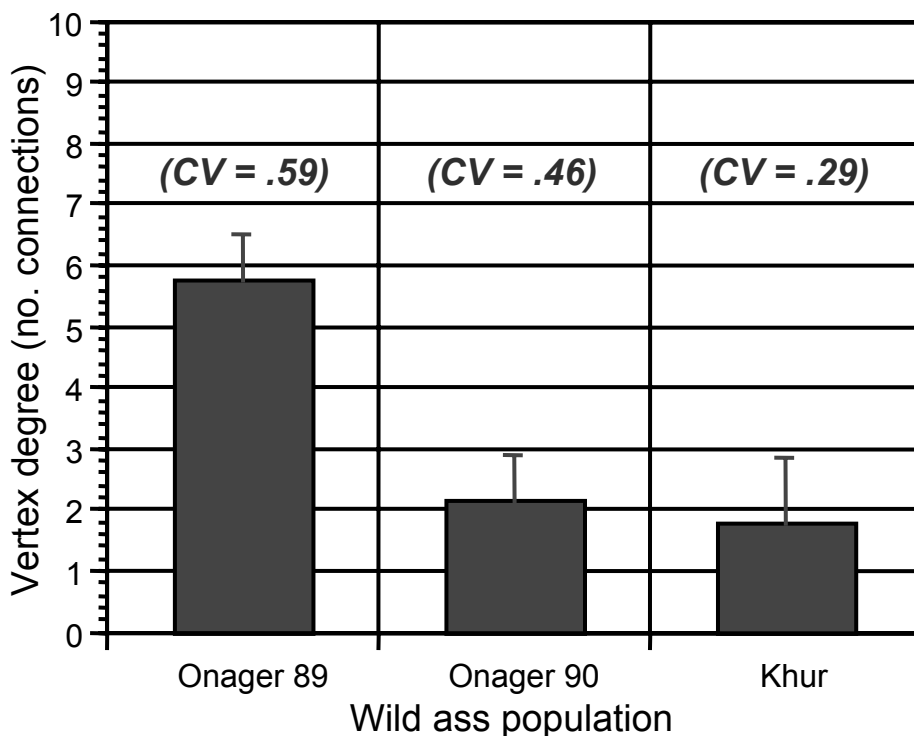


Fig. 11: The average number of associates and coefficient of variation for individuals in each population. Individuals in the 1989 cohort have significantly more associates than individuals in the other populations ($F[2,16] = 6.54$; $p < .01$). The coefficients of variation for the different populations are similar.

Cluster Coefficient

Onagers appear to be more cliquish than khur. For onagers, especially the 1989 cohort, clustering is high for a wide range of association thresholds (fig. 12). As the non-zero network of 1989 onagers depicted in fig. 3 illustrates, every individual is connected to every other individual. Thus all friends are friends of friends and the cluster coefficient is 1 for $AI < .1$ (fig. 12a). Even when the threshold for defining strong associates becomes more stringent ($AI = .5$), onager cluster coefficients for this cohort remain high, averaging .85. Cluster coefficients for the 1990 cohort are also high (.85) when association thresholds for 'friendship' are low, but once the threshold reaches $AI = .5$, the cluster coefficient drops dramatically to .55 and cliques of 'triads' become less common (fig. 12b). The relationship between cluster coefficient and AI threshold for khur resembles the shape of the 1990 onagers (fig. 13). The step-wise pattern remains, but cluster coefficients are lower than those for onagers at all AI thresholds. At $AI = .5$, for example, the cluster coefficient for khur drops to .30. Overall, cliquishness is lowest for khur and lower for larger rather than smaller onager populations.

Path Length

In non-zero networks virtually all individuals in our two populations are connected within one large component. In general, average path lengths for all wild asses in these networks are low (fig. 14), but individuals appear to be more distant in larger populations. For the 1989 onagers mean path length is 1 as every individual is connected to every other individual. For the 1990 onagers and the khur, pairs of individuals tend to be slightly, but significantly, more distant since the average path length increases by approximately 50 % to 1.5 and 1.6 respectively.

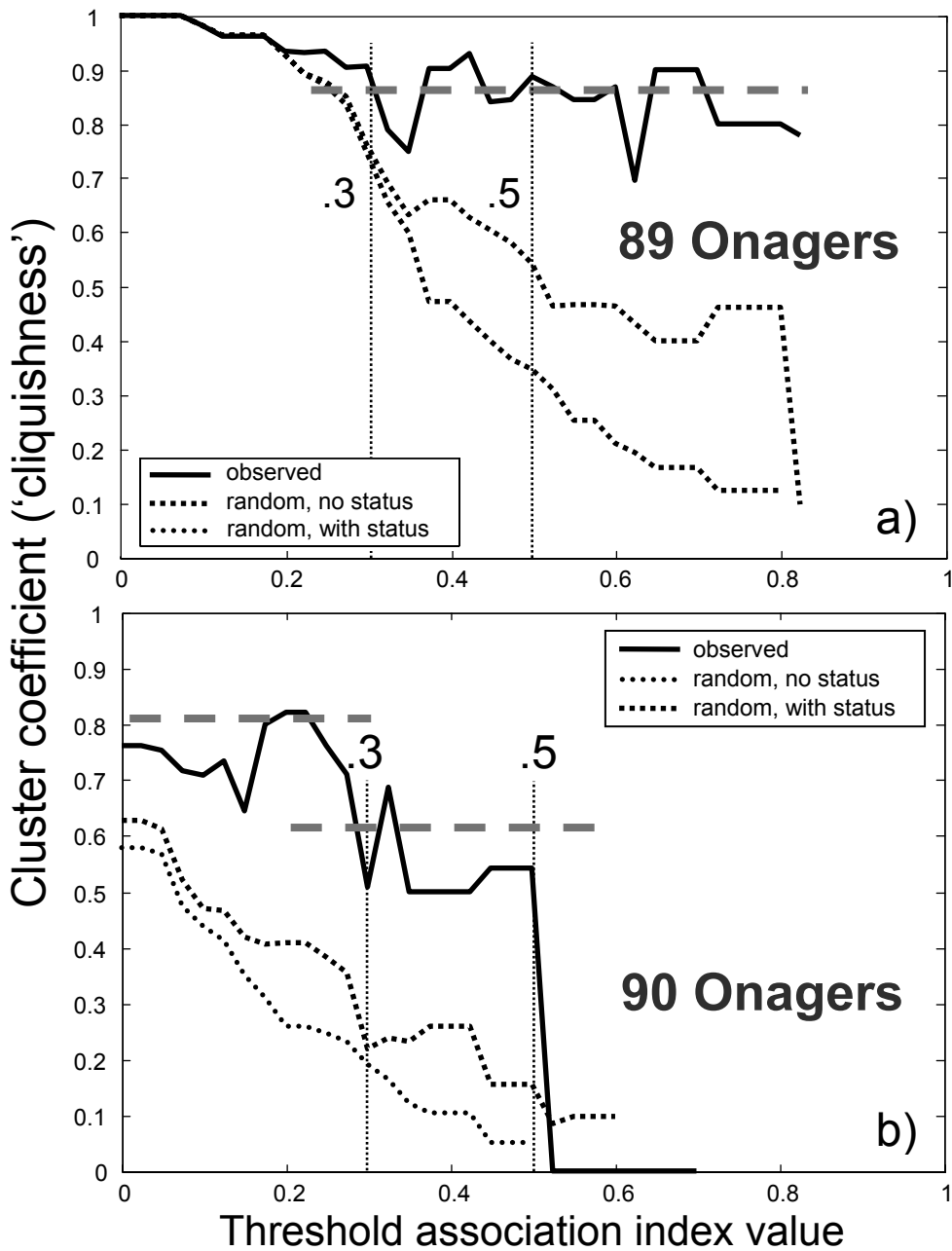


Fig. 12: Relationship between cluster coefficient and association thresholds for onagers: a) 1989 cohort and b) 1990 cohort. The solid line depicts values from the observed network, whereas the two different dotted lines show values for the two 'null models'. The dashed line indicates average tendency for a range of AI thresholds. In both cohorts, when thresholds are low clustering is high, but clustering decreases as association thresholds increase. The smaller 1989 cohort shows more cliquishness than the larger 1990 cohort at all AI thresholds. Non-random linkages appear for a wide range of moderately high AI thresholds in both populations.

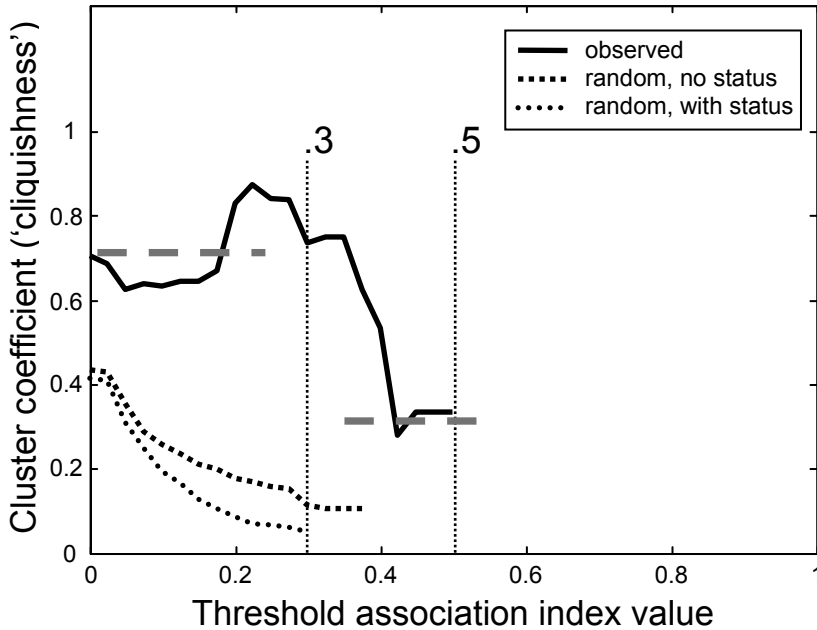


Fig. 13: Relationship between cluster coefficient and association thresholds for khur. The solid line depicts values from the observed network, whereas the two different dotted lines show values for the two 'null models'. The dashed line indicates average tendency for a range of AI thresholds. As with the 1990 onagers, cliquishness decreases in a stepwise manner as AI thresholds increase.

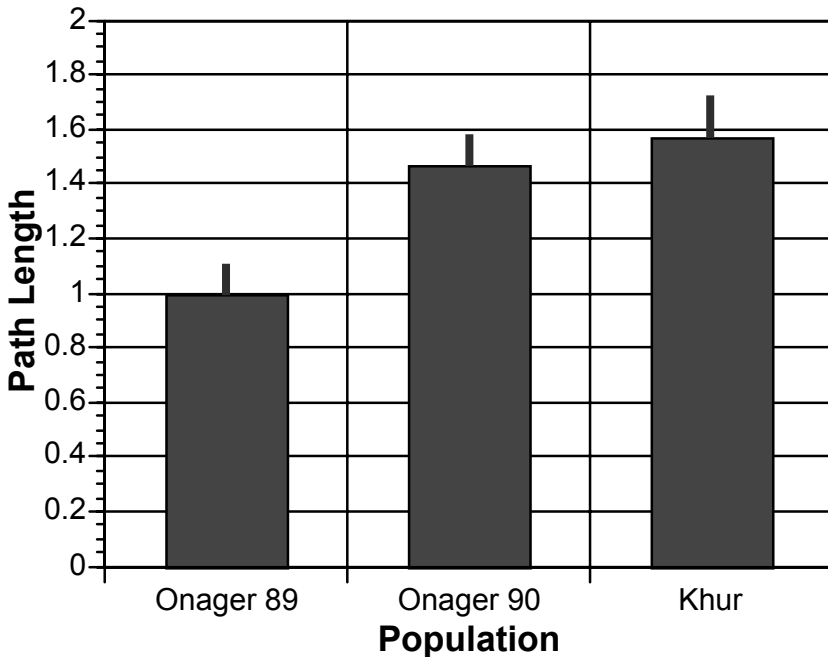


Fig. 14: Average path lengths in the three wild ass populations. Path lengths are significantly shorter in the 1989 onager population ($F [2,16] = 4.43$; $p < .05$) than in the other populations.

Discussion

The results of this study show that although populations of onagers and khur live in fission-fusion societies, the fine-grained structure of their societies differ. Hints about these differences can be gleaned solely from inspection of the distribution of AI values. Most onagers in 1990 and khur in 2003 roam as singletons and for the pairs that form, most show weak associations. This contrasts markedly with the pattern shown by the 1989 onager cohort in which strong associations are common among most pairs.

Inspection of the networks and comparison of the derived metrics, however, provides deeper insights into social structure as well as its determinants and potential consequences. Comparisons of the metrics enable us to test our predictions as to how demographic, phenotypic and environmental factors shape social structure.

First, networks show non-random structure for each population regardless of locale or year. Based on number of connected components, observed networks tend to be more segregated than random networks. Yet within the largest connected components of each population or cohort, individuals in observed networks tend to have more associates and these associates tend to form stronger cliques than in random networks. These patterns suggest that bonds among wild asses do not form at random but involve active choice.

Second, demography matters since networks change as populations grow. The 1990 onager population grew as juveniles matured into adults and as sub-adult males returned from distant bachelor male groups (RUBENSTEIN & SALTZ pers. obs.). Integrating these new members into the population, especially the second territorial male (SALTZ, ROWEN & RUBENSTEIN 2000) appears to have dramatically altered the structure of the population. The changed AI distribution shows weakened association strengths overall. Increases in population size also leads to a decrease in average number of associates of each onager, a decrease in cliquishness within components and an increase distance among associates. As we predicted, the overall social structure of a population as it expands becomes diminished in virtually all dimensions.

Third, although changes in number of strong associates do not universally vary with female reproductive state, there is some support from our large populations for our prediction that non-lactating females are somewhat more selective in their choice of strong partners than lactating females. Bonding strongly to a few individuals presumably lets non-lactating females reap the benefits of sharing information about the locations of hard to find resources. In addition, comparison of fig. 4 and 6 shows that population growth also leads to changes in nature of bonds that the sexes establish. While males tend to become less selective with whom they associate, females appear to become more selective as they split their allegiance among the males, bonding to one or the other.

Fourth, network metrics provide insights into how ecological factors help shape the social structure of populations. Onager and khur populations are ecologically similar in many ways, but they differ at least with respect to seasonality of rainfall and availability of watering points. In the Negev, rainfall is much more episodic and watering points are fewer and further apart than in the Little Rann of Kutch. In the Negev, any means augmenting the sharing of information among neighbours about the location of the best places to forage and drink would be favoured by natural selection; social structures that facilitate mutualistic or reciprocally altruistic actions would be adaptive. Societies in which numbers of connected components are low, path lengths within components are small and both vertex degree and cluster coefficients are high will be those where individuals will be tied to many friends who will be friends of other friends. In such settings, long-term bonds would minimize costs associated with cooperative behaviour. Onager networks, especially those shown by the 1989 cohort, exhibit lower values in the number of components and path length and higher values in vertex degree and cluster coefficients than networks of khur. These findings support our prediction that for fission-fusion societies inhabit-

ing highly variable environments, few, large connected components each containing tightly knit cliques will form. In general our findings suggest that a population's structure is coupled to its ecology and that network analysis can help identify mechanisms underlying particular couplings.

Lastly, examination of the networks based on weak and strong association provides insights into the way information, beneficence, pathogens and genes may potentially spread in populations. Much depends on whether non-zero networks resemble those based on more stringent criteria for determining bonds. If both non-zero and more stringently defined networks are similar in structure, as is the case for the 1989 onagers, then transmission dynamics involving single contacts will be the same as those requiring repeated contacts. If the networks are different, as is the case in the 1990 onagers and the khur, then spread of pathogens or even alarm calls that can be transmitted by a single contact will be much higher than the spread of memes or genes that typically require repeated contact before they are accepted by others. In general, networks that facilitate rapid spread should have few connected components, high cluster coefficients and short path lengths. Such networks are often called 'small world networks' (LUSSEAU 2003, CROFT et al. 2004) and all non-zero networks in our wild ass populations meet this criterion; only the networks of the 1989 onagers preserve this feature as the threshold for defining strong friendships increases.

Biologists have long been challenged to understand the determinants of social structure in open membership societies (WHITEHEAD & DUFAULT 1999, KRAUSE & RUXTON 2002). It is clear from the above analyses that network theory provides an important means of understanding the structure of complex animal populations whose societies involve fissioning and fusing of individuals. Insights from inspection of the networks and comparison among network metrics illustrate ecological causes and potential consequences of social structure on transmission processes involving the spread of ideas, beneficent behaviour, pathogens and genes.

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