BEHAVIORAL ECOLOGY

Network metrics reveal differences in social organization between two fission–fusion species, Grevy's zebra and onager

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Abstract For species in which group membership frequently changes, it has been a challenge to characterize variation in individual interactions and social structure. Quantifying this variation is necessary to test hypotheses about ecological determinants of social patterns and to make predictions about how group dynamics affect the development of cooperative relationships and transmission processes. Network models have recently become popular for analyzing individual contacts within a population context. We use network metrics to compare populations of Grevy's zebra (*Equus grevyi*) and onagers (*Equus hemionus khur*). These closely related equids, previously described as having the same social system, inhabit environments differing in the distribution of food, water, and predators. Grevy's zebra and onagers are one example of many sets of coarsely similar fission–fusion species and populations, observed elsewhere in other ungulates, primates, and cetaceans. Our analysis of the population association networks reveals contrasts consistent with their distinctive environments. Grevy's zebra individuals are more selective in their association choices. Grevy's zebra form stable cliques, while onager associations are more fluid. We find evidence that females associate assortatively by reproductive state in Grevy's zebra but not in onagers. The current approach demonstrates the utility of network metrics for identifying fine-grained variation among individuals and populations in association patterns. From our analysis, we can make testable predictions about behavioral mechanisms underlying social structure and its effects on transmission processes.

Keywords Individual associations · Equids · Animal groups · Social structure

Introduction

Emergence of social structure from individual relationships is a key organizing problem for the study of animal behavior (Couzin and Krause 2003; Hinde 1976; Whitehead and Dufault 1999). In turn, social structure shapes the development of social relationships, such as dominance or cooperation (Hemelrijk 1999), and transmission of ideas (McComb et al. 2001), pathogens (Keeling and Eames 2005), and genes (Altmann et al. 1996). Describing variation in individual association choices and social structure is particularly challenging in populations where individuals frequently change associates, as groups form and disintegrate (Chapman et al. 1993; Whitehead 1997; Whitehead and Dufault 1999). Many mammals exhibit such fission–fusion patterns, including equids (Ginsberg 1987; Rubenstein 1986), chimpanzees (Symington 1990), dolphins (Brager 1999), buffalos (Cross et al. 2005), and humans. Among these species, we observe great variation in ecology and sociality, including group size and degree of mixing among individuals. How can we

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characterize the distinctions in sociality among fission–fusion populations? Do individuals form preferred bonds, or do associations reflect chance encounters? How does phenotype shape individuals' decisions about group membership? Until we characterize the patterns and processes of associations, it is difficult to understand how ecology drives social behavior (Krause and Ruxton 2002; Rubenstein and Wrangham 1986), or how population social structure feeds back on social relationships and constrains transmission processes.

Social networks offer a powerful set of tools for characterizing and analyzing individual associations within a population-level social context (Croft et al. 2004; Lusseau 2003; Newman 2003; Wasserman and Faust 1994). Biologists have modeled networks in which individuals are vertices and behavioral interactions define edges linking individuals. Depending on the process of interest, an interaction could be defined as shared group membership, sexual contact, affiliation, or antagonism. Using networks, we can quantify complementary aspects of sociality: population substructure, individual variability, and association preferences. Based on the association matrix that defines a network, researchers have searched for clusters using various algorithms (Whitehead and Dufault 1999). Lusseau and Newman (2004) found that key individuals maintain social structure in dolphin networks. Size and sex can affect social preferences in dolphins and guppies (Croft et al. 2005; Lusseau and Newman 2004). Network structure has been used to make predictions about the course of disease or innovation spread (Keeling and Eames 2005)

We apply network methods to quantify differences between two fission–fusion equids having broadly similar social organization: Grevy's zebra (*Equus grevyi*) and onagers (*Equus hemionus khur*). We define bonds in the network based on shared group membership because we are interested in individual association choices. Grevy's zebra and onagers are grazers inhabiting arid and semi-arid landscapes. Social organization in both species falls under the category of resource defense polygyny: males seek to control access to unstable groups of females by defending areas with critical resources (Ginsberg 1987; Klingel 1998; Rubenstein 1994; Rubenstein 1986). In Grevy's zebra, differences in water needs of lactating and nonlactating females result in partial segregation among females by reproductive status; it is not known how lactation state affects female associations in onagers (Ginsberg and Rubenstein 1990). Past studies on the two species have described coarsely similar unstable female groups. But this past research has left unexamined possible differences between populations of the two species in

individual association patterns. Ecological variation is known to underlie differences across populations in social structure (Rubenstein 1994; Rubenstein and Wrangham 1986).

Our study populations differ in key ecological aspects that we expect drive distinct patterns of individual association and, therefore, population-level network properties. Onagers are found in open desert habitat and can therefore easily find other conspecifics if they break an association. In the bushier habitat of Grevy's zebra, it may be difficult to find new associates after leaving a group. If a Grevy's zebra individual wants to be in a group, then it is important for it to choose associates with whom it can easily coexist, because opportunities to meet other associates are infrequent. Thus we expect Grevy's zebra to prefer associates with common needs, and to form cliques through persistent group membership. In onagers, on the other hand, ease of exchanging associates reduces the benefit of choosing particular individuals as associates.

Grevy's zebra and onagers differ further in predation danger and forage distribution in ways that predict larger optimal groups in Grevy's zebra than in onagers. Our Grevy's zebra population faces predation, while the onagers do not (Moehlman 2002). Compared to Grevy's zebra, the more arid onagers' environment has sparser forage (S. R. Sundaresan, I. R. Fischhoff, and D. I. Rubenstein, unpublished data). Once in a group, predation danger is expected to result in high costs for Grevy's zebra of leaving a group by oneself, compared to onagers. Furthermore, reduced forage competition is expected to result in a low cost of maintaining group associations in Grevy's zebra; by comparison, movement into sparser forage may prompt onagers to break associations. Taken together, ecological factors predict differences between the populations in group sizes and the individual association patterns that shape social structure.

We use network metrics to compare social structure between our study populations, and among reproductive classes within each population. We extend the utility of network metrics that have previously provided powerful tools for analyzing variation within a single population. We use frequency of membership in the same group as a measure of association strength among dyads. We define two types of associations: those between individuals seen together at least once and those seen together more than would be expected through random encounters (Bejder et al. 1998). On a continuum of social bond strength, these two criteria represent two points that may be relevant to different social processes.

Using recent advances in network theory (Newman 2003; Watts and Strogatz 1998), we demonstrate how simple network metrics provide richer insights into association patterns than are possible from examination of group size and association strength distributions alone. We show that Grevy's zebra individuals form tightly knit cliques which themselves occasionally associate, while onager individuals change groups more frequently. As demonstrated in past studies, we confirm that Grevy's zebra females are more selective in their choices of associates, tending to form bonds with others in the same reproductive state. We find no evidence that onager females choose associates based on reproductive state. Because we are only analyzing data from one population of each species, our conclusions are limited to comparisons between these populations. In our discussion, we suggest how comparisons across further populations may allow us to determine the effects of specific ecological factors on association patterns.

Materials and methods

Study sites and field methods

Data on Grevy's zebra are from Mpala Ranch, a semi-arid bushed grassland in the Laikipia ecosystem of Kenya. Onager data were gathered in the Little Rann of Kutch (LRK), a desert in Gujarat, India. Both study sites cover approximately 40 km^2 and include populations of similar size and sex structure. Our population of 28 Grevy's zebra consists of eight males, 15 nonlactating females, and five lactating females. The 29 onagers include eight males, 12 nonlactating females, and nine lactating females. Mpala averages 500 mm rainfall annually; in LRK annual rainfall averages less than 300 mm. Grass in Mpala tends to be greener and more abundant than in LRK. In the dry season, Grevy's zebra drink at fewer waterholes (eight) than do onagers (fourteen, most artificial). Predation pressure in Mpala is strong. In contrast, within the onager study area there are no recent reports of large carnivores.

For Grevy's zebra, our study period is June–August 2002. The onager data are from January–May 2003. All study periods are dry seasons. In both study sites, we searched the area for groups every day by driving all the roads and going offroad to check certain frequently used locations. We define a group as a set of one or more individuals that is spatially cohesive and distinct from other groups at the time of observation. In the field, we can readily distinguish among groups based on close proximity of individuals within a group, on the order of several meters between individuals, and large

distances (hundreds of meters to several kilometers) separating groups. Within each group encountered, we identify individuals and classify their reproductive status. In this paper, we use three reproductive classes: males, lactating females, and nonlactating females. We exclude dependent offspring from all analyses, based on the assumption that their mothers determine their association choices. For Grevy's zebra, we identify individuals using stripe patterns. We identify onagers based on scars, ear notches, tail variation, and other unique markings. On average, we identify 80% of individuals we encounter. Unidentified individuals are excluded from all analyses presented here.

For every pair of individuals in each population, we define the strength of their bond using the half-weight index (HWI), twice the number of observations of two individuals together, divided by the sum of observations for each (Cairns and Schwager 1987). We compare population-level HWI and group size distributions. To test for significant difference between the group size means, we use a permutation test because our data are not normally distributed (Good 2000).

Network definition

We construct two sets of networks for each species. One we base on all bonds with HWI above zero, indicating two individuals were seen together at least once. We term this the "nonzero" network. For some biological processes, such as transmission of certain diseases, reproduction, or one-trial learning, even a single contact may be significant. For other processes, such as development of cooperative relationships, reinforcement of dominance hierarchies, or cultural transmission of complex behaviors, individuals need to interact repeatedly. To capture the network possibly appropriate for these processes, we define a second set of networks, the "preferred associates" network based on significantly preferred associations. We identify preferences using the randomization method of Bejder et al. (1998). We randomly permute individuals within groups, maintaining both original group sizes and the number of times we observed each animal. After each permutation, we recompute the HWI of all dyads. After making 10,000 randomizations, we identify as preferred associates those dyads having an observed HWI greater than 95% of the randomized values for the pair. We use 10,000 exchanges because this is the number of permutations necessary to achieve a stable P value (Bejder et al. 1998).

We use the following standard network properties to compare populations and reproductive classes: connected components, vertex degree, cluster coefficient,

and mean path length (Wasserman and Faust 1994). A connected component is a set of individuals, any pair of which is linked by a continuous path. We use the number of connected components (NCC) and size of the largest component as measures of social substructure within the population. Vertex degree is the number of bonds for an individual. We can use degree distributions to determine if individuals in the two populations tend to differ in their number of associates. We can further test if individuals prefer associates of particular reproductive classes. Cluster coefficient is the proportion of an individual's associates who are also bonded to each other. It is a measure of integration of individuals' local neighborhoods, or "cliquishness" (Watts and Strogatz 1998). We compute the cluster coefficient for only those individuals with at least two associates. Finally, within each connected component, we find the length of the shortest path connecting each pair. For each connected component within the population, we find the mean shortest path length, also known as the characteristic path length (Watts and Strogatz 1998). From path length we can infer how quickly information or disease would spread through a component. Short paths indicate that transmission would rapidly occur over the entire component (Newman 2003). Together with cluster coefficient, path length indicates the potential for rapid spread of information or disease (Watts and Strogatz 1998).

To identify the importance of individual choices to observed network properties, we compare the observed network properties to those of random networks. We generate equivalent random networks, containing the same number of bonds and individuals, by reassigning associations randomly among all dyads (Lusseau 2003). Comparison of observed and random networks allows us to test whether observed network properties reflect biologically meaningful social structure or are simply the outcome of having a certain number of edges and vertices. To compare the values of metrics in the observed and equivalent random networks, we perform two-tailed Monte Carlo tests. We define as significantly different from random an observed value that falls within the top or bottom 2.5% of the distribution for the statistic generated from our randomizations (Bejder et al. 1998; Manly 1995).

We use a two-sample permutation test for all comparisons of network metrics between populations (Good 2000). For each comparison, we present the P value, the estimated difference between the two group means, and the 95% confidence interval around the estimated difference. Within a population, we test for effects of reproductive state on network metrics using a permutation ANOVA (Good 2000). We perform multiple pairwise comparisons among reproductive classes using a

Bonferroni correction to the critical P value. With three reproductive classes, our critical P value is 0.05 divided by 3, or 0.017. Consequently, for each pairwise comparison we report 98.3% Bonferroni confidence intervals. To determine whether females tend to preferentially associate with other females in the same reproductive state, we perform Monte Carlo permutation tests. We compare the observed total number of bonds between females in the same lactation state to the same total after randomly reassigning female lactation state. The randomization maintains the observed number of females in each state, total number of bonds in the network, and number of bonds held by each individual.

We used Matlab and R for randomizations and data analysis; we drew graphs with UCINET (Borgatti et al. 2002). Matlab and R scripts are available from the authors.

Results

We begin by identifying coarse population-level differences revealed by the distributions of HWI association and group size. We then present the richer inferences we can draw by using these HWI values in a network framework. By comparing observed nonzero and preferred networks to equivalent random networks, we confirm that both populations exhibit nonrandom social structure. To compare the two populations, we use network metrics to quantify visually apparent differences in their nonzero and preferred networks.
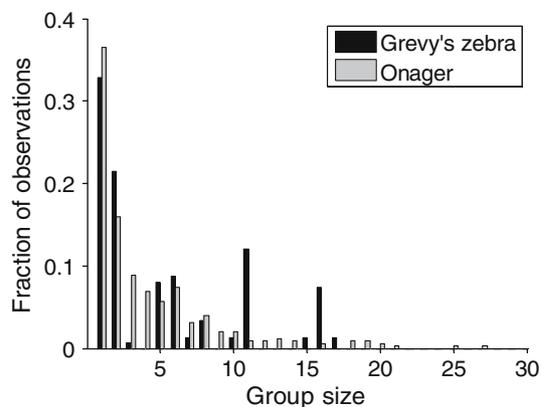
HWI and group size distributions

Grevy's zebra exhibit a greater number of associations with high HWI values; in onagers, no dyad has an HWI above 0.7 (Fig. 1). The percentage of possible dyads with nonzero HWI values is higher in onagers (43%) than it is in Grevy's zebra (33%).

In Fig. 2, we plot group size distributions for each population. Group size is larger in Grevy's zebra (mean = 5.1, N=149 groups), than in onagers (mean = 4.1, N=350) (P=0.02, difference in means = 1.07, 95% CI [0.16, 1.91]). Visually comparing the distributions, in onagers there appears to be a slightly greater tendency for individuals to be observed alone. For groups larger than two, the variation in group size for onagers appears to be more continuous, whereas the Grevy's zebra distribution exhibits multiple peaks around 6, 12, and 17. These patterns suggest that changes in Grevy's zebra groups involve subgroups of certain sizes, whereas in onagers group changes do not involve clusters of stereotypical size.
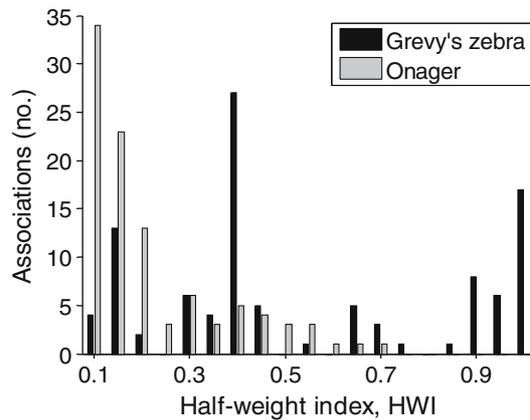
Fig. 1 Frequency distribution of half-weight index (HWI) association strengths among dyads in Grevy's zebra (*Equus grevyi*) (*black bars*) and onager (*Equus hemionus khur*) (*gray bars*) populations. The HWI is computed for each dyad as twice the number of times the dyad has been seen in the same group divided by the sum of the observations of each individual (Cairns and Schwager 1987)

Fig. 2 Group size distributions for Grevy's zebra (*black bars*, *n*=149 groups) and onager (*gray bars*, *n*=350)

Network analysis

Observed versus random networks

Comparisons of observed and random networks reveal that both populations exhibit significantly nonrandom social structure, as shown by the metrics in Table 1. The observed networks have a significantly higher number of connected components in both the nonzero and preferred cases (Monte Carlo randomization test, *P*<0.0001). Consequently, the number of individuals in the largest component is significantly lower in the observed network than in random networks (Monte Carlo randomization test, *P*<0.0001). Further, both populations exhibit significantly greater cluster coefficients

than expected from equivalent random networks, at the levels of both nonzero and preferred associates (Monte Carlo randomization test, *P*<0.0001).

In Grevy's zebra and onagers, path length in observed networks is similar to that for the equivalent random networks for nonzero bonds. Characteristic path length in the onager preferred network shows nonrandom substructure that distances individuals more than in equivalent random networks. For the Grevy's zebra network of preferred bonds, every component contains all possible bonds, resulting in a minimum path length of 1 for each component. By comparison, the minimum path length in the largest component of equivalent random networks averages 2.9. However, a higher proportion of dyads in the Grevy's zebra observed preferred network are in separate components. For these dyads in separate components, it is not possible to compute a finite path length. Thus, characteristic path length also indicates nonrandom structure in the observed preferred network for Grevy's zebra.

Grevy's zebra versus onager

In Fig. 3, we draw the nonzero associates and preferred associates networks for both species. Visual examination of the Grevy's zebra nonzero network points to distinct cliques, which become more obvious in the preferred network. Each clique appears relatively homogeneous with respect to individuals' reproductive state. Inspection of the onager nonzero network indicates no such cliques, but the preferred associates network suggests relatively weak groupings within the large component. Assortative associations by reproductive state are less obvious in the onager preferred network.

Analysis of network metrics quantifies these visual patterns. Onager individuals appear to be less selective in their association choices, based on comparison of vertex degree in the two populations. For the nonzero associates network, onagers have significantly higher vertex degree, indicating that individuals tend to be seen at least once with a larger number of other animals (*P*=0.01, difference in means = 3.4, 95% CI [0.7, 6.1]). In the preferred networks, on the other hand, onagers and Grevy's zebra do not significantly differ in their number of associates (*P*=1, difference in means = 0.03, 95% CI [−1.1, 1.1]). No individual in either species has more than seven preferred associates.

We find greater segregation in Grevy's zebra than onagers for both the nonzero and preferred networks, using number of components and size of largest component as measures of population social structure. In the nonzero bonds network, onagers have two components,

Table 1 Metrics for observed and equivalent random networks for Grevy's zebra and onager

Metric	Grevy's zebra nonzero		Onager nonzero		Grevy's zebra preferred[1]		Onager preferred	
	Observed	Random[3] mean (SE)	Observed	Random mean (SE)	Observed	Random mean (SE)	Observed	Random mean (SE)
Number of connected components	3	1 (0.03)	2	1 (0)	11	2.1 (0.95)	6	2.1 (0.94)
Size of largest component	23	28 (0.03)	28	29 (0)	7	26.8 (1.07)	24	27.8 (1.05)
Cluster coefficient	0.91	0.30 (0.06)	0.71	0.41 (0.02)	1	0.11 (0.03)	0.57	0.11 (0.06)
Characteristic path length[2]	1.9	1.7 (0.01)	1.6	1.6 (0)	1	2.9 (0.17)	3.5	2.9 (0.16)

[1] The preferred network contains edges only between dyads seen together more often than expected by chance (Bejder et al. 1998)

[2] Characteristic path length is shown for only the largest connected component

[3] Equivalent random networks contain the same number of bonds and vertices as in the observed case. Metric values for random networks are means of 10,000 realizations with the standard error shown in parentheses. All differences between observed and equivalent random networks are significant (Monte Carlo randomization test, $P<0.0001$)

a Grevy's zebra
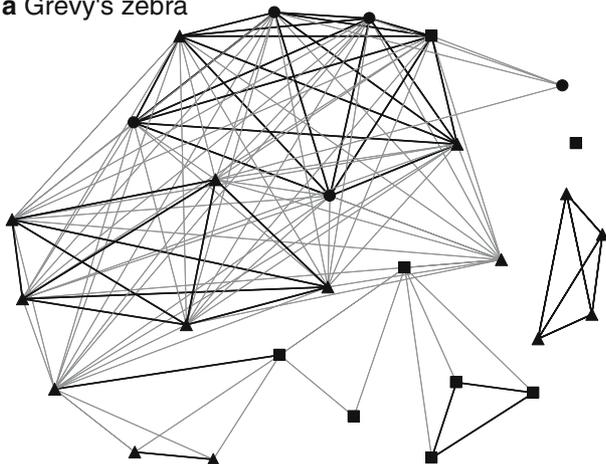
b Onager
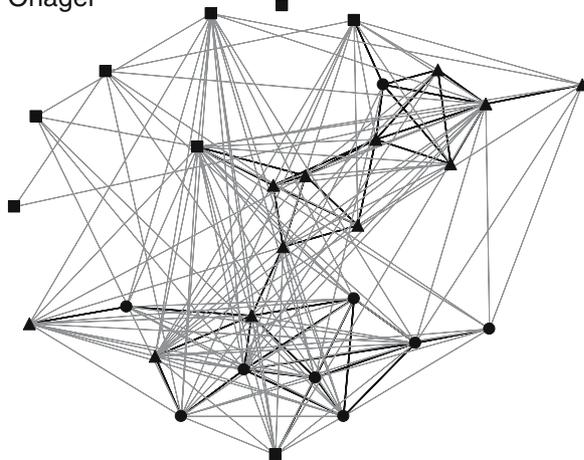
Fig. 3a–b Observed networks for **a** Grevy's zebra (28 individuals) and **b** Onagers (29 individuals). Individuals are vertices, with reproductive status indicated by shape: males (*squares*), lactating females (*circles*), and nonlactating females (*triangles*). *Thin gray lines* join individuals observed together at least once (nonzero network). *Thick black lines* represent statistically significant associations (preferred network)

one of 28 individuals and the other a singleton. Grevy's zebra have three components, of sizes 23, 4, and 1. The onager preferred associates network has six connected components, the largest of which includes 24 individuals. The remaining five individuals are all in singleton components. The Grevy's zebra preferred associates network has 11 components, the largest of which has seven individuals. There are five other nonsingleton connected components in Grevy's zebra.

Grevy's zebra exhibit greater cliquishness than onagers. Grevy's zebra have higher cluster coefficient for both nonzero networks ($P<0.001$, difference in means = 0.19, 95% CI [0.11, 0.28]) and preferred networks ($P<0.001$, difference in means = 0.43, 95% CI [0.27, 0.58]). Mean Grevy's zebra cluster coefficient is 0.9 for the network of nonzero bonds and 1 for the preferred associates network. The latter reflects the fact that all possible bonds within components exist in this network. For onagers, mean cluster coefficient is lower for the network of preferred associations (0.57) than it is for the network of nonzero bonds (0.71).

Pairs of individuals in the largest component tend to be more distant in Grevy's zebra than in onagers for the nonzero and preferred networks. The distribution of shortest paths among all dyads significantly differs between the Grevy's zebra and onager nonzero networks ($P<0.001$, difference in means = 0.29, 95% CI [0.20, 0.40]). For the Grevy's zebra network of preferred bonds, every component contains all possible bonds, resulting in a minimum path length of 1 for each component. For the onager preferred network, observed mean minimum path length is 3.47 for the largest component of 24 animals; the remaining five individuals are singletons. Although path length within a component is shorter in the Grevy's zebra preferred network, Grevy's zebra pairs nonetheless tend to be more distant at the population level because individuals in a higher fraction of possible pairs are in different components.

Reproductive state comparisons

Individual reproductive state influences association decisions more strongly in Grevy's zebra than in onagers. Comparing vertex degree among reproductive classes within the onager nonzero network, our permutation ANOVA indicates no significant effect of reproductive class (*P*=0.29). Further, we find no significant pairwise difference between males and lactating females (*P*=0.34, difference in means = 2.9, 98.3% Bonferroni CI [−4.8, 10]), males and nonlactating females (*P*=0.36, difference in means = 2.7, 98.3% Bonferroni CI [−4.3, 10]), or nonlactating versus lactating females (*P*=0.9, difference in means = 0.2, 98.3% Bonferroni CI [−4.0, 4.5]). For the Grevy's zebra nonzero network, however, we observe significant differences in number of associates among reproductive classes using an overall permutation ANOVA (*P*=0.03). However, our pairwise comparisons among different classes cannot detect significant differences between any pairs at the 1.7% level defined by our Bonferroni correction: males and lactating females (*P*=0.03, difference in means = 7.2, 98.3% Bonferroni CI [0, 12.5]), males and nonlactating females (*P*=0.05, difference in means = 4.8, 98.3% Bonferroni CI [−1, 10.5]), or nonlactating and lactating females (*P*=0.22, difference in means = 2.5, 98.3% Bonferroni CI [−3.7, 10.5]). There appears to be a trend toward differences between males and both female classes.

The number of associates of individuals varies significantly by reproductive class in the preferred networks of both onagers (permutation ANOVA, *P*=0.0001) and Grevy's zebra (permutation ANOVA, *P*=0.035). Onager males are significantly different from both lactating females (*P*<0.001, difference in means = 3.5, 98.3% Bonferroni CI [1.5, 5.3]) and nonlactating females (*P*<0.001, difference in means = 3.5, 98.3% Bonferroni CI [1.7, 5.2]), but female classes do not differ from each other (*P*=1, difference in means = 0, 98.3% Bonferroni CI [−2.2, 2.2]). In Grevy's zebra we again detect no significant differences between any pair: males versus lactating females (*P*=0.06, difference in means = 3.2, 98.3% Bonferroni CI [−1, 6]), males versus nonlactating females (*P*=0.09, difference in means = 1.5, 98.3% Bonferroni CI [−0.8, 3.8]), or nonlactating versus lactating females (*P*=0.12, difference in means = 1.7, 98.3% Bonferroni CI [−1, 4.5]). As for the Grevy's zebra nonzero network, we observe a nonsignificant trend toward differences in degree between males and both female classes.

As expected from past research, female Grevy's zebra exhibit a significant tendency to associate with other females in the same reproductive state (Monte Carlo permutation test, *P*=0.023). In contrast, we detect no assortative associations among onager females (Monte Carlo permutation test, *P*=0.95). The reproductive status of an individual does not significantly influence its membership in cliques. Cluster coefficient of an individual does not significantly vary by reproductive class in nonzero and preferred networks of either onagers (permutation ANOVA, *P*=0.44 and *P*=0.98, for nonzero and preferred networks, respectively) or Grevy's zebra (*P*=0.14 and *P*=1).

Discussion

For species in which group membership frequently changes, it has been a challenge to characterize fine-grained variation in social patterns (Krause and Ruxton 2002; Whitehead and Dufault 1999). Quantifying this variation is necessary to test hypotheses about ecological determinants of social patterns and to make predictions about how variation in group formation and breakdown affects development of social relationships and transmission processes. As a pair, our study populations of Grevy's zebra and onagers exemplify many sets of coarsely similar fission–fusion species or populations, such as chimpanzees and spider monkeys, or among bottlenose dolphin populations. Grevy's zebra and onagers are closely related grazing ungulates inhabiting varied environments in Africa and Asia, respectively. Until now they have been ascribed the same general social organization, in which males defend areas to gain access to females in unstable groups. However, differences in predation danger, forage distribution, and rainfall between the two populations all suggest that onagers should form smaller groups with less stable membership than Grevy's zebra.

We find a small but significant trend toward greater group size in Grevy's zebra, as predicted by differential ecological pressures. Examination of the distributions suggests that Grevy's zebra fission and fusion events tend to occur when a social subunit of several individuals splits or joins others. This may be the mechanism for the apparently multimodal group size distribution. In the high-risk environment of Grevy's zebra, this mode of group changes may allow individuals to avoid the dangers of being alone. The apparently exponential group size distribution in onagers is consistent with individuals being relatively indifferent about minimum group size (Bonabeau et al. 1999). However, Bonabeau et al. (1999) demonstrate that diverse mechanisms of fission and fusion, including splitting by cliques, can produce such a distribution. Thus, although we may draw some insights from the group size distributions, we can make

more powerful comparisons by investigating individual associations and their resulting social structure.

One population measure that offers insight into group stability is HWI distributions. The HWI distributions show that some Grevy's zebra dyads have stronger associations than onagers. The onager population, on the other hand, has more bonds with HWI greater than zero. Both patterns are consistent with Grevy's zebra individuals exerting greater selectivity in their associations. Population-level HWI distributions do not allow us to address questions about stability of group membership, clustering, or individual preferences. By using the dyadic HWI to create association networks, we bring more powerful tools for investigating how these fine-grained aspects of sociality vary between and within two populations. We combine tools for defining preferred associations with network models previously applied to single populations (Croft et al. 2004; Lusseau 2003).

We compare the populations using two thresholds for bonds within a network. In the nonzero network we join all dyads seen together at least once, while in the preferred bonds network we link only those individuals whose HWI indicates statistically significant preference for being in the same group. The network that emerges from preferred bonds is relevant for addressing processes that require strong connections, such as dominance, cooperation, and observational learning of complex behaviors. However, even the rare contacts that do not define significant preferences may be critical to certain phenomena. Many transmission processes require only a single contact to occur, including some aspects of cultural learning, or the spread of information about resources, disease, or even genes. The nonzero network is appropriate for such single-contact processes.

Having constructed a network, we must analyze it in ways that provide greatest insight into the questions and population of interest. Many past applications of network methods to animal societies have focused on evaluating whether a social network is a "small world" (Croft et al. 2004; Lusseau 2003).

In a small world network, highly clustered localities are connected to other such localities by shortcuts. These shortcuts result in the network having low characteristic path length. Disease or information is expected to spread rapidly in a small world network (Watts and Strogatz 1998). The largest connected component in each nonzero network of our populations appears to meet the criteria of a "small world" network, having higher cluster coefficient but similar characteristic path length when compared to equivalent random networks. Neither the onager nor Grevy's zebra preferred networks appear to be small-world. In

onagers, path length is higher compared to the equivalent random networks. In the Grevy's zebra preferred network, every component contains all possible bonds, rendering the small world concept irrelevant. Classifying networks as small-world or not does not allow us to make fine-scale comparisons between the populations.

Direct comparisons of metrics derived from association networks of our two study populations provide a clearer picture of their similarities and differences. The populations are similar in containing nonrandom social structure, as shown by differences between observed networks and equivalent random ones. Observed networks have more connected components and higher cluster coefficients. A second similarity is that networks of nonzero associations show that almost all individuals in both populations exist in a common community, in which each individual is accessible from any other by an unbroken path. Any idea or disease that requires only a single contact to spread may be expected to do so through almost all individuals.

While onagers tend to have more nonzero associates, individuals in both populations have similar numbers of preferred associates. A possible explanation for this pattern, also observed in primate societies, is that there are constraints on the number of close associates an individual can cultivate (Kudo and Dunbar 2001). The number of preferred associates may both constrain and reflect the pool of other individuals with whom an animal can develop cooperative relationships such as mutual grooming or male coalitions.

Network metrics identify a key difference between the Grevy's zebra and onager study populations: Grevy's zebra form groups with relatively stable membership, compared to the onagers. Grevy's zebra have a higher number of connected components, for both nonzero and preferred networks. In the Grevy's zebra nonzero network, the visually apparent substructure clearly foreshadows the distinct components of the preferred network. The bonds present in the nonzero network and absent in the preferred are those signifying infrequent interactions between tightly knit groups. Onagers, by contrast, do not show the same substructure in terms of the number and size of connected components. Greater cliquishness in Grevy's zebra is further indicated by their higher cluster coefficient. The higher number of nonzero bonds held by onager individuals suggests less selectivity about associates.

From the structure of observed networks we can make predictions about how the two populations may differ in the spread of pathogens or information. Disease transmission in mammals typically occurs through contact among individuals in groups such as those analyzed here (Altizer et al. 2003). In ungulates, it is likely

that information about resource locations spreads through copying, as naïve individuals move with knowledgeable ones (Galef and Laland 2005). In the networks of onager nonzero and preferred associations, most individuals are in one component. Thus we would expect diseases and information to spread through most of the onager population. The higher path length in the onager preferred network suggests that transmission through the population is much slower for processes requiring multiple contacts. In contrast to onagers, in Grevy's zebra there are more components for both networks. Transmission processes may be expected to be contained within one of the Grevy's zebra components, if only introduced once. The higher cluster coefficient and lower path length within a Grevy's zebra component predicts more rapid, complete spread of ideas and diseases than within an onager component.

Network structure may further shape differences in social relationships between the two populations. In particular, high clustering in Grevy's zebra may promote development of reciprocal relationships, such as dominance and mutual grooming, among individuals in a component. We predict these behaviors are more common in Grevy's zebra than in onagers.

Reproductive state is an important basis for the greater selectivity in associations shown by Grevy's zebra females. The number of bonds held by an individual varies by its reproductive state in both the nonzero and preferred Grevy's zebra networks, but only in the preferred onager network. Further, in their preferred bonds, Grevy's zebra females associate assortatively by reproductive class, but onagers do not. One explanation for this difference is that higher costs of changing associates in Grevy's zebra force individuals to choose others with similar needs. In equids, female reproductive state strongly influences resource requirements because lactation increases water and energy use (Ginsberg 1987). For onagers, by contrast, low predation danger and high visibility reduces the costs of individuals changing groups when their needs diverge from those of current associates.

In onagers, greater turnover of individuals within groups and lower selectivity in association choices appear to result in nonconcurrent interactions: individuals tend to be in groups with their various preferred associates at different times, rather than occurring with all these associates in the same group. We can infer this pattern from the presence of most onagers in one component of the preferred network, combined with its high path length and low mean cluster coefficient. If an individual formed a group with all its associates at the same time, the associates would then be bonded to each other as well, in which case cluster coefficient

would be high and path length low. It is possible that the onagers tend to associate nonconcurrently, because individuals spend time with different associates depending on activity, time of day, or location. Because onagers tend to associate nonconcurrently with preferred associates, the order of interactions may have importance for how diseases or ideas spread through the onager network. If we are to test hypotheses about how timing of interactions relates to ecology and transmission processes, we will need a network framework that explicitly accounts for temporal dynamics of interactions (Keeling and Eames 2005).

We have demonstrated the use of network metrics in comparing association patterns of two populations with broadly similar fission–fusion grouping patterns. The approach arrives at a more nuanced understanding of how social structure between the two populations differs, in ways that are consistent with ecological drivers. We suggest that network analysis offers simple and powerful tools for characterizing patterns of individual variation and emergent population structure. These patterns may otherwise be difficult to discern in fission–fusion species, where group turnover is frequent. The key biological differences we infer from network metrics, in cliquishness and group turnover, are not apparent from analyses limited to group size and association strength distributions. We also find patterns within and between populations in individuals' number of associates. Although it is possible to compute number of associates without explicitly using a network framework, the metric of vertex degree is a straightforward result of constructing a network.

The ways in which our current study populations differ in network properties follow predictions from ecological factors: forage, predators, and water points. For these two populations, the differences in all three ecological variables should influence social decisions towards a common direction of greater group stability and individual selectivity in the Grevy's zebra population. Using the present methods to analyze associations in populations that represent a greater range of ecological variation, we can develop a predictive model relating network properties to particular ecological factors. Then we can identify the relative importance of each ecological feature, and how they may interact in producing network properties. Fission–fusion equids exist under varying ecological conditions, which appear to drive distinctive patterns among populations within each species. For example, onagers are reported to form stable groups in Mongolia, where they experience predation by wolves (Feh et al. 1994). In a more open habitat and at higher population density than our population, Grevy's zebra form unstable groups (Ginsberg

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