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Comparative social network analysis in a leaf-roosting bat

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Abstract Even though social network analysis provides an important tool to characterize and compare societies, no studies have used its analytical applications to characterize patterns of sociality in bats. Here I use social network analysis to characterize and compare patterns of sociality between three populations of the leaf-roosting bat *Thyroptera tricolor*. Sites differed in the density of furled leaves used by *T. tricolor* for roosting. Finca had more leaves per hectare (77), followed by Ureña (58), and Esquinas (7). The time period over which the probability of association is halved based on fitted models was 1,086 days for Finca, 714 days for Ureña, and 303 days for Esquinas. Finca and Ureña had very similar network topologies, with several small clusters, high-clustering coefficients, short path lengths, low node betweenness, and high network robustness. Social networks at Esquinas were composed of one large cluster and several small isolated ones. Esquinas also had high-clustering coefficients, but path length and node betweenness were high. Network resilience was lower in Esquinas compared to Finca and Ureña. These results show that, unlike many other forest-dwelling bats that switch roosts regularly, *T. tricolor* does not exhibit a typical fission–fusion social system, and that resource availability seems to affect social networks in this bat. In addition, this study highlights the importance of emigrating individuals in maintaining social cohesion, establishing network connectedness, and determining network robustness.

Keywords Association patterns · Cooperation · Lagged association rates · Network robustness · Roost density · Social network

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Introduction

Societies are formed by individual interactions that vary in their type, frequency, and duration (Hinde 1976). Such interactions are difficult to understand and characterize by using only traditional measures of social structure, such as group size or mating patterns, because these seldom account for interactions among multiple individuals. Social network analysis, the study of social groups as networks of individuals connected by social ties, provides an important basis for identifying properties of societies because it accounts for reticulate multi-actor interactions (Albert and Barabási 2002; Newman 2003; Wasserman and Faust 1994). By using social network analysis, it is possible to visualize and analyze networks of variable complexity and topology using advanced analytical tools, and to explore the structural properties of societies by applying null models and simulation techniques (Croft et al. 2008). Thus, the analytical applications of social network analysis, through their use in visualizing and quantifying social relationships, have the potential to revolutionize how we think about and categorize social structure, as more traditional categories, such as polygynous mating systems or dominance hierarchies do not really capture the dynamic nature of individual interactions or the variation within and among populations. Unfortunately, the field of animal behavior and behavioral

ecology have thus far benefited little by the analytical advances of social network analysis (Krause et al. 2009).

Social networks have local and global properties that can be understood by a set of metrics describing the connectedness, closeness, and centrality of individuals (Table 1). Such node and group-based metrics not only allow the classification of societies into modeling paradigms (Barabási and Albert 1999; Erdős and Rényi 1959; Watts and Strogatz 1998), but also allow us to define social groups, identify important individuals and their structural roles, understand flow of disease and information, and quantify anthropogenic effects on animals (Wey et al. 2008). Of particular interest has been the use of network metrics to assess the role of individuals within their network, and to model the effect of node removal on network functioning (e.g., Flack et al. 2005; Lusseau 2003; Lusseau and Newman 2004; Manno 2008; McComb et al. 2001; Williams and Lusseau 2006), since this provides clues as to the possible effects of natural mortality, culling, or live captures on natural populations. Thus, social network analysis is not only a powerful descriptive tool that allows us to characterize and compare societies, relationships, and interactions, but is also a crucial tool to understand network responses to environmental and anthropogenic disturbances because removing key individuals from natural populations and observing its effect on social systems may not always be feasible nor desirable.

In this study, I use social network analysis to characterize and compare patterns of sociality between three populations of the leaf-roosting bat *Thyroptera tricolor*, which occupy areas that differ in the density of available resources. Specifically, I address how the differences in temporal patterns of associations observed between populations influence network topology and robustness. Network topology was addressed in terms of node and group-based metrics describing the connectedness, closeness, and centrality of individuals (Table 1). Network robustness was addressed in terms of tolerance against the removal of individuals, where greater tolerance, and hence greater robustness, represents networks whose diameter and fragmentation remain constant after experimentally removing nodes from the network.

T. tricolor is a small (3–4 g) insectivorous bat found in lowland Neotropical forests from southern Mexico to southeastern Brazil (Wilson and Findley 1977). This species is highly morphologically specialized for roosting in furled leaves of members of the order Zingiberales (primarily in the genera *Heliconia* and *Calathea*), which are suitable as roosting resources for very short periods of between 5 and 60 h (Findley and Wilson 1974; Vonhof and Fenton 2004). These plants are typically found in secondary forests and clearings, and there is extensive temporal and spatial variation in their density due to succession, the distribution of canopy gaps, and the stochastic nature of disturbances (Dobkin 1984; Horvitz and Schemske 1994; Seifert 1982; Stiles 1975). The only study addressing *T. tricolor*'s social behavior (i.e., Vonhof et al. 2004) found that this leaf-roosting species formed distinct

Table 1 Terminology

Basic terms

   Social network: a set of interactions or associations between social entities (e.g., individuals, corporations) typically represented as dots (nodes, or vertices) connected by lines (edges, or links).

   Nodes, vertices: a component of a network representing an individual or social entity.

   Edges, links: a network component that represents a relationship between two nodes. In social networks, edges may represent any type of relationship, such as association, information transfer, and amicable or antagonistic interactions.

   Community: set of individuals that are more closely associated with each other than with the rest of the population.

   Cluster: an isolated subset of interconnected nodes within a community. Clusters are typically formed by several communities.

   Network topology: patterns of interconnections between network components (nodes and edges).

   Network resilience, robustness, tolerance: the ability of a network to maintain a similar topology despite the removal of components.

   Random and targeted attacks: removal of network components in a random fashion or based on a specified criterion.

   Network metrics: set of node and group-based measures used to describe networks.

Node-based metrics

   Betweenness: the number of shortest paths between pairs of individuals that pass through a particular individual.

   Degree: number of immediate neighbors.

Group-based metrics

   Clustering coefficient: the degree to which an individual's immediate neighbors are connected.

   Density: the proportion of edges in a network relative to the total number possible.

   Diameter: average length of the shortest paths between any two nodes in the network.

   Fragmentation: the separation of clusters of nodes from the main cluster.

   Path length: number of connections on the shortest path between two individuals.

mixed-sex social groups, which maintained stable dyadic associations that sometimes lasted over 420 days. However, the majority of dyads (i.e., 85%) remained together for shorter periods of time, typically less than 100 days. Vonhof et al. also found that all members of a social group rarely occupied the same roost at the same time, and that individuals typically spent short periods of time apart from long-term companions. Because of these findings, Vonhof et al. suggest that *T. tricolor* exhibits a fission–fusion social system, and that the functional social unit may not be defined by roost occupancy, but rather by relative levels of social interactions. Additionally, *T. tricolor* is known to perform cooperative signaling behaviors when displaced individuals attempt to locate conspecifics (Chaverri et al. in press). During the process of searching for roosts, *T. tricolor* emits calls to inquiry about roost, or roostmate, location, frequently eliciting a response from individuals who have already entered a tubular leaf. These response calls, in turn, often drive the flying individual into the roost. Hence, the use of social network analysis to characterize sociality in three populations of *T. tricolor* will not only allow us to further understand this species' social system, but will also provide clues as to the possible effects of network topology and robustness on flow of information, particularly regarding roost location.

Materials and methods

Field methods

This study was conducted at three sites located in and around the Golfito Wildlife Refuge (GWR) and Piedras Blancas National Park (PBNP), in southwestern Costa Rica, from October 2006 through February 2009. The first site, Finca (8°38′ N, 83°05′ W), is located near the town of Rio Claro, and is mostly surrounded by primary forest, but its northern range borders pasturelands. The dominant understorey plant species are *Heliconia imbricata* and *Calathea lutea*. The second site, Esquinas (8°42′ N, 83°12′ W), is located near the Esquinas Rainforest Lodge, which is surrounded by the PBNP. This site is mostly composed of primary and late secondary forests, and *Heliconia* spp. patches are scattered and never too dense. The other site, Ureña (8°40′ N, 83°12′ W), is located near the town of Golfito, inside the GWR. Ureña is located within disturbed secondary forests, and its understorey is dominated by *C. lutea* patches. These three sites were selected among a total of 16 based on the density of tubular leaves and recapture rates, such that the widest possible range of leaf densities was represented, and that bats were being recaptured often enough to accurately represent their social behavior.

At these sites, I consistently surveyed a pre-established area (Size: Finca=0.78 ha, Ureña=0.81 ha, Esquinas= 3.30 ha) once or twice a month. During these surveys, bats were captured in all identified roosts by pinching the top of the leaf and directing them into a cloth-holding bag. Bats were then fitted with individually numbered metal wing bands, sexed, aged, and their reproductive condition assessed. I quantified the number of tubular leaves (i.e., potential roosts) per site by counting the number of unoccupied and occupied (i.e., roosts) leaves. Tubular leaves were only counted if their diameter of opening ranged between 4 and 20 cm, as this is the preferred size range of roosting leaves selected by *T. tricolor* (Vonhof and Fenton 2004). To estimate tubular leaf density per site, I mapped the surveyed area and calculated the number of tubular leaves ha^{-1}, then compared tubular leaf density among sites using One-way ANOVA, and used Tukey's pairwise comparison at an alpha of 0.05 to identify differences between sites. Tubular leaf availability was not measured during every visit, only a total of 16 times in Finca, 17 in Ureña, and 18 in Esquinas.

Collection and organization of social data

For each sampling day, I noted the identity and location of individuals within sampling areas. I recorded the composition of groups within single roosts, and constructed a similarity matrix based on the proportion of time that pairs of individuals were observed associating (i.e., in the same roost) during the 29-month study period using SOCPROG version 2.3 (Whitehead 2009). To determine patterns of association among individuals, I used the simple ratio association index (Cairns and Schwager 1987; Ginsberg and Young 1992). This index estimates the proportion of time that two individuals (or dyad) spent in association, and ranges from zero (no association) to one. The simple ratio association index was calculated as $X/(X+Y_{AB}+Y_A+Y_B)$, where X is the number of observations during which bat A and bat B were observed together in the same roost, Y_{AB} is the number of observation periods during which A and B were observed in separate groups, Y_A is the number of observation periods during which only A was observed, and Y_B the number of observations in which only B was observed.

Association data were converted to a binary matrix in which 0 and 1 represent absence or presence, respectively, of an association between two individuals. Even though many authors advocate the use of weighted, rather than binary, social networks (e.g., Lusseau et al. 2008; Whitehead 2008), I preferred the latter for the following reasons: 1) *T. tricolor* has a social system in which roosting groups maintain very stable associations, and exchange of individuals among roosting groups is rare (Vonhof et al. 2004; G. Chaverri, unpubl. obs.), thus avoiding the problem of linking transient

associations that is often used to justify the use of weighted networks (Lusseau et al. 2008). 2) Many node-based measures used for binary networks are not available, or are difficult to interpret, for their weighted counterparts (Croft et al. 2008; Whitehead 2008), limiting the range of possible descriptors available to this study. 3) Some of the roosting groups considered in this study were recaptured within an extended time period (2+ years), which allowed me to record the arrival and departure of group members. Other groups, however, were only recaptured within a short time period (a few weeks), which precluded me from observing changes in group composition. By using a weighted network approach, I would have overestimated association rates of these latter groups, and underestimated rates of association in the former, even though the two may not have differed when compared along the same time scale.

Temporal stability of associations

To address the scales of temporal patterning of social relationships within the three study sites, I estimated lagged association rates. The lagged association rate $g(\tau)$ represents the probability of association τ time units after a previous association. A dyad is always associated τ time units later if $g(\tau)=1$, whereas if associations always disband and never reform within τ time units, $g(\tau)=0$. The values associated with lagged association rates if animals associated randomly represent the null association rates, with $g(\tau)=n/N$, where n represents the number of recorded associations and N represents pairs of sampling periods τ units apart (Whitehead 2008). Because not all individuals were captured during each survey, and because the identification rate of individuals and their associates varied among sampling periods, I used the standardized lagged association rate, or $g'(\tau)$ (Whitehead 2008). The standardized lagged association rate represents the probability that, if X and Y associate, randomly choosing an associate of X after a time lag of τ would result in Y.

Standardized lagged association rates were plotted against time lag, in days, to describe how relationships change with time. To produce smooth curves of lagged association rates, without compromising the precision of τ, I adjusted the moving average in SOCPROG to 10,000 for data from Finca, 1,500 for Ureña, and 400 for Esquinas. To assess the precision of the estimated lagged association rates, I used standard errors calculated using the temporal jackknife method (Whitehead 2008). Standardized lagged association rates were then compared to the standardized null association rate to determine whether preferred associations were present in the population. The standardized null association rate represents the lagged association rate if individuals were associating at random, and is the inverse of the number of identified individuals minus one, which does not change with time lag (Whitehead 2008).

Model fitting to standardized lagged association rates was conducted using the four default models in SOCPROG, namely constant companions (CC), casual acquaintances (CA), constant companions and casual acquaintances (CC+CA), and two levels of casual acquaintances (2CA) (Whitehead 2008). In the CC model, where $g'(\tau)=a$, all associations persist throughout the study, typical of closed, non-interacting units. Hence, in this model there is no change in association rate with lags of one sampling period or more. The CA model ($g'[\tau]=a \times e^{-b\tau}$) assumes very large populations in which animals associate for about $1/b$ time units. Other scenarios under which CA may also occur include smaller populations where individuals avoid previous associates, or populations with high mortality or emigration rates of about b per sampling period. In the CC+CA model ($g'[\tau]=a+c \times e^{-b\tau}$), association rates fall with time lag and then level off, which could indicate casual acquaintances within a closed population if the leveling of lagged association rates occurs at the null association rates. If the long-term lagged association rate occurs above the null, then this model indicates a social system in which individuals associate temporally; casual, but preferred associations; and a scenario in which some individuals form permanent units while others are "floaters" who move between social units. The duration of associations for this model is $1/b$. The final model, 2CA ($g'[\tau]=a \times e^{-b\tau}+c \times e^{-d\tau}$), represents the short-term movement of strongly associated individuals among social groups, and the long-term disassociation of these bonds because of movement between social units, shifts in preferred companions, mortality, emigration, or a combination of these. To determine which of these models best fit the data, I used the quasilikelihood version of the Akaike Information Criterion (QAIC) in SOCPROG (Whitehead 2007).

Social network analysis

Network density (ρ, the proportion of links, or relationships among individuals, in a network relative to the total number possible), mean path length (L, number of connections on the shortest path between two individuals), mean clustering coefficient (C, the degree to which an individual's immediate neighbors are connected), mean degree (k, number of immediate neighbors), and mean node betweenness (B, the number of shortest paths between pairs of individuals that pass through a particular individual; Table 1) were estimated for the three networks using Ucinet version 6.205 (Borgatti et al. 2002). These network metrics were compared to the average value of 20 random networks that contained the same number of links and vertices.

To determine network robustness, I removed individuals (i.e., nodes) from social networks at the three study sites and measured network diameter (i.e., average length of the

shortest paths between any two nodes in the network) and fragmentation (i.e., the separation of clusters of nodes from the main cluster). First, to measure the effect of node removal on network diameter, and to compare the effect of removing arbitrary and specific individuals, I simulated random attacks by removing up to 50% of nodes chosen at random and subsequently measured the diameter of attacked networks using Pajek version 1.24 (Batagelj and Mrvar 2008). I then performed targeted attacks by removing up to 50% of nodes with high degree and betweenness, and measured their effect on network diameter. I repeated random and targeted attacks ten times. To determine the effect of attacks on network fragmentation, I removed nodes with high degree and betweenness, and measured their effect on the total number of clusters remaining in the network, proportion of nodes left in the largest cluster (S), and the average size of isolated clusters ‹s› (i.e., clusters other than the largest one). I repeated attacks ten times, and removed up to 50% of nodes in NetDraw version 2.082 (Borgatti 2002).

Results

During the study period of 29 months, I captured a total of 163 individuals across the three study sites. I captured 50 individuals in Finca, 42 in Ureña, and 71 in Esquinas (Table 2). Recapture rates were highest in Finca (mean 10.36±SD 8.00, min 1–max 24), followed by Ureña (7.31± 5.27, 1–22), and Esquinas (4.70±4.01, 1–15). Similarly, the proportion of individuals identified per sampling period was greatest in Finca and lowest in Esquinas (Table 2). All sites differed significantly in the density of furled leaves (One-way ANOVA, $F_{2,48}$=77.65, $p<0.001$; Tukey's post hoc test: $p<0.05$ for all pairwise comparisons). Finca had the greatest amount of furled leaves per hectare (77), followed by Ureña (58). Esquinas had a density of only seven tubular leaves per hectare (Table 2).

Associations among individuals were quite stable within all study sites. Group composition remained constant (i.e., no immigration or emigration of group members) for long periods, with standardized lagged association rates above

null rates (random association) across time lags of up to 500 days (Fig. 1). However, the standardized lagged association rate decreased over increasing time lags, and the best-fitting model was one of casual acquaintances, indicating that dyads slowly dissociate over time (Table 3). The time period over which the probability of association is halved based on fitted models was 1,086 days for Finca, 714 days for Ureña, and 303 days for Esquinas. The longest period of time in which the same set of individuals were observed together, without immigration of individuals from other groups or emigration of group members, was 22 months at Finca, 13 months at Ureña, and 6 months at Esquinas. Additionally, a large proportion of dyads captured over periods longer than 12 months were observed together on more than 90% of sampling periods in which those individuals were captured, and average maximum associations were 0.79 (±0.26) at Finca, 0.75 (±0.17) at Ureña, and 0.74 (±0.22) at Esquinas (Fig. 2).

The social network at Finca was composed of three non-interacting, densely connected clusters, each with relatively few individuals (Fig. 3). Similar patterns of network topology occurred at Ureña, whose network was composed of four non-interconnected clusters. At Esquinas, I observed one large, sparsely connected cluster and three smaller ones. The large cluster at this site formed slowly over the study period, while the smaller ones correspond to individuals that were added to the network towards the end of the study period. Most clusters were formed by smaller "communities", or sets of individuals that were more closely associated with each other than with other members of the cluster. At all sites, communities were connected to other such structures by one or several individuals (i.e., individuals with high betweenness; Fig. 3) who, in the majority of cases, permanently switched social units. High betweenness values were observed largely in males at Finca and Ureña. At Esquinas, both males and females exhibited high node betweenness, with the latter having greater values.

Network density was highest in Finca and lowest in Esquinas (ρ_{finca}=0.20, $\rho_{esquinas}$=0.10; Table 4). Average clustering coefficient was very similar for all three sites ($C_{finca,\ ureña}$=0.87, $C_{esquinas}$=0.86), while mean degree was

Table 2 Summary statistics for each network, including number of individuals identified, leaf density (number of furled leaves per hectare), number of sampling periods (days), number of identifica-tions, mean individuals identified per sampling period, and proportion of individuals identified per sampling period

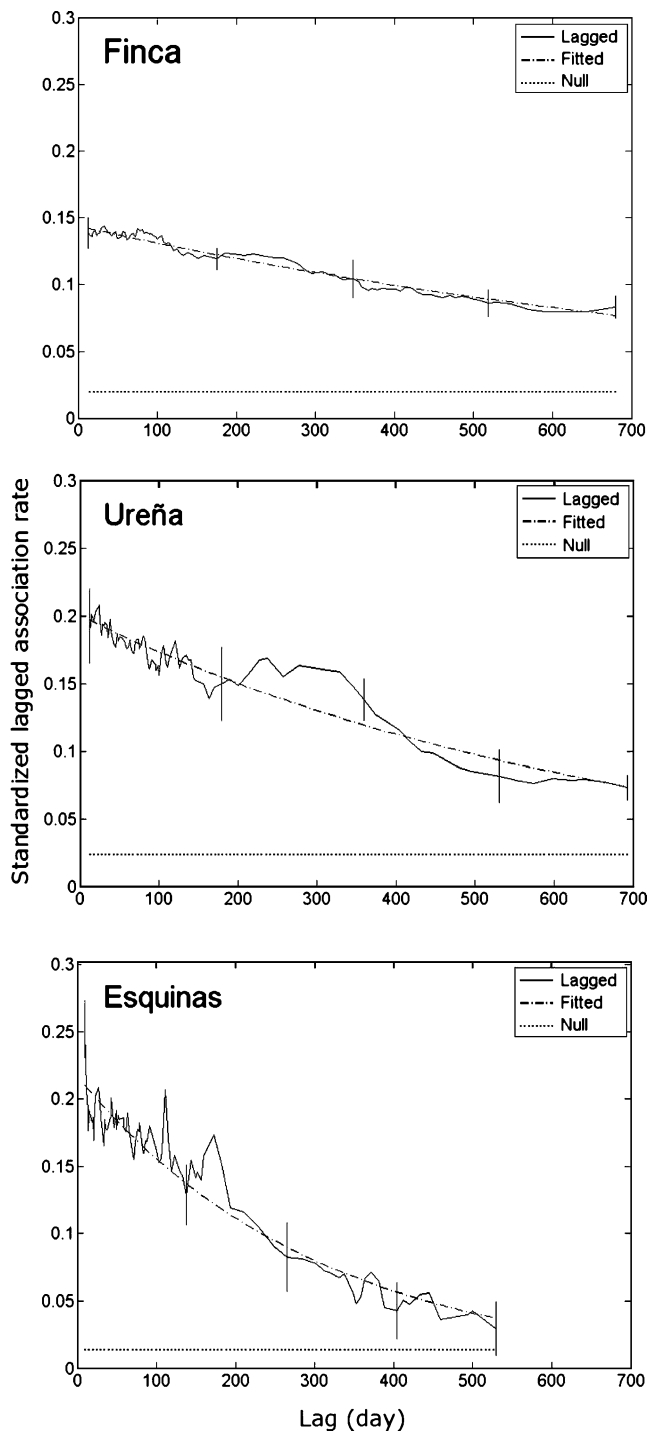| Site	Individuals	Leaf density	Sampling periods	Identifications	Individuals per sampling period	
	n	fl/ha	n	n	Mean	Proportion
Finca	50	77	30	518	17.27	0.34
Ureña	42	58	30	308	10.23	0.24
Esquinas	71	7	31	334	10.77	0.15

Fig. 1 Standardized lagged association rates showing fitted model and standardized null associations for each study site. *Vertical bars* indicate approximate standard errors calculated using the temporal jackknife method. For details on model fitting and selection see Table 2

50.50). Real values for clustering coefficient were larger than the average of 20 random networks, whereas they were lower for degree. In addition, the degree standard deviation for real networks was lower than the average standard deviation for all 20 random networks at all three sites. Comparison of real and random networks generated similar trends in path length and node betweenness, with real values below random at Finca and Ureña, and random values below real for Esquinas (Table 4).

Networks at Finca and Ureña were highly resilient in terms of diameter to both random and targeted attacks, even after the removal of an unrealistic number of vertices (Fig. 4). Network diameter remained fairly constant at around three at Finca and approaching two at Ureña after removing 50% of individuals. Despite an increase in the number of clusters at Finca and Ureña, and hence greater fragmentation, the relative size of the largest cluster remained fairly constant (Figs. 4 and 5). However, the size of isolated clusters, those other than the largest one, decreased considerably at Finca and, to a lesser extent, at Ureña. At Esquinas, in contrast, network diameter was very susceptible to random and targeted attacks, decreasing from seven to almost one after the removal of vertices with high betweenness. These changes in diameter at Esquinas are most likely explained by network fragmentation and by the considerable decrease in the size of the largest cluster with the removal of an increasing amount of vertices, particularly those with high betweenness (Figs. 4 and 5). Thus, unlike Finca and Ureña, Esquinas had a larger number of clusters whose size differed considerably when only a few nodes had been removed (i.e., low f), and whose fragmentation at high values of f produced a considerable amount of very small clusters (Fig. 5).

Discussion

Despite the diversity and complexity of social structures observed in bats, there are no published studies applying social network analysis to characterize patterns of sociality in this diverse taxon (but see Rhodes et al. 2005 and Fortuna et al. 2009 for the use of network analysis on roosting networks). Moreover, very few studies have evaluated social networks across populations within single species (but see Naug 2009; Godfrey et al. 2009; Croft et al. 2006), even though social network analysis, compared to other more traditional measures of sociality, has a greater potential to elucidate how differences in ecological conditions could have resulted in the evolution of different behavioral and morphological patterns (Krause et al. 2007). Thus, this study not only uses social network analysis to study sociality in bats for the first time, but is also one of the first studies to explicitly use a comparative

highest at Finca and lowest at Ureña (k_{finca}=3.93, $k_{ureña}$= 2.61). Path length and node betweenness followed a similar pattern of lowest values at Ureña, and very high values for Esquinas ($L_{ureña}$=1.43, $L_{esquinas}$=3.35; $B_{ureña}$=2.10, $B_{esquinas}$=

Table 3 Model fit (τ is time lag in days) to the data on standardized lagged association rates (g') of *Thyroptera tricolor* at the three study sites, Finca, Ureña, and Esquinas

Site	Model	Best fit	QAIC	ΔQAIC	TP
Finca	CC	$g'=0.118$	55,484	313	
	CA	$g'=0.144e^{-0.00092\tau}$	55,171	0	1,086
	CC+CA	$g'=0.118+0.567e^{-0.724\tau}$	55,486	315	
	2CA	$g'=-0.021e^{-0.218\tau}+0.144e^{-0.00092\tau}$	55,175	4	
Ureña	CC	$g'=0.158$	16,861	222	
	CA	$g'=0.20e^{-0.0014\tau}$	16,639	0	714
	CC+CA	$g'=0.158+0.594e^{-0.708\tau}$	16,865	226	
	2CA	$g'=-3955.87e^{-1.634\tau}+0.201e^{-0.0014\tau}$	16,641	2	
Esquinas	CC	$g'=0.144$	12,434	422	
	CA	$g'=0.217e^{-0.0033\tau}$	12,012	0	303
	CC+CA	$g'=0.135+0.867e^{-0.194\tau}$	12,386	374	
	2CA	$g'=2.032e^{-0.509\tau}+0.215e^{-0.0032\tau}$	12,013	1	

Models tested include constant companions (*CC*), casual acquaintances (*CA*), constant companions and casual acquaintances (*CC+CA*), and two levels of casual acquaintances (*2CA*). Best-fitting model was determined using the quasilikelihood version of the Akaike Information Criterion (*QAIC*) (Whitehead 2007). For details on models and model fitting see Whitehead (2008). Time period (*TP*) over which the probability of association is halved, in days, was estimated only for the best-fitting model

approach to explore a social network structure. Given that social network analysis has been widely used to study societies that exhibit a more fluid social organization (i.e., fission–fusion societies), this study also provides a valuable step towards understanding social systems with more stable associations.

The results of my study highlight some interesting properties of social networks in *T. tricolor*. First, social networks in *T. tricolor* are composed of stable communities (i.e., sets of individuals that are more closely associated with each other than with other individuals within a cluster; Croft et al. 2008), or roosting groups, whose composition remained unchanged for up to 22 months. Hence, unlike many other forest-dwelling bats that switch roosts regularly (see Kerth 2008 and references therein), *T. tricolor* does not seem to exhibit a typical fission–fusion social system whereby groups temporarily split and reform. Since my sampling protocol did not allow me to observe daily movements of individuals, however, I cannot be entirely sure that fission–fusion did not occur in the populations sampled. Notwithstanding the fact that roosting groups may remain unchanged for almost 2 years, despite multiple capture events conducted over extended periods of time, provides an interesting finding that demonstrates the stability of social units in *T. tricolor*. To date, there has only been one study reporting such stable composition of groups in bats, specifically in the cave-roosting bat *Phyllostomus hastatus*, in which up to 87% of females remained in their original harem group after 1 year (McCracken and Bradbury 1981).

Communities in *T. tricolor* were also highly interconnected, as confirmed by clustering coefficients larger than 0.86 for all three social networks considered in this study. In contrast, lower clustering coefficients reported for some mammals (e.g., 0.11 to 0.30 in bottlenose dolphins [Lusseau et al. 2006; Wiszniewski et al. 2009]; 0.2 to 0.35 in sperm whales [Lusseau et al. 2008]; 0.32 in killer whales [Guimarães et al. 2007]; 0 to 1 in meerkats [Drewe et al. 2009]; 0.81 in Columbian ground squirrels [Manno 2008]) imply that many social networks are not as interconnected as those in *T. tricolor*. Clustering coefficients are typically larger in tight and closed societies, while societies in which individuals only associate with their neighbors, who may not associate with each other, exhibit lower clustering coefficients (Whitehead 2008). Thus, unlike many mammals studied to date, *T. tricolor* seems to have societies formed primarily by very tight communities that seldom interact with individuals outside their social unit.

Another interesting characteristic of social networks in *T. tricolor* is that these appeared to be influenced in an almost linear fashion by resource availability. Finca and Ureña, the most similar sites in terms of furled leaf abundance, had the most similar network topologies, with several relatively small isolated clusters, high-clustering coefficients, short path lengths, low node betweenness, and relatively high network robustness. Social networks at Esquinas, in contrast, were composed of one very large cluster and several small isolated ones. The large cluster was formed primarily by the departure of group members from one community to another. Like Finca and Ureña, Esquinas had high-clustering coefficients, although the distance between pairs of nodes was higher for real data in Esquinas compared to random networks. Network resilience was also lower in Esquinas compared to the other
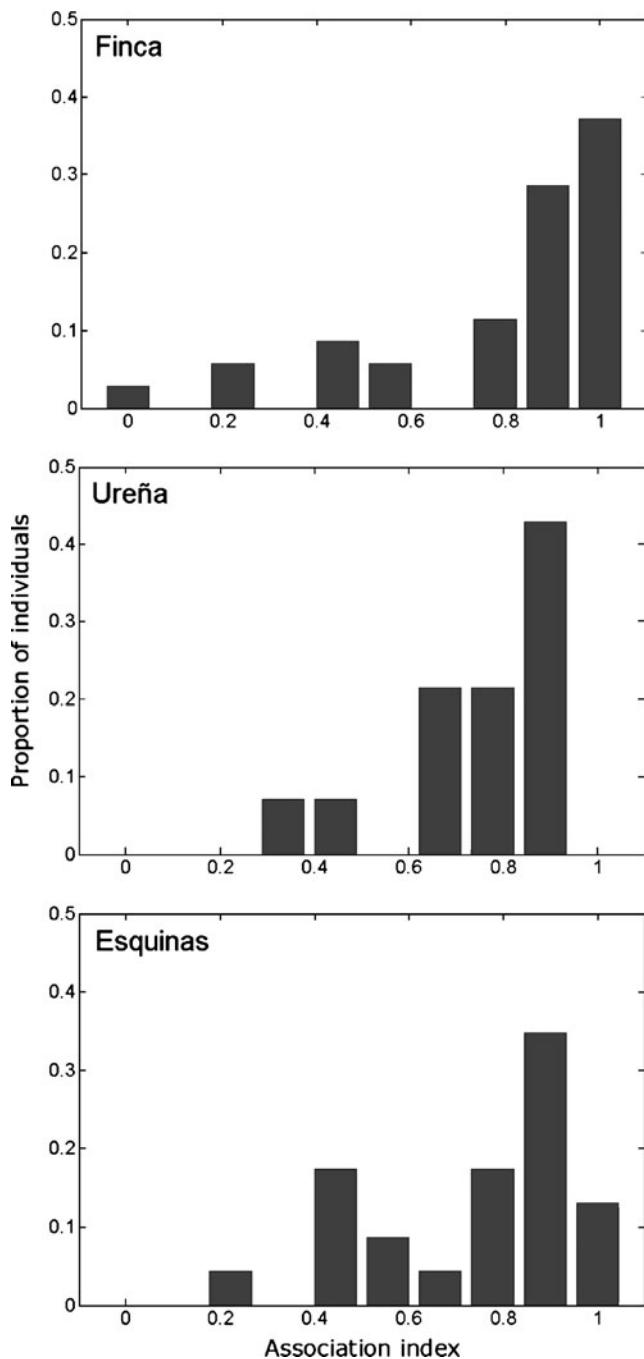
Fig. 2 Plots showing the maximum association values for bats captured over periods of a minimum of 12 months

the site with the fewest roosting resources, because individuals tend to exhibit lower spatial fidelity when they reside in habitats with fewer resources (Forero et al. 2002; Gaillard et al. 2008; Kokko and Lundberg 2001). Thus, after removing the effect of emigrating individuals on social network topology, it is possible to observe similarities between the three societies considered in this study, particularly in regards to connectedness among community members and size of communities.

Societies with fairly discrete communities, such as those observed in *T. tricolor*, often incur in the loss of emigrating
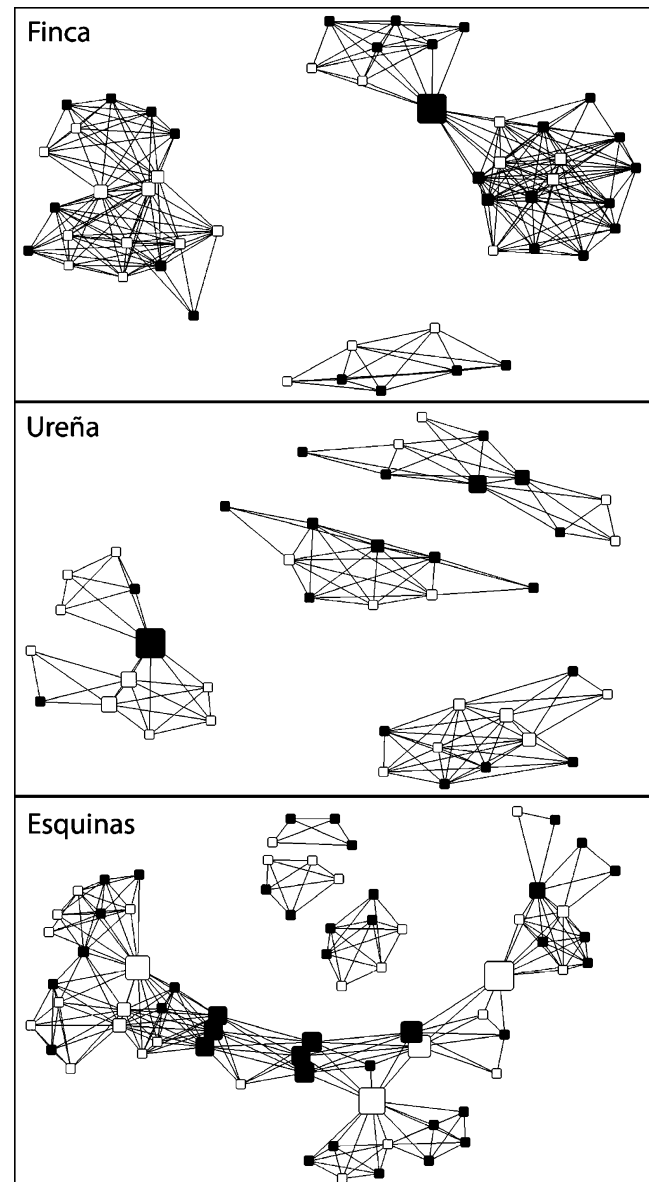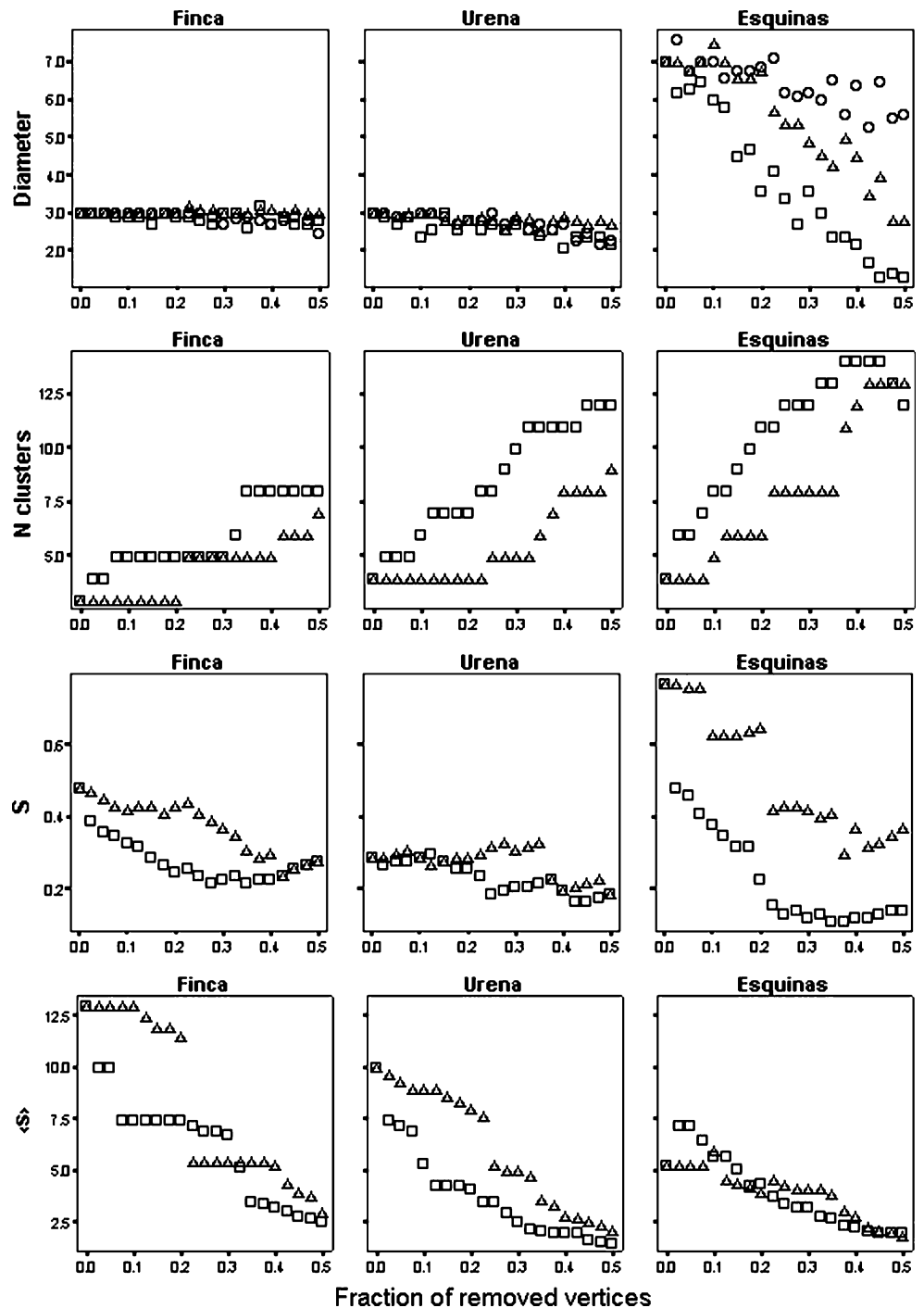

Fig. 3 Social networks of *T. tricolor* at the three study sites in southwestern Costa Rica drawn using the spring embedding method in NetDraw. Each node represents a bat, with *black* representing males and *white* females, and the size of a node is proportional to the betweenness value for that individual

sites, as random and targeted attacks decreased network diameter and the size of the largest cluster, and increased the number of clusters in the network considerably. All of these differences in network topology among sites may be explained by the pervasiveness of emigrating individuals (i.e., nodes with high betweenness) at Esquinas, which decreased association strength and hence, social stability within clusters, and increased connectedness among clusters. Emigration may be more common at Esquinas,

Table 4 Edge density (ρ), path length (L), clustering coefficient (C), degree (k), and node betweenness (B) for real data from each site compared to random graphs generated using the same number of links and vertices as the original networks

Site	ρ	L_{real}	L_{random}	C_{real}	C_{random}	k_{real}	k_{random}	B_{real}	B_{random}
Finca	0.20	1.60	1.92	0.87 (0.13)	0.21 (0.06)	3.93 (1.87)	9.80 (2.94)	5.68 (16.49)	22.44 (14.69)
Ureña	0.14	1.43	2.16	0.87 (0.17)	0.14 (0.14)	2.61 (1.01)	5.76 (2.22)	2.10 (4.89)	26.19 (20.31)
Esquinas	0.10	3.35	2.37	0.86 (0.19)	0.10 (0.08)	2.81 (1.04)	7.01 (2.56)	50.50 (109.29)	48.24 (34.52)

Values in parentheses are standard deviation for real networks and the average standard deviation for the 20 random networks

Fig. 4 Changes in diameter, number of clusters (N), size of the largest cluster (S), and average size of isolated clusters ‹s› of social networks at the three research sites in relation to the fraction of removed nodes. *Circles* represent random removal of individuals (i.e., random attacks). Targeted attacks were focused on individuals with many links (i.e., individuals with high degree, *triangles*) and towards individuals connecting two otherwise discrete clusters (i.e., individuals with high node betweenness, *squares*)
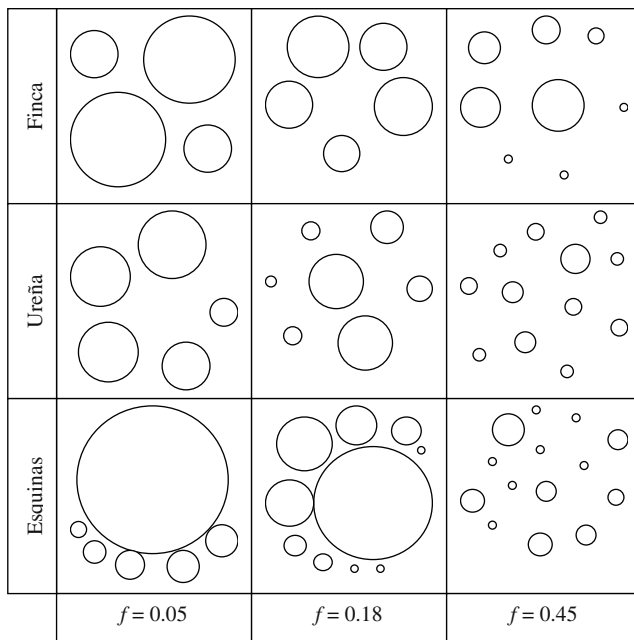
Fig. 5 Response of social networks to the removal of individuals with high betweenness. *Circles* represent clusters, with size proportional to the number of individuals in the cluster. *Rows* represent networks at the three study sites, while *columns* represent networks with a specific fraction of removed nodes (*f*=fraction of removed vertices)

group members, who may subsequently join other social units. These individuals are often detected using social network analysis, particularly through the use of centrality measures such as node betweenness (Whitehead 2008). Based on network measures alone, these emigrating individuals seem to play central roles within their networks, as their betweenness values suggest they are well-connected. However, because emigrating individuals permanently leave their original cluster, their role in network structuring is not really that of "society's glue" (Lusseau and Newman 2004), but rather "socially exploratory" (Whitehead 2008). These individuals may be a particularly valuable asset in *T. tricolor*'s societies, and consequently accepted into new groups, as their explorations may provide information about other roosting or foraging habitats. Thus, as more individuals switch social units, apparently there will be more efficient transfer of information about food and roost location, which could be particularly critical at sites where resources are scarcer.

While information transfer is a well-studied aspect of the social behavior of bats, and has been used to explain sociality in these mammals (Safi and Kerth 2007), no studies have provided conclusive evidence of the presence of cooperative signaling behaviors of roost location towards flying conspecifics, even though previous studies on bats suggest the presence of information transfer of roost location (Kerth and Reckardt 2003; Ruczynski et al. 2007; Ruczyński et al. 2009; Wilkinson 1992). Data available for

T. tricolor show that during the process of searching for roosts, *T. tricolor* emits calls to inquiry about roost location, frequently eliciting a response from individuals who have already entered a tubular leaf. These response calls, in turn, repeatedly attract the flying individual into the roost (Chaverri et al. in press). Thus, *T. tricolor* is the only species for which there are not only data available on social networks, but also on cooperative signaling behaviors of roost location, allowing me to formulate predictions regarding information transfer and cooperation in this species. Based on the results of network topology in *T. tricolor*, for example, I can predict greater reciprocity in networks with higher clustering coefficients, shorter path lengths, and larger stability of associations, such as those observed in Finca and Ureña, because it may be easier to identify the reputation of each individual (Ohtsuki et al. 2006; Suzuki and Akiyama 2005). In contrast, I expect lower levels of reciprocation at Esquinas since there is greater movement of individuals between clusters, which may decrease the predictability of an individual's social environment (Beletsky and Orians 1989), decreasing encounter rates and hindering reciprocation (Ferriere and Michod 1996). Because network diameter and fragmentation characterize the ability of nodes to communicate with each other, and because the absence of nodes in general increases the distance between the remaining nodes (Albert et al. 2000), I can also predict that a better flow of information among individuals will exist in social networks at Finca and Ureña despite mortality of group members, since diameter and fragmentation remained fairly constant even after removing a large proportion of nodes. Social networks at Esquinas, in contrast, exhibited a considerable increase in network fragmentation as nodes with large degree and betweenness values were removed, suggesting that communication within the network would be severely affected by the death of these individuals. However, because communication occurs on shorter time scales than movement between communities, and because stability and connectedness within communities may be similar between sites after removing the effect of emigrating individuals, it is possible that efficient flow of information is still possible despite lower network resilience in Esquinas.

Despite the similarities in some of the methods used to explore the social structure of *T. tricolor*, I found a few discrepancies in the results of my study and that of Vonhof et al. (2004). For example, because my study was conducted over a longer period of time, I was able to record dyadic associations that lasted more than 1,086 days, compared to the period of 420 days recorded by Vonhof et al. I also observed very stable social units in which the same set of roosting individuals remained unchanged for periods of up to 22 months. In contrast, Vonhof et al. observed that social units rarely occupied the same roost at the same time, and

that individuals typically spent short periods of time apart from long-term companions. Thus, it seems that *T. tricolor* in southwestern Costa Rica does not exhibit a similar fission–fusion social system described by Vonhof et al., and that the functional social unit may be, in fact, defined primarily by roost occupancy. Because the study conducted by Vonhof et al. did not compare populations inhabiting areas with different resources, they were also unable to address whether environmental constraints influence the social behavior of this leaf-roosting species. By using social network analysis, my study also provides additional information regarding the social behavior of *T. tricolor*, such as the structural role of individuals within networks, and the possible consequences of death or departure of group members to communication patterns within social units.

Based on the analysis of its social networks, I can conclude that *T. tricolor*'s social structure conforms to the small world modeling paradigm, characterized by highly structured subgroups and short path lengths (Watts and Strogatz 1998). Like the social networks in *T. tricolor*, small world networks are very robust to the removal of random edges, but selectively removing nodes that play pivotal roles in maintaining network connectivity (i.e., individuals with high node betweenness in *T. tricolor*) has considerable effects on network topology (Albert and Barabási 2002; Albert et al. 2000; Crucitti et al. 2004). By having short path lengths and high-clustering coefficients, small world networks are systems in which information is exchanged very efficiently (Latora and Marchiori 2001; Watts and Strogatz 1998). Because cooperative signaling behaviors play a significant role during the location of very ephemeral, and often sparse, roosts in *T. tricolor*, efficient flow of information is a fundamental requirement of this species social network. In addition to having a more efficient flow of information, the social network topology of *T. tricolor* favors cooperation among group members because interacting with a relatively small number of individuals is known to increase the occurrence of cooperation (Santos et al. 2006; Suzuki and Akiyama 2005). Hence, the use of social network analysis to study three populations of *T. tricolor* has allowed us to further understand this species' social system, to address the possible effects of resource abundance on social behavior, to understand potential network responses to environmental and anthropogenic disturbances, and has also provided clues to understand cooperation in a species which uses very ephemeral roosting resources. Additional comparative network analyses in bats could significantly advance our understanding of ecological selection pressures that shape social behavior in this diverse and ecologically significant taxon.

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