METHODS

Using home range estimates to construct social networks for species with indirect behavioral interactions

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Abstract Social network analysis has become a vital tool for studying patterns of individual interactions that influence a variety of processes in behavior, ecology, and evolution. Taxa in which interactions are indirect or whose social behaviors are difficult to observe directly are being excluded from this rapidly expanding field. Here, we introduce a method that uses a probabilistic and spatially implicit technique for delineating social interactions. Kernel density estimators (KDE) are nonparametric techniques that are often used in home range analyses and allow researchers studying social networks to generate interaction matrices based on shared space use. We explored the use of KDE analysis and the effects of altering KDE input parameters on social network metrics using data from a natural population of the spatially persistent forked fungus beetle, *Bolitotherus cornutus*.

Keywords Social networks · Kernel density estimation ·
Home range · *Bolitotherus cornutus* ·
Indirect behavioral interactions

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Introduction

Due to the logistical constraints on defining interactions, organisms that rarely interact physically, or do so in contexts that are difficult to observe (e.g., at night or underground), have been left out of the recent exploration of social networks in population biology. Moreover, indirect interactions are an important component of social behavior in many animal species. Critical information may be exchanged or social influence propagated among individuals even if they do not share the same space at the same time. Scent marking behavior, for example, is a primary mode of communication in a variety of taxa including mammals (e.g., Smith and Abbott 1998; Washabaugh and Snowdon 1998; White et al. 2002; Scordato and Drea 2007), salamanders (e.g., Jaeger and Gabor 1993; Gautier and Miaud 2003), anurans (Byrne and Keogh 2007), and both social and non-social insects (Colwell et al. 1978; Epple et al. 1987; doNascimento and Morgan 1996; Fitzgerald et al. 2004; Morgan 2009). Chemical signals may persist in an area long after an individual has departed. The information contained in chemical communication can be complex and often includes information on identity, sex, health status, hormonal and reproductive state, and even genetic composition of the applier. Other ecologically important factors, such as environmentally persistent diseases or parasites (e.g., Perkins et al. 2009), or spatial distributions of risk or resources also generate interactions among individuals even when they do not occupy a space at the same time. To consider indirect interactions such as these in a social network framework, we require an approach that defines individual interactions on the basis of space use that does not require simultaneous occupation.

Network analyses typically use one of two techniques for defining interactions—observations of animals seen

together sharing space in isolated groups or direct observation of social interactions. The first method is useful in species that naturally form groups and can be easily observed or captured together (such as herds of ungulates or schools of fish; Croft et al. 2005, 2008; Sundaresan et al. 2007) but requires additional statistical steps and specialized permutations in order for complete analyses (termed the "gambit of the group"; Croft et al. 2008). The second method requires the researcher to define the contacts or behaviors among individuals that are considered to be interactions (typically those that involve physical contact such as grooming, fighting, or copulating) and to be able to directly observe such actions.

A few studies have successfully defined interaction matrices on the basis of shared space use (Corner et al. 2003; Vonhof et al. 2004) but have typically been confined to animals that simultaneously utilize common nests or dens (although see Wolf and Trillmich 2008). To investigate taxa that might utilize common space, but at different (or difficult to observe) times, we need a probabilistic method for delineating social interactions based on independent movement patterns. Space utilization models of animal home ranges are probabilistic, spatial estimates of where individuals tend to be located during a given time (Burt 1943; Worton 1989, 1995; Seaman and Powell 1996). Because these spatial home range models are estimates of where an individual spends the majority of its time, observations of "intrusions" into residents' home ranges can be used to define potential direct interactions, indirect interactions, or chances for indirect disease transfer. The generation of animal home ranges is relatively straightforward, and spatial location data for many animal species already exists in the form of radio tracking or GPS and can be collected relatively easily through scan sampling or directed searching of an animal's habitat.

Probabilistic home range models may also provide a novel and additional method of constructing social networks that reveal patterns in social structure and ecological space use that have been previously undetectable using other social network construction methods. Kernel density estimation (KDE) is a nonparametric method that is often used to describe the utilization distribution of animals in two-dimensional space (Worton 1989, 1995; Seaman and Powell 1996). When applied to animal home ranges, the KDE generates a continuous, space-filling model that estimates the relative amount of time a resident individual spends in a particular space.

The primary goal of this paper is to suggest the use of indirect interactions and KDE methods in delineating potential social interactions. In this study, we explore the use of KDE home range methods to define indirect interactions and construct social networks with a behavioral data set collected on *Bolitotherus cornutus* (the forked

fungus beetle). Limited migration, genetic substructure, long lifespan (up to 8 years), and total dependence on a spatially clumped resource suggest that *B. cornutus* populations should have a stable social structure with repeated social interactions, making them an ideal subject for exploring this new social network method. The goals of this study were (1) to use empirical data from the field in a KDE analysis to generate social networks of a wild population and (2) to explore the effects of altering parameters of the KDE models on commonly calculated social network metrics. To illustrate the utility of the space use methodology, we examined possible biological correlates of social network metrics in forked fungus beetles, including spatial attributes that could not be generated using other methods.

Methods

GIS analysis and generation of KDE home ranges

KDE home ranges can be generated using a number of available software programs. The critical data require only a unique identifier for each individual, and X and Y locations on any Cartesian coordinate systems. Our KDE home ranges were generated using the Animal Movement Extension (Hooge and Eichenlaub 1997) for ArcView 3.4 (ESRI, Redlands, CA, USA); the remaining Geographical Information System (GIS) analyses were done in ArcGIS 9.1 (ESRI, Redlands, CA, USA) with the Hawth's Tools extension (Beyer 2004). After generating the space-filling KDE model, the researcher must choose a particular contour level with which to draw the boundaries of the home range. For statistical comparison, percent volume contours must be drawn at a selected contour level (Silverman 1986; Worton 1995; Kernohan et al. 1998). Such contours are analogous to drawing topology contours on a topographic map, but instead of elevation, the KDE contour levels describe the probability that a focal individual would be observed within the contour level at any given time. Typically, 90–95% volume contours are used to delineate the boundaries of animal home ranges, and 50–60% contours are generated to represent "core" areas (Worton 1989, 1995; Seaman and Powell 1996).

There is some evidence from Monte Carlo simulations that KDE can overestimate the home range size of animals when sample sizes are low (Worton 1995; Fieberg 2007). One way to conservatively draw the boundaries of home ranges is to choose a smaller kernel size (i.e., contour level). However, the contour level selected directly affects the location of home range boundaries. On one hand, choosing a smaller contour level may be considered conservative, as it generates smaller home ranges and may counteract the overestimation of the utilization distribution

often seen in data sets with small sample sizes. However, smaller contour levels describe a smaller percentage of the total space that is used by an individual. A smaller contour level may also arbitrarily exclude space that is important to the social biology of the resident (e.g., the location of a socially important resource). As the contour level increases, so too will the percentage of total space incorporated within the home range boundary increase. In terms of social network identification, this might include more social partners in the interaction graph and might affect the social network parameters at both the population and individual level.

Study species and field observations

The forked fungus beetle (*B. cornutus*, Coleoptera: Tenebrionidae) is an ideal system for spatial studies of social interactions because they spend their entire lives on or near the fruiting bodies of wood-decaying shelf fungi (*Ganoderma applanatum*, *Ganoderma tsugae*, or *Fomes fomentarius*) and perform the majority of their social and mating behavior on the surface of the fruiting bodies (brackets) of the fungi between 0100 and 0900 hours in the morning (Liles 1956; Pace 1967; Heatwole and Heatwole 1968; Conner 1988, 1989). The brackets also serve as the sole food source and oviposition site of *B. cornutus*. Direct social interactions (i.e., that involve individuals making physical contact) in this species can last for seconds (e.g., antennation and fighting) or several hours (e.g., courtship). Chemical communication is likely to be important for *B. cornutus*, as it is for most insects (Tschinkel 1975a, b; Bell and Cardé 1984; Conner et al. 1985; Holliday et al. 2009). The nocturnal behavior of *B. cornutus* and difficulty observing many direct social interactions (due to extended periods of activity) further make this species an excellent candidate in which to investigate spatial utilization analyses for the construction of social networks.

The beetle deme examined was a fallen log with a large patch of *G. applanatum* brackets arranged along the log in a linear fashion in the forest near Mountain Lake Biological Station (37.376°, −80.523°). We consider the surface of the log a landscape and treat it as a two-dimensional topology, employing spatial analysis tools in the same fashion as researchers who study larger organisms on a larger spatial scale. In order to map beetle locations, a central meridian was placed along the most dorsal length of the horizontal log, and 10 cm square pieces of paper were then laid over the surface of the log proceeding from the meridian. Numbered galvanized steel nails were placed at each corner to generate a Mercator-like Cartesian coordinate system in which the surface area of each grid cell equals 10 cm^2. Locations of brackets, branches, and other important landscape features were digitized into a GIS.

The deme was surveyed 30 days prior to behavioral observations, and all *B. cornutus* found on this patch were captured. The dorsal and ventral sides of captured beetles were photographed with a Nikkor 105 mm micro lens and Nikon D200. The photographs contained a 2 mm stage micrometer in the same plane as the focal traits for scale. Each beetle was then labeled with a uniquely coded tag printed on fluorescent paper. These tags were affixed with a light-cured acrylic (Tuffleye™ Wet-A-Hook Technologies); the tags fluoresce when exposed to UV light and are easily observed from several meters away. Once labeled and photographed, beetles were returned to the same bracket or log grid cell at which they were captured. Measurements of elytra length were completed using ImageJ (National Institutes of Health) for all beetles.

Scan sampling was conducted from 22 June 2008 to 20 July 2008. During each sampling period, three different trained observers using both ultraviolet and white light scanned the log, brackets, and surrounding vegetation. The individual ID, location (grid square or bracket ID), and behavior were recorded for all *B. cornutus* present. These individual observations were then incorporated into the spatial data of the GIS. Newly observed, unlabeled beetles were also noted and collected for labeling. Sampling periods rotated through four possible time sets: 0300–0700, 0800–1200, 1300–1700, and 2100–0100 hours. Sampling was done twice in 24 h (once during the day and once at night); there was no sampling every third day. This schedule resulted in a total of 40 scan periods.

Estimating beetle KDE home ranges

A KDE home range was generated for all individuals (both male and female) that had at least three observations, the minimum required to construct a kernel (mean number of observations=16.6±1.7 SE). We utilized the least-squares cross validation (LSCV; Silverman 1986) to correct for possible effects of small sample sizes. For our initial analyses, we used a conservative 60% kernel contour level to estimate home range size. A 60% kernel contour level generates home range boundaries while still allowing for individual forays outside of the home range area, even for individuals with only a few observations. Additionally, this contour level is the largest level that generates home ranges contained mostly on the log; in other words, contour levels above 60% often estimate that individual *B. cornutus* utilize space outside of their ecological context (in areas where individuals have never been observed). Although not entirely unbiased, a 60% kernel contour level also reflects the closest space use predicted by experienced observers. We also generated home ranges using 20%, 40%, 80%, and 90% kernel contour levels (Fig. 1a) to examine potential effects of kernel contour level on size and shape of

Fig. 1 Kernel density estimator (KDE) home ranges. **a** An example of the components of a home range for one individual. *Contours* represent the various kernel levels. *Black circles* represent direct observations of the focal individual. The *size of the black circles* indicates the relative number of times the focal individual was seen at that location. *Dashed lines* represent the borders of fungal brackets. **b** Examples of KDE home ranges (*shaded area*) for seven individual *Bolitotherus cornutus*, constructed with a kernel contour level of 60%. The *thin gray line* represents the edges of the log, while the *small dark areas* are the location of fungal brackets. The *black line to the left of each log* is a 1-m scale bar
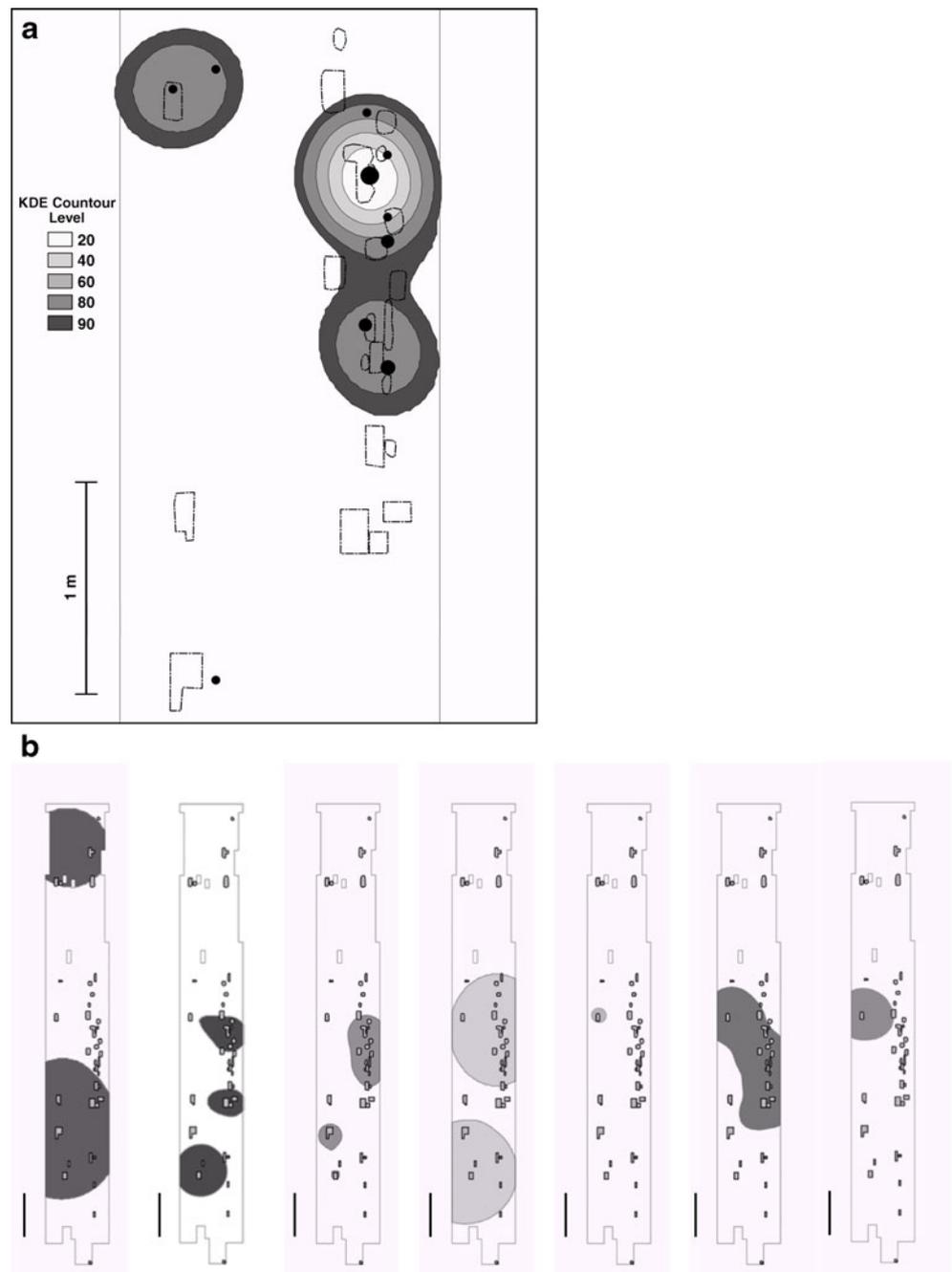
estimated home ranges, and resulting networks and their metrics.

Delineation of social partners and networks

We considered all conspecifics observed within the boundaries of a focal individual's home range to be part of the focal individual's social environment. Individuals were only considered focal individuals (residents) in the analysis if they were observed at least three times (the number of observations required to generate a KDE home range; $N=$ 55 individuals); however, all individuals had the potential to be considered social partners ($N=61$). In graph theory terminology, each individual is termed a "node," and each connection between two individuals is termed an "edge." In animal social networks, the weight of an edge is often represented by an association index that is typically calculated from the number of times individuals interact or the number of times two individuals are seen in the same group. These associations are then scaled between zero and 1, often by dividing by the number of observation periods or the overall activity of the individuals (for a review of

various association indices, see Croft et al. 2005 and citations therein). To calculate our association index (and edge weight), we divided the number of times a social partner was seen inside a focal individual's home range by the total number of scan sampling periods ($N=40$). Current analyses on animal social networks are typically limited to symmetrical graphs, and so to symmetrize our graph, the mean association index for two social partners was used in both cells of the matrix.

The data from the GIS were imported into UCINET (Borgatti et al. 1999) to calculate the association index and to symmetrize the graph. The social networks generated were symmetrical, weighted, and non-directional. From these networks, the following social network metrics were calculated in the program SOCPROG (Whitehead 2009): strength, eigenvector centrality, reach, clustering coefficient, and affinity (see Appendix for definitions and interpretations of these parameters).

Testing biological hypotheses with KDE social networks

Once the social networks were generated with our KDE methods, we explored which biological variables correlated with various network metrics at the 60% contour level. To this end, we conducted multiple regressions with sex, elytra length, and the number of brackets within a home range. Regressions included each of the social network metrics as separate independent variables. Sex is often examined in social network analyses (e.g., Lusseau and Newman 2004; Croft et al. 2006; Bezanson et al. 2008; Sueur and Petit 2008), whereas quantitative measures of phenotypes have yet to become commonplace (although see Croft et al. 2005). We included body size because it is known to be an important factor influencing reproductive success in *B. cornutus* (Conner 1988, 1989; Formica et al., unpublished data). We included the number of brackets in an individual's home range as an independent variable because the fungal brackets are the total resource for this species, and most observable social and reproductive interactions occur on the surface of the brackets.

Social networks, and the resultant metrics, were generated using all 61 *B. cornutus* that met our criteria as potential social partners (see above); however, statistics involving components of the home ranges (e.g., number of brackets in a home range) could only be calculated for individuals for which we estimated a KDE home range (i.e., those observed three or more times on the surface of the log; $N=55$). Calculation of network metrics, even those for individuals, involves consideration of the entire network. Therefore, values assigned to individuals are not statistically independent, and tests involving network metrics must be conducted using a permutation method. Multiple regressions involving network metrics were conducted in

UCINET, and *P* values are reported as percentages of 10,000 permutations that are as extreme as the values that were calculated from the population. All other statistics were calculated with JMP 7 (SAS, Cary, NC, USA).

Results

KDE home ranges and initial network
(60% kernel contour level)

Using the initial kernel contour level of 60%, the KDE generated home ranges of wild *B. cornutus* with a wide range of sizes (range, 0.008–10.10 m²; mean, 1.54 m²± 0.27 SE; for examples, see Fig. 1b). Although the home ranges were spatially distributed across the entire log, the majority of the home ranges contained a section of the log with a high density of brackets (middle and right of log; Fig. 1b). The number of observations was significantly negatively correlated with home range area, which is often a concern with KDE home ranges. However, of the network metrics, strength and eigenvector centrality were the only variables that correlated with the number of observations, and so variance in the number of observation does not appear to greatly affect our social network results. Most of the network metrics correlated with each other, the exception being clustering coefficient, which only correlated with affinity (Table 1). The social network, overall, appears highly connected (Fig. 2).

Effects of kernel contour level on network metrics

Changing the kernel contour level had similar effects on most network metrics, although the magnitude of this change differed (Fig. 3a–e). Increasing the kernel contour level tended to include more potential social partners in each focal individual's network, causing the estimated network to become more decentralized and individuals to become more connected. Strength, reach, and affinity increased with increasing kernel contour level. Significantly different values for these metrics could be produced by kernel contour levels divergent by 40% (Fig. 3a–c). Clustering coefficient also increased with increasing contour level; however, it is doubtful that the small increase (0.32–0.42 between 20% and 90%) has much biological meaning (Fig. 3d). Eigenvector centrality, however, did not change significantly as a function of kernel contour level (Fig. 3e).

Phenotypic and ecological correlates of network metrics
(60% kernel contour level)

Network strength, affinity, eigenvector centrality, and reach were all positively correlated with the number of brackets

Table 1 Bivariate correlation matrix of variables used in the creation and analysis of *Bolitotherus cornutus* social networks

|	Sex	Home range area	No. of brackets within home range	No. of observations	Elytra length (mm)	Strength	Reach	Affinity	Clustering coefficient
Home range area	−0.214								
No. of brackets within home range	−0.064	0.778**							
No. of observations	0.173	−0.419*	−0.248						
Elytra length (mm)	0.245	−0.257	−0.176	0.283*					
Strength	0.094	0.104	0.496**	0.610**	0.057				
Reach	0.123	0.057	0.492**	0.575	0.051	0.990**			
Affinity	0.161	−0.137	0.341*	0.075	−0.006	0.499**	0.605**		
Clustering coefficient	0.138	−0.434*	−0.107	−0.003	0.047	0.128	0.246	0.774**	
Eigenvector centrality	0.127	0.034	0.481**	0.570**	0.056	0.984**	0.998**	0.625**	0.275*

*$P<0.05$

**$P<0.001$

in the focal individual's home range, but not with sex, or elytra length (see Table 2 for statistical details). Clustering coefficient was not correlated with any of the independent variables. Home range area and the number of observations were correlated with the number of brackets and so were not included in the regression analyses to avoid non-independence and multicollinearity. The univariate correlation matrix is included (Table 1) for comparison. These analyses were also conducted for networks that contained only males and only females. Sex-specific network results were identical to those of the total network and so are not reported here.

Discussion

Identifying social interactions based on shared space utilization distributions describes a highly connected social network (Fig. 2). The use of KDE to identify home ranges allowed us to consider indirect interactions among *B. cornutus* individuals that might take place through non-simultaneous occupation of a given area. Such temporally dispersed interactions are expected to occur more broadly than more commonly considered physical contacts, so the high connectivity of the network is not surprising.

The values of metrics that describe network structure are influenced by kernel contour levels in different ways. For all measures except eigenvector centrality, a 20% difference in contour could generate significant differences in network statistics. The metrics most susceptible to influence were strength, reach, and affinity. Differences between clustering coefficient values were all statistically significant, but the most extreme difference in mean (between 20% and 90%) of 0.1 may not be of biological importance. These observations are consistent with the expected effects of altering kernel contour. Lower kernel levels define a home range that includes less of the space likely to be used by an individual. As a result, interaction matrices based on lower kernel contours might be expected to miss some pairs of individuals that use common space. Conversely, the largest kernel contours describe the broadest probability distributions of space use and potentially identify interactions that are unlikely to occur. Eigenvector centrality did not differ significantly even
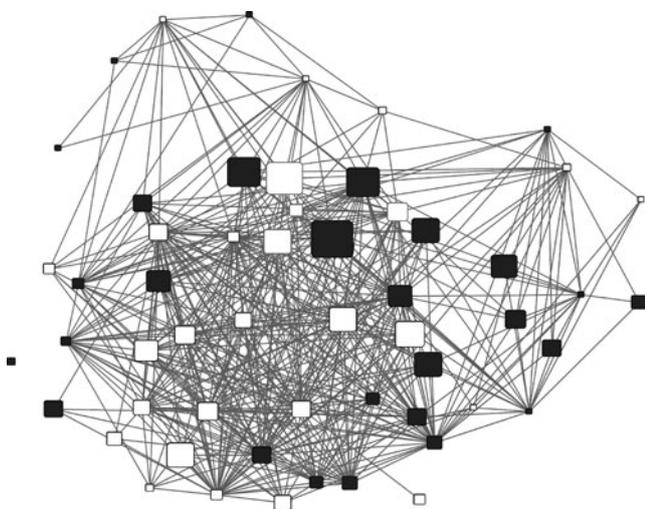
Fig. 2 Spring-embedded social network, generated using kernel density estimator at the 60% kernel contour level. Spring-embedded visualizations of social networks place more connected individuals towards the center of the two-dimensional network and less connected individuals toward the periphery. For visualization purposes, only edges with an association index of 0.25 or greater (at least ten indirect interactions between individuals) are displayed. The size of each node (males, *white*; females, *black*) is relative to the number of fungal brackets in each individual's home range
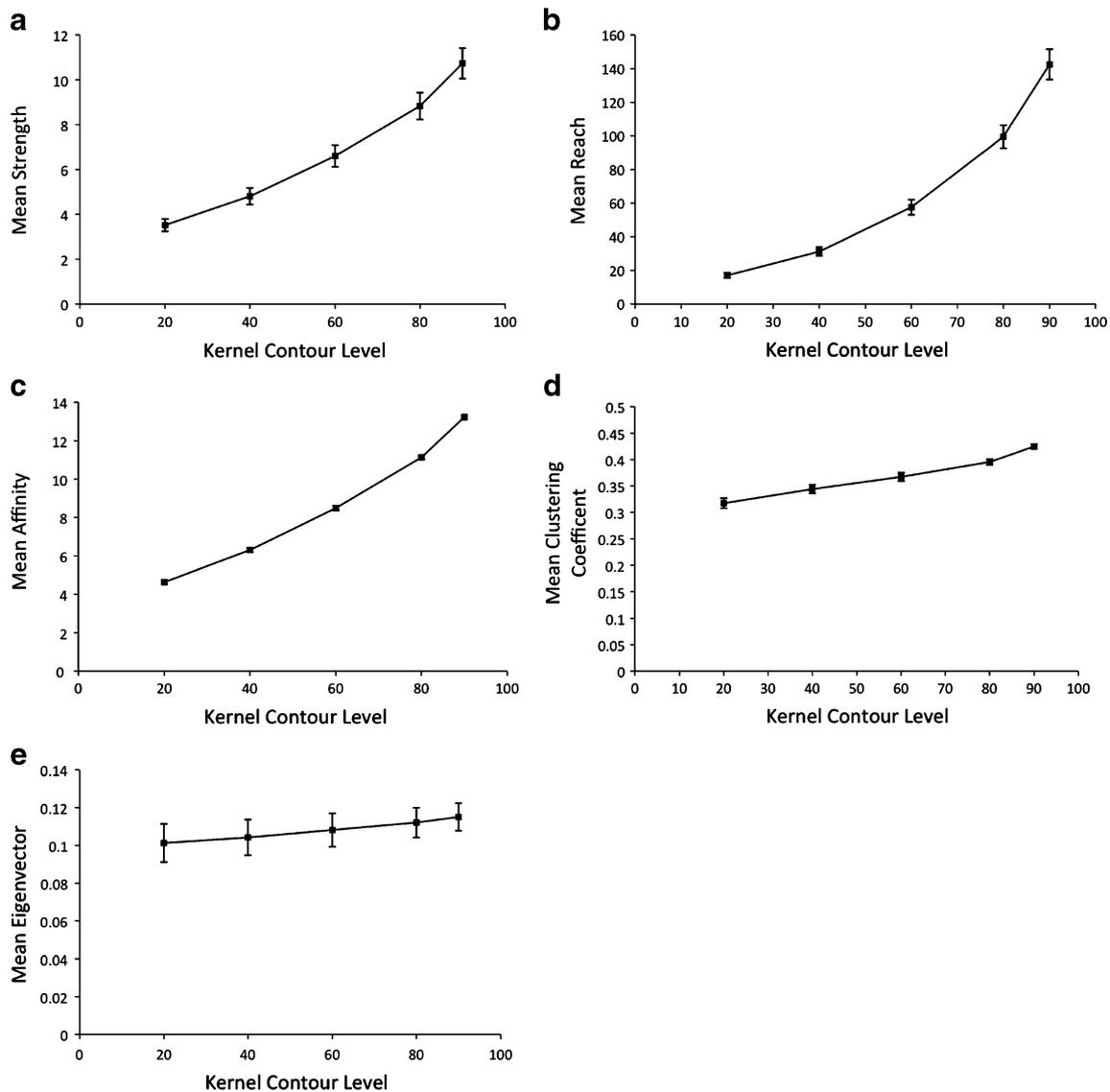
Fig. 3 Effects of altering kernel density estimator contour level on mean (**a**) strength, (**b**) reach, (**c**) affinity, (**d**) clustering coefficient, and (**e**) eigenvector centrality for a single population of *Bolitotherus cornutus*. Error bars are ±SE; error bars for (**c**) affinity and (**e**) clustering coefficient are too small to print

Table 2 Multiple regression results for each network metric

Network metric	Model P	Model F	Model R^2	Sex standardized coefficient	Sex proportion as extreme (P)	Elytra standardized coefficient	Elytra proportion as extreme (P)	Number of brackets standardized coefficient	Number of brackets proportion as extreme (P)
Strength	0.003	6.501	0.277	0.097	0.512	0.125	0.392	0.525	<0.001
Affinity	0.054	2.996	0.150	0.181	0.223	0.012	0.934	0.354	0.013
Reach	0.004	6.507	0.277	0.129	0.353	0.111	0.456	0.519	<0.001
Eigenvector centrality	0.009	6.236	0.268	0.132	0.356	0.113	0.436	0.510	<0.000
Clustering coefficient	0.678	0.502	0.029	0.132	0.372	−0.003	0.979	−0.099	0.496

Each test was completed using UCINET's permutation tests. P values are reported as percentage of permutations not as extreme

between the most extreme contour levels (20% vs. 90%). An eigenvector centrality value for an individual explains his or her relative contribution to the eigenvector, and so even if the network becomes more connected in general, an individual's contribution to the eigenvector may not change.

There are no clear rules to guide the choice of the best kernel contour level for the construction of home ranges. We suggest that choice of kernel contour level should be based both on the biology of the study organism as well as the spatial dispersion of the data. Small sample sizes, even with LSCV correction, have a tendency to overestimate the area utilization distributions (Seaman and Powell 1996; Fieberg 2007), and so we also suggest using smaller contour levels (40–60%) if some focal individuals have smaller numbers of observations (i.e., <30). It is clear from previous studies that accuracy of the estimate of space utilization improves with increased observations (Seaman and Powell 1996; Fieberg 2007). For studies involving organisms with few direct interactions, large home ranges, and social interactions mediated by temporally persistent signals such as scent marking (e.g., large mammals, Gorman 1990; Gosling and Roberts 2001; Rozhnov 2004), the choice of larger kernel contour levels may be appropriate for the construction of social networks. For taxa with many direct interactions, more limited or consistent space use, or more commonly shared space, lower contours may be more insightful. In any case, it will be critical to explore the results from social networks using more than one KDE contour level, if only as a sensitivity analysis of parameter choice.

KDE methods will not be appropriate for all biological systems. KDE assumes that observations in a two-dimensional space are a sample of an individual's movements within that space. In cases where individuals are constrained from freely moving within the two-dimensional space, either physically or through their biology, KDE-based network methods may not be appropriate. Temporally variable effects of shared space utilization may also render a simple KDE inappropriate, as when movement is sporadic or nomadic, or the salient signal or ecological factor (e.g., disease transmissibility) degrades with time. In such cases, KDE home ranges may be generated for specified time windows to consider the specific temporal context of indirect interactions.

Environmental and biological correlates of beetle networks

Defining social partners based on shared space utilization by forked fungus beetles revealed the importance of environmental variables in determining network structure. Individuals with home ranges that encompass a larger number of fungus brackets are more central to the social network (higher eigenvector centrality and reach), have more social partners (higher strength), and interact with social partners who are themselves more connected (higher affinity). Body size, a critical mediator of interactions both among males and between the sexes, did not influence network structure.

The positive partial regression between strength and number of brackets is unsurprising but may not be detectable without a shared space use approach to understanding social networks. As individuals move to new brackets, they have the potential to interact with a larger number of unique individuals more often. This would also explain the significant relationship with reach; as individuals sample a greater diversity of resource patches, they become more connected to the overall population and attain a shorter network distance from any given social partner. The correlation between both reach and eigenvector centrality with the number of brackets suggests that as individuals sample more brackets, they are not only interacting with more social partners but also those social partners are highly connected themselves.

In the population studied herein, the role of fungus bracket number in structuring networks may be driven by the non-uniform dispersion of brackets. A large proportion of the brackets is clumped (the middle right of maps in Fig. 1b). Therefore, individuals whose home ranges are near this section of the log may have the opportunity to visit more brackets and interact with other individuals who are doing the same, where as focal individuals who are on the periphery of the log-landscape may visit fewer brackets and interact with social partners who are themselves limited in the diversity of their social partners. This hypothesis, however, cannot completely explain all of the social structure we observed. The lack of significance in the partial regression between clustering coefficient and the number of brackets suggests that although focal individuals increase the diversity and frequency of social partners by visiting many brackets, those social partners are not interacting with each other. These results describe a social structure that is somewhat spread across the landscape and not entirely localized on the area of clumped fungal brackets in the middle of the log.

Conclusions

Ecological processes such as predation, competition, and resource availability often have spatial components and have been shown to have effects on social behaviors (e.g., Brown et al. 1999; Giraldeau and Caraco 2000; Shuster and Wade 2003). The inclusion of such spatial and environmental variables in social network analyses may be vital to understanding the mechanisms that drive social structure in wild populations. Only a few social network studies have

addressed such ecological factors (e.g., Rhodes 2007; Sundaresan et al. 2007). We hope that the integration of spatial tools, such as KDE home range analysis, with current social network techniques will increase the consideration of the role ecology may play in animal social structure.

Appendix

Definitions and descriptions of common weighted social network metrics (for an in-depth discussion and mathematical explanations, see Whitehead 2008).

Strength: *the sum of the weights of edges connected to a node*. This is the weighted number of interactants that an individual experiences. For our data set, strength represents the sum of weighted association indices, which essentially represents the frequency of potential social interactions. Depending on the data used to construct the social network, strength might represent the conspecific density experienced by an individual, the number of aggressive encounters it has participated in, or the frequency of matings.

Reach: *the sum of the strengths of an individual's social partners*. Reach is a measure of how well the social partners of a focal individual are connected. A focal individual may only have a few social partners, but if those partners are well connected in the network, then the focal individual will have a high reach. Reach can be thought of as an indirect measure of connectedness, and Flack et al. (2006) suggest that reach can access the ability of a behavioral contagion (e.g., aggression) to spread from individuals.

Affinity: *the ratio of how well connected a focal individual is to how well connected its social partners are*. Affinity examines a focal individual's connectedness by taking into account the weights of connections to social partners and then how well connected those social partners are to the rest of the network. Mathematically, this becomes the weighted mean strength of a node or an individual's reach divided by its strength.

Eigenvector centrality: *a more abstract metric that relates how highly connected an individual is within the entire network*. Eigenvector centrality does not discriminate whether has many social partners or associates with highly connected social partners. Mathematically, eigenvector centrality is the first eigenvector of the weighted association matrix.

Clustering coefficient (CC): *how well connected a focal individual's social partners are to each other*. An individual's (or node's) CC score is calculated as the sum of the weights on all three connections of each triangle (between three individuals) divided by the maximum weight in the network. In other words, the clustering coefficient measures how many and how often the focal individual's social partners are themselves social partners.

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