Research

Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception

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Understanding the spatial structuring of animal behaviors and how they link landscapes can be critical for conservation management. This emerging field has been greatly facilitated by technologically advanced acquisition and analysis of data on animal movements. The framework of graph theory, which directly quantifies network connectivity properties, provides a useful addition to this tool set. Using a novel application of graph theory, we investigate the structure and patterning of African elephant *Loxodonta africana* rest sites, a potentially critical feature structuring spatial properties of animal populations. Elephants in the study rested intermittently and for short durations (1–3 rests d⁻¹, lasting 3–5 h total). They switched circadian rest patterns according to landscape attributes, resting more during the day and further from permanent water in areas with high human density outside protected areas. Within protected areas and during the dry season, elephants showed clustering and sequential use of rest nodes (repeated motifs). Repeated use of specific rest nodes (self-looping) was more frequent than expected if rest nodes were chosen at random, particularly when outside protected areas further from water, indicating the importance of preferred rest sites. Our results suggest that elephants adjust resting behavior when in human-dominated areas, using preferred resting sites presumably in locations that reduce the risk of interactions. This study demonstrates how graph theory may be used practically to gain novel insight into behaviours, such as resting, that are discrete in time and space. Furthermore, analysis of the spatial and network properties of rest sites, given an individual's susceptibility when engaged in rest behavior, allowed characterization of spatio-temporal risk perception, providing a powerful behavioral based means to quantify the landscape of fear.

Analysis of an animal's space use was traditionally focused on Eulerian (diffusive) characterizations of animal distribution patterns (Turchin 1998). With our increasing ability to collect accurate location data, that focus is shifting to explore the details of individual movements (Lagrangian characterization). This significant shift in emphasis allows for a more accurate characterization of the influence of exogenous and endogenous processes, and thus provide deeper insight to animal spatial behaviors (Nathan et al. 2008). In particular, the quantification of location-specific movement patterns and properties has been applied to infer landscape use patterns (McClintock et al. 2012, Polansky et al. 2015) and also to quantify the impacts of habitat selection on inter-specific interactions (Northrup et al. 2015). Such approaches allow the extension of animal cost-benefit and risk analysis beyond the traditional focus on foraging theory (Marquet et al. 2014) and foraging strategies (Morales et al. 2004) to other spatially structured behaviors, such as rest, which can be as important (Lima et al. 2005).

Sleeping behavior is a critical but understudied aspect of animal spatial ecology, with selection of daily rest stops fundamental to survival (Lima et al. 2005). An animal tends to be most vulnerable to predation during sleep, which makes sleep for most animals a risky behavior (Anderson 1998). In addition, lack of and disruption to sleep can have serious physiological costs (McCoy and Strecker 2011). Rest/sleep site use has been linked to parasite prevalence (Butler and Roper 1996) and access to critical resources (Janmaat et al. 2014). As such, investigations into the spatial arrangements of rest and sleep behavior can offer important insights to animal ecology.

Graph (network) theory provides a powerful framework for investigating processes that have some aspect of connectivity (Newman 2010), with recent applications in biology studying the effect of landscape structure (Minor and Urban 2007, Garroway et al. 2008). While widely used to assess contact structure in animals (Newman 2003), application of graph theory to study animal spatial behavior has been limited to the analysis of array based data (Jacoby et al. 2012). Graph theoretic approaches allow the analysis of movement-based connectivity in animal ranges and spatially discrete behaviors such as resting. Rest sites can be conceived

as spatially static nodes connected across the landscape by movement (simplified as connections between nodes or network edges). Leveraging graph theory to investigate the spatial structure of this behavior can offer insight to rest site connectivity and spatially and temporally structured use patterning (Barthelemy 2011, Holme and Saramäki 2012).

Here we investigate resting behavior of free-ranging African elephants *Loxodonta africana*, a generalist herbivore, using a graph theoretic approach to identify patterns of movement across defined rest site networks, with particular attention paid to the patterning of rest site visitation. The manner in which elephants alter rest behavior relative to risk (nocturnal/diurnal patterning in and outside protected areas), permanent water and ecological dynamics (seasonality) were assessed. Given the importance of rest site selection to animal survival, our analysis provides important insight to species perceptions of their landscape of fear (Brown et al. 1999). The implications of results to elephant ecology, risk assessment and the utility of graph theoretic approaches for examining the spatially structured behaviors are discussed.

Methods

GPS positions were collected on nine female elephants (representing nine socially distinct core groups (Wittemyer et al. 2005) containing 8–17 individuals) monitored as part of a long term research project (Wittemyer et al. 2013) in and around the Samburu and Buffalo Springs National Reserves Complex (lying approximately 0.5°N, 37.5°E) in northern Kenya from January 2000 to March 2007. The reserves complex covers a 220 km², though the ranges of the studied elephants encompass a region greater than 4000 km². GPS sampling resolution was predominantly on an hourly basis, with fix success per collar exceeding 90%. On average, 25 413 h were collected per group (minimum: 14 529 h, maximum: 43 072 h where the variation in coverage was attributable to differences in collar life span).

Resting event definition and analysis

Resting events were defined using activity sensors and displacement distances collected from GPS collars (see supplemental information) and categorized based on the time of day (nocturnal or diurnal), season (wet or dry) and protective status of a rest location (within or outside a nationally designated protected area). Wet or dry season was defined using normalized difference vegetation index (NDVI) as described elsewhere (Wittemyer et al. 2007b) and rest events were categorized temporally as 'day' (between 06:00 and 17:59) or 'night' (between 18:00 and 05:59) (note: seasonal differences in daylight hours are minor since the study site is near the equator). We then quantified the 1) mean number of day and night rests per day, 2) mean day and night rest duration, and 3) mean day and night restlessness index, defined as the proportion of days or nights an elephant did not rest. The mean number of rests per day and the restlessness index were calculated from days and nights with complete data (i.e. 12 GPS points for each day or night).

We investigated the relationship between these three measureable quantities and covariates representing a rest site's 1) protected area status (in or out), 2) timing (day or night), and 3) season (wet or dry) using generalized linear mixed effect models (GLMMs) implemented in the lme4 R package (Bates et al. 2013). Elephant identity was incorporated as a random effect in the models. We used AIC to rank models composed of main, additive, and interactive effects (Burnham and Andersen 1998). Where models were marginally different (difference in AIC weight ≤ 0.95), parameter coefficients in secondary models were inspected for influence (95% confidence intervals did not overlap 0). The top ranked model was used to infer relationships in all cases given that the additional parameters in secondary models were weakly informative (Arnold 2010). Models accounting for ≥ 95% of the AIC weight are presented in the Supplementary material Appendix 1.

Spatio-temporal resting network

Resting events were collated into nodes by clustering event locations using the hclust function in the 'stats' R library (R Core Team) using the best fitting average-linkage hierarchal clustering method (Supplementary material Appendix 1, Table A1). The spatio-temporal structure of rest nodes was then analyzed using a graph-theory framework, with rest nodes in the graph connected by edges defined by observed movements between nodes. In this network, edge weights represent the number of times resting occurred consecutively in two nodes and node strength (i.e. weighted degree) represents the number of rests that occurred in a node.

We analyzed this resting network as: a) an undirected unweighted static network, b) an undirected weighted static network (i.e. edge weights representing movement between nodes), and c) a time-ordered network (i.e. edges ordered sequentially in time) constructed for each of four treatment categories (i.e. wet/dry and protected/unprotected). From these networks, we derived three metrics (see Supplementary material Appendix 1 for formal definitions) that capture different structural components of the rest network: 1) global clustering coefficient (i.e. transitivity) of the undirected unweighted static network (a measure of network interconnectedness), 2) the mean fraction of node strength from self-loops in the undirected weighted static network (a measure of the propensity of consecutive return to nodes), and 3) the normalized number of repeated paths in the time-ordered network (a measure of the propensity to consecutively use three rest nodes). The normalized number of repeated paths in the time-ordered network is an example of a temporal motif (repeated sequence), since it represents a subgraph with topologies that re-occur in time (Holme and Saramäki 2012).

On each network, 10 000 iterations of a random walk (see Supplementary material Appendix 1 for details) were implemented in order to derive distributions of each network metric and the degree for each node that would be expected if rest sites were selected at random (Supplementary material Appendix 1, Table A2). The observed network structure and node use statistics were then compared to the distributions obtained from the results of the 10 000 random walks. Significance was defined as the observed metric or node value being larger than or equal to the 95th percentile of

the corresponding distribution (for the specific node or metric) derived from the random walks. Preferred nodes were defined as nodes with a strength (i.e. number of rests) that was significantly larger than expected based on the random walks.

Network metrics were analyzed using a GLMM framework with model selection as described previously, where elephant group identity was included as a random variable and all continuous covariates were standardized $\left(\frac{x - \bar{x}}{\sigma}\right)$. We modeled node degree (count data) using the negative binomial distribution (to avoid over-dispersion) in relation to a location's 1) protected status, 2) node size (km^2), 3) nearest node distance, 4) proportion of node use that was diurnal, 5) group dominance rank (as defined previously in Wittemyer and Getz (2007)) and 6) distance to water. Preferred nodes (1 or 0) were modeled as a Bernoulli-distributed variable with a logit-link function in relation to 1) protected status, 2) node size, 3) nearest node distance, 4) proportion of node use that was diurnal, 5) group dominance rank, and 6) distance to water. The propensity to self-loop (proportion data) was modeled using a binomial link function in relation to 1) rest node size, 2) nearest node distance, 3) location protected status, 4) season, 5) elephant group dominance rank and 6) distance to water. The numbers of repeat motifs (here defined as consecutive use of three nodes in a specified order resulting in 0 biased count data) were modeled using a zero-inflated Poisson model as a function of 1) location protected status, 2) proportion of node use that was diurnal, 3) group dominance rank and 4) distance to water. Dominance rank data were derived from previous studies (Wittemyer and Getz 2007). Clustering coefficients, given that they were network wide metrics and

therefore could not be assigned spatially or temporally specific attributes, were not modeled. All metrics and models were computed using R (R Core Team).

Results

Elephants tended to rest in the late night hours between midnight and dawn, with a less predictable resting bout during midday (Fig. 1a). When resting, rest duration tended to be short (Fig. 1b), averaging 1.4 (standard deviation: 0.78) h during the day and 1.8 (standard deviation: 1.3) h during the night. In addition to time of day, rests were also structured by season and location (Fig. 2). The top models of rest properties (rest duration, number of rests/day and rest-lessness; Supplementary material Appendix 1, Table A3) demonstrated more and longer resting during the night, outside protected areas and during the dry season (Table 1). Rest events were markedly closer to rivers during the day relative to night within protected areas (Wilcoxon sign-ranked test V = 4, p = 0.027), but demonstrated the opposite effect outside protected area though the differences in distance were weaker (V = 37, p = 0.098). Seasonal differences were also apparent with fewer rests in protected areas during the wet season (relative to the dry season, Fig. 2).

Clustering of rest events into nodes demonstrated that elephant groups used a diverse array of rest sites, averaging 402 unique sites within their range. Rest nodes were typically larger within protected areas (13 ha) than outside protected areas (7.6 ha; Fig. 3a, b). In addition, node density was larger within protected area, averaging 0.46 nodes km^{-2} (standard deviation: 0.18) relative to 0.17 nodes km^{-2} (standard deviation: 0.06) outside protected areas. Degree (number of adjacent vertices) per node averaged 6.8 across
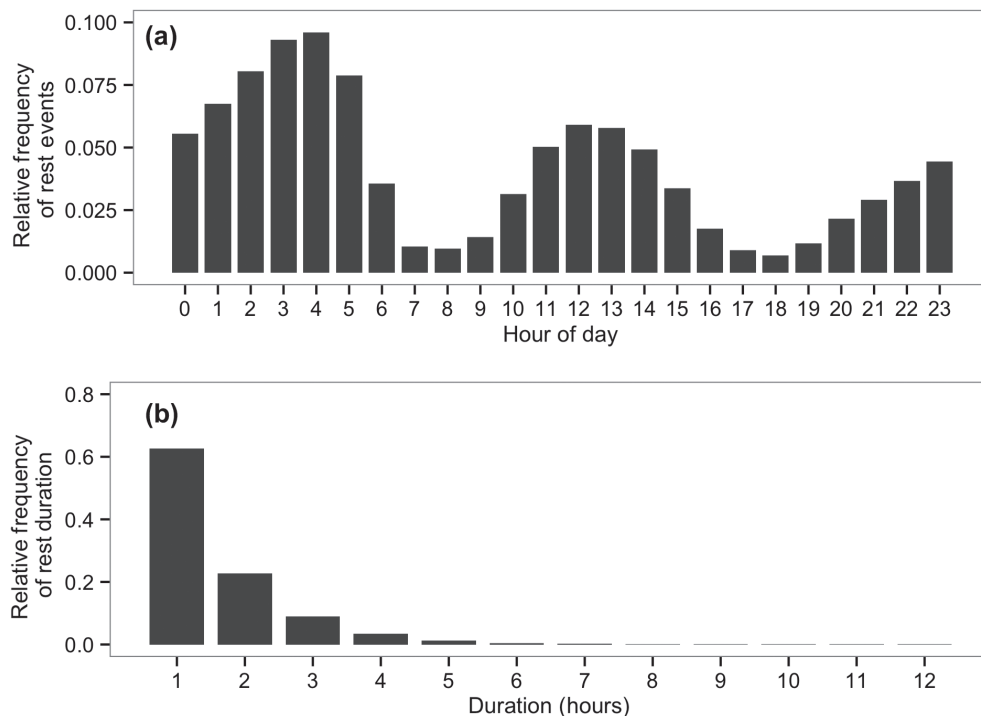

Figure 1. Histograms of the timing and duration of rest events demonstrated that (a) rest events most commonly occurred during the late night hours or midday and (b) rest events tended to be short in duration.
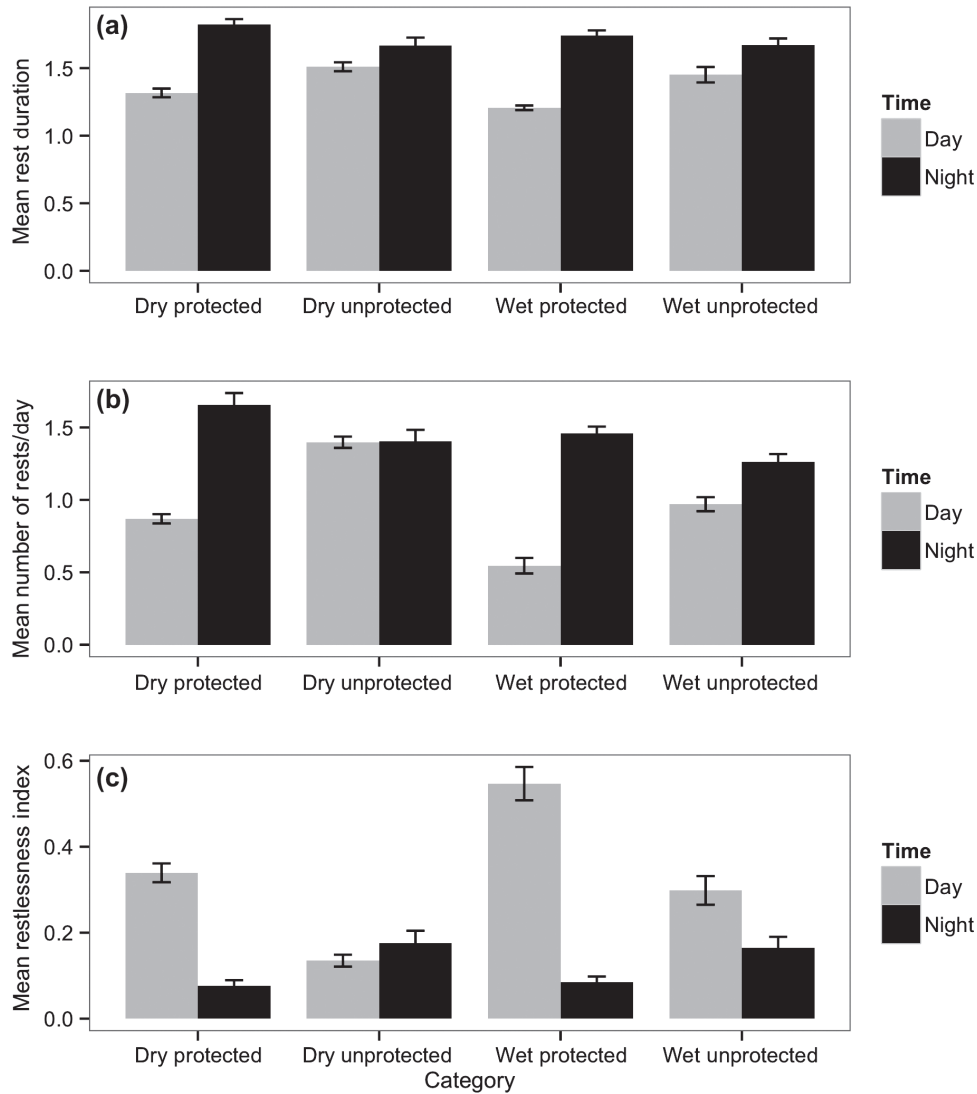
Figure 2. (a) Number of rest bouts per day, (b) duration and (c) restlessness by treatment (season and location specific protective status) and temporal (day and night) category. Values presented are means (with standard errors) across the nine elephants.

Table 1. Results from the top models of rest properties (rest duration, number of rest d^{-1}, and restlessness).

Response variable	Covariate	Coefficient (95% CI)	
Rest duration			
	Season	0.488	(0.466–0.510)
	Protected	0.047	(0.022–0.072)
	Time	−0.135	(−0.166–−0.104)
	Protected × Time	−0.218	(−0.263–−0.173)
No. rests d^{-1}			
	Season	0.173	(0.134–0.212)
	Protected	0.167	(0.122–0.212)
	Time	−0.245	(−0.304–−0.186)
	Protected × Time	−0.706	(−0.773–−0.639)
	Season × Time	0.202	(0.141–0.263)
Restlessness			
	Season	0.169	(0.022–0.316)
	Protected	0.858	(0.687–1.029)
	Time	−0.637	(−0.792–−0.482)
	Protected × Time	−1.934	(−2.134–−1.734)
	Season × Time	0.596	(0.420–0.772)

elephant groups, but varied relative to protected status of location (Fig. 3c, d). The top model of degree demonstrated an increase with node size, proximity to permanent water and inside protected areas (where the water effect was pronounced inside protected areas), but decrease of degree when closer to its nearest neighbor node (Table 2). In addition, nodes used more frequently during the day tended to have a larger degree than those used more at night (Table 2).

Analysis of rest node network structure revealed heterogeneity driven by strong rest node preferences. An average of 44% of rest bouts occurred in preferred nodes, which represented less than 10% of all nodes. These preferred nodes were larger, used more often during the day, tended to be in protected areas, further from permanent water (unless inside protected areas) and closer to other nodes relative to non-preferred nodes (Table 2).

Assessment of rest network structure indicated that for most individuals dry season clustering coefficients, self-loop strength and number of repeated motifs were significantly
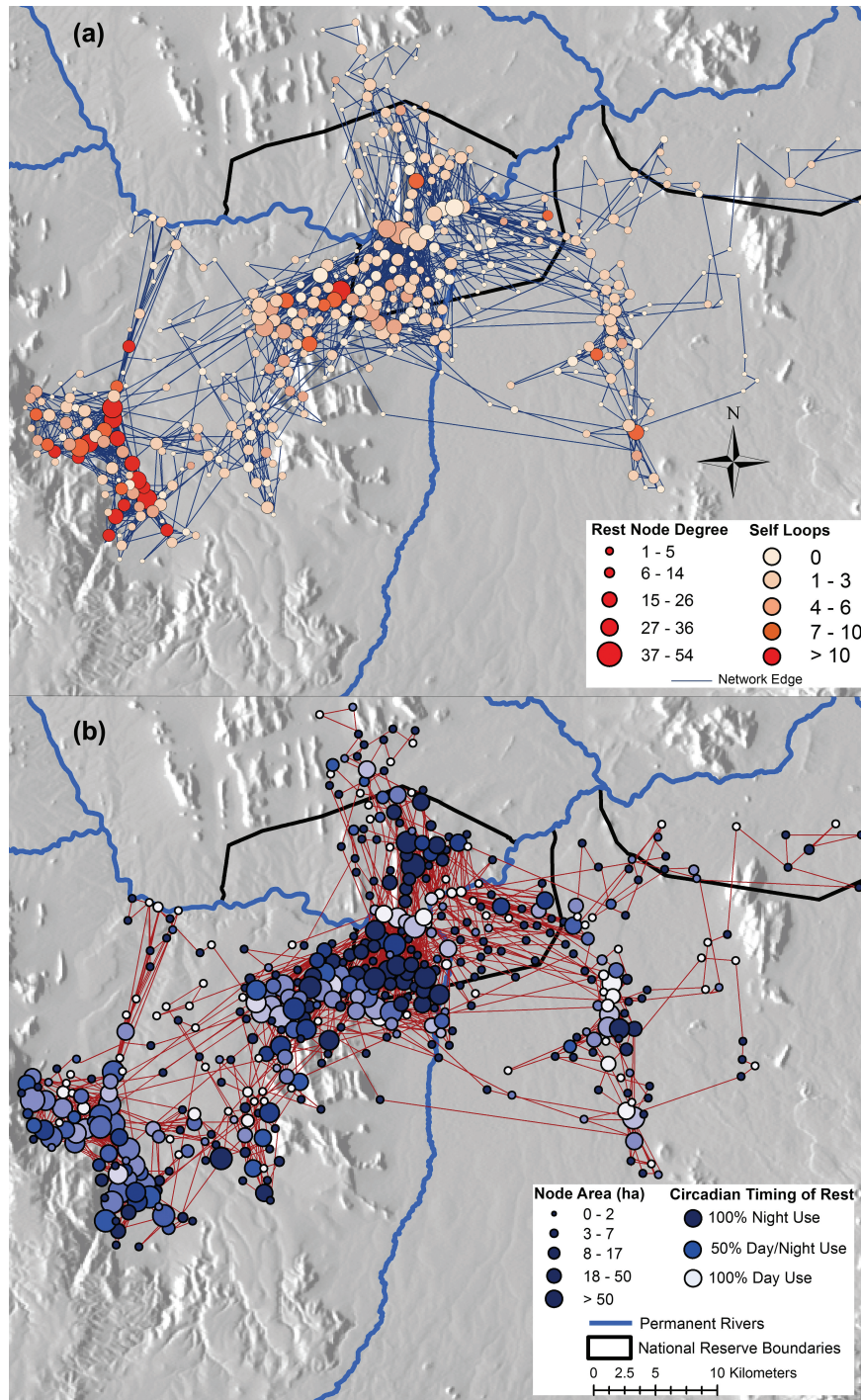
Figure 3. The resting network of the elephant 'Amina' in northern Kenya. Across all elephants studied, (a) rest node degree (node size) tended to be higher inside protected areas (black polygons), while self looping (node color scale) tended to be greater outside protected areas. (b) Circadian patterns in rest node use (proportion night versus day; color scale) related to proximity to water and differed strongly in versus out of protected areas, while rest site area (node size) varied across the landscape. Lines between nodes are the network edges (i.e. connecting consecutive rests).

greater than predicted from random networks (Table 3). Conversely, wet-season network repeated motifs did not differ from random expectation, while for some individuals clustering coefficient and self-loops strength were significantly larger than random. Stronger clustering of rest networks occurred within protected areas relative to outside (Table 3), while self-looping was more common outside

protected areas, further from water and during the dry season (Table 2). Repeat motifs were found to be more common in nodes in protected areas, closer to permanent water (though further inside protected areas) and those used primarily during the day (Table 2). Dominance rank was not included in any of the top models of network metrics (Supplementary material Appendix 1, Table A4).

Table 2. Results from the top models of network properties (degree, preference, repeat motifs, and self-loops).

Response variable	Covariate	Coefficient	(95% CI)
Degree			
	Node area	0.376	(0.368–0.383)
	Protected	0.177	(0.140–0.214)
	Time	0.232	(0.191–0.273)
	Distance to nearest neighbor	−0.418	(−0.479–−0.357)
	Water	−0.020	(−0.044–0.004)
	Protected × Water	−0.079	(−0.116–−0.042)
Preferred nodes			
	Node area	2.061	(1.869–2.531)
	Time	1.784	(1.312–2.256)
	Distance to nearest neighbor	−1.319	(−2.236–−0.402)
	Protected	0.761	(0.379–1.143)
	Water	0.683	(0.454–0.912)
	Protected × Water	−0.420	(−0.753–−0.087)
Repeated paths			
	Protected	1.128	(0.809–1.447)
	Time	0.632	(0.391–0.873)
	Water	−1.117	(−1.485–−0.749)
	Protected × Water	0.877	(0.495–1.269)
Self-loops			
	Season	0.393	(0.107–0.679)
	Protected	−0.313	(−0.599–−0.027)
	Water	0.160	(0.040–0.280)

Discussion

Rest, and its absence, can strongly influence an animal's health and performance, while also affecting social interactions and predation (Anderson 1998). Clearly, the study of rest strategies can provide important ecological insight on a species, yet generally rest patterns and locations tend to be ignored in studies of behavior and movement ecology. Our study characterized African elephant resting strategies, determining that elephants generally had short rest periods multiple times a day (1–3 d^{-1}, lasting 3–5 h total). These relatively short rest periods are likely a function of forage requirements related to body size (Owen-Smith 1988). Rests occurred in numerous sites, spaced across the ecosystem, though preferences for sites were apparent and important to gaining understanding of landscape use patterns more generally.

There was a marked behavioral shift in rest strategies relative to the protected status of a location, with all rest properties being strongly influenced by the rest site's (node) protective status. For example, unprotected areas saw more frequent, longer rests further from water during the day (when humans are most active) versus less frequent resting (a higher restlessness index) during the night and during the dry season. Within protected areas, rests were more common and longer at night and occurred markedly further from water (average twice as far from water) relative to day time rests. Regardless of time of day, rest sites outside protected areas were further from permanent water. In addition, we found repeated use (self-loops as discussed below) to be most common outside protected areas (Fig. 3a). This location mediated circadian switch in rest likely reflects a tactic aimed to minimize interaction with humans and livestock, comparable to shifts recorded in elephants' movement patterns (Wittemyer et al. 2008), nocturnal reliance on water sources (Wittemyer et al. 2007a) outside relative to inside protected areas, and crop raiding strategies (Graham et al. 2009). By resting more during the day in preferred (safe) locations when outside protected areas, elephants minimize their likelihood of interacting with people, their primary predator in the system (Wittemyer et al. 2013). Thus, resting strategies in elephants offer insight to the spatio-temporal structure of risk perception as has been found for other species (Anderson 1998) allowing characterization of species' 'landscape of fear' (Brown et al. 1999). Applying telemetered movement behavioral analysis (as done here with rest) to characterize and interpret risk perception offers an important avenue for landscape risk mapping that improves upon some of the limitations of applying mortality site or point observational data to such aims. Specifically, continuous tracking data avoids sampling bias introduced by the latter and increases sample size relative to the former.

Interpreting rest network structure

Network-based approaches were recently applied to study the spatial connectivity of habitat use in animal ecology (Jacoby et al. 2012). Here, we used movement to define network attributes and examine their spatial context, specifically defining nodes as the spatial locations of discrete resting behavior and their edges as observed movements between nodes. Comparable to effects in social networks (Newman 2003), we found strong heterogeneity in node degree driven

Table 3. Resting network metrics, presented as means and standard error across the nine elephants, by treatment group. Values in brackets represent the number of elephant resting networks with metrics that were significantly higher than that of the corresponding random networks (p ≤ 0.05; see Supplementary material Appendix 1 for a description of how the random networks were generated).

Treatment group	Global Clustering Coefficient	Mean Fraction Self-Loop Strength	Repeated Paths (size 3)
Wet, protected	0.154 ± 0.021 (3)	0.204 ± 0.013 (9)	0.006 ± 0.003 (2)
Dry, protected	0.229 ± 0.022 (7)	0.259 ± 0.017 (9)	0.031 ± 0.009 (5)
Wet, unprotected	0.129 ± 0.016 (1)	0.207 ± 0.011 (9)	0.005 ± 0.002 (1)
Dry, unprotected	0.188 ± 0.028 (7)	0.261 ± 0.015 (9)	0.014 ± 0.006 (4)
Overall	0.203 ± 0.015 (7)	0.213 ± 0.010 (9)	0.022 ± 0.005 (5)

by rest site preferences which structured network properties. Approximately half of all resting events took place in less than 10% of nodes.

Node degree, the number of connections to other nodes, was primarily a function of the node size (positively correlated with rest site area) and location (further from their nearest neighbor) within the network. In addition, degree was larger in nodes used more during the day and in protected areas (particularly when closer to permanent water), with the latter potentially reflecting the higher density of nodes in protected areas relative to outside (Fig. 3a). Correlates of preferred nodes were somewhat parallel to those of degree, with larger nodes and those further from other nodes being preferred. However, a strong preference for nodes further from permanent water (particularly outside protected areas) was found. Observationally, these patterns are likely influenced by avoidance of humans (as discussed) and elephants' apparent resting preference for certain woodland structure, namely canopy cover, that provide required shade for midday rests, though we lack data on woodland structure to test this assumption.

Across all elephants studied, self-looping or sequential use of a node for rest events was more common than expected at random, and occurred more often outside protected areas, further from water and during the dry season. As discussed, the structuring of rest location relative to protected status and water proximity likely reflects the influence of human activity where, in this case, elephants likely repeatedly used nodes with characteristics that minimize the potential for interaction with people. Lower node density outside protected areas, which may itself reflect higher selectivity in rest node sites, may have contributed to this. Interestingly, node sizes were smaller outside protected areas, another potential indication of specificity in rest sites attributes. It is likely the propensity for smaller dry season range (Wittemyer et al. 2007a) contributes to the increased propensity of self-looping during that season.

Results from analysis of repeat motifs (i.e. consecutive use of three nodes in a specified order) and clustering coefficients were less definitive. Both network metrics were structured by season in the majority of individuals, with significantly more repeat motifs and clustering than random networks during the dry season (Table 3). The seasonal structuring probably reflects, at least in part, the increased physiological stresses during the dry season, as demonstrated demographically for Asian elephants (Mumby et al. 2013). The larger productivity, more homogenously spread in the study ecosystem during the wet-season, reduces intra-specific competition for resources, including rest sites (Wittemyer and Getz 2007). More randomness in rest timing and location during the wet season may reflect a release from these social and environmental constraints.

Despite the importance of social rank in space use (Wittemyer et al. 2007a) and movement strategies (Wittemyer et al. 2008, Polansky et al. 2013), dominance did not seem to play a role in properties of rest locations. Rather, it appeared that elephants used relatively similar resting strategies, irrespective of social factors. While previous work suggests that social subtleties are likely to affect rest locations, with more dominant families displacing subordinates from resting spots (Wittemyer and Getz

2007), we could not discern connotations of this in our rest networks.

Applications of the network approach to animal movement

Studying spatial behavior patterns using graph theory, in this case the use of rest sites, provided insights to interconnectivity of sites, both temporally and geographically. Elephant rest site use demonstrated strong patterning, structured in part by season, landscape context (protected area status and distance to permanent water) and node location within the network. Our results identified landscape features apparently important to the elephants, which is an output that may be generally applicable to other species and systems.

While a powerful tool for the study of connectivity, graph theoretic approaches may not be as powerful to assess site specific characteristics in comparison to other methods such as a resource selection framework (Manly et al. 2002). Information on landscape-level covariate information was limited in our system; in particular, information on canopy height and density (related to shade and cover) and human activity given the semi-nomadic lifestyles of pastoralists in the region, precluding such an approach. Holistic studies assessing the spatial properties of different behaviors are needed to ensure proper inference on animal ecology. Last, we point out that this study concerns rest and resting patterns, and makes no inferences as to when and where in the observed patterns the elephants actually slept, as defined by REM sleep. Analysis of activity sensor data conducted here suggests that midday rest is mostly that, often standing up, while early morning rest (around 4 am) may often be sleep, lying down.

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Supplementary material (Appendix ECOG-02379 at <www.ecography.org/appendix/ecog-02379>). Appendix 1.