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Emerging Issues

Structure and Resilience of Bald Eagle Roost Networks

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ABSTRACT The recognition that communal roosts are important elements within the life cycle of bald eagles (*Haliaeetus leucocephalus*) led to their protection under the "disturb" clause of the Bald and Golden Eagle Protection Act. The regular roost-switching movements of bald eagles imply that roosts are part of an interactive network where roosts represent nodes linked by birds moving between them. Network analysis holds promise for informing management decisions by assessing the effect of roost removal on the resilience of the broader network. We tracked nonbreeding bald eagles ($n = 56$) within the upper Chesapeake Bay (2008–2013), USA, to evaluate roost characteristics and network structure. We used midnight locations ($n = 14{,}464$) to assess the use of communal roosts ($n = 212$) and movement of birds among roosts ($n = 2{,}634$) on successive roost nights to evaluate the pattern and strength of connections. We performed a sensitivity analysis to assess the response of the roost network to roost loss. Structure of the roost network approximated that of a scale-free network where the distribution of connections follows a power law of the form $P(k) = Ak^{-\gamma}$ and $\gamma = 1.1$. Unlike random networks, connections within scale-free networks are concentrated within a few highly connected nodes (hubs). These hub roosts serve as bridges between large numbers of other roosts, have the shortest travel times to other roosts and greatest overall influence on network functioning. The effect of roost removal on overall network function was directly proportional to the connectivity of the roost being removed. The targeted removal of the majority (>90%) of roosts had very little effect on the network. Network sensitivity was high in response to the loss of roosts within the highest 10% of connectivity. This small ($n = 18$) subset of roosts makes a disproportionate contribution to network function and the protection of these roosts should be a stated management objective with high priority. Network analysis represents a powerful tool with the potential to inform management decisions. © 2018 The Wildlife Society.

KEY WORDS bald eagle, Chesapeake Bay, communal roost, *Haliaeetus leucocephalus*, networks, resiliency.

The gathering together of individuals to rest has been documented within a wide range of animals across varied taxonomic groups, suggesting that the behavior has evolved independently numerous times (Allen and Young 1982, Eiserer 1984, Lewis 1995, Grether and Donaldson 2007, Kerth 2008). Proposed benefits to individuals participating in communal roosts are species-specific, but include a reduction in the cost of thermoregulation (Beauchamp 1999, McKechnie and Lovegrove 2001, Hatchwell et al. 2009), a reduction in the likelihood of being predated either through safety in numbers or improved predator detection (Krause and Ruxton 2002, Finkbeiner et al. 2012), and access to information about the location of food (Ward and Zahavi 1973, Rabenold 1987, Buckley 1996). Recognition of ecological benefits provided by roosts to participating individuals has resulted in a wave of research focused on the effects of roost loss (Brigham and Fenton 1986, Burton et al. 1996, Chaverri and Kunz 2011) and efforts to protect significant roost sites for species of conservation concern (Rehfisch et al. 2003, Rhodes et al. 2006, Fortuna et al. 2009).

Bald eagles (*Haliaeetus leucocephalus*) are highly social and nonbreeding individuals frequently utilize communal roosts that form around important feeding sites (McClelland 1973, Isaacs and Anthony 1987, Keister et al. 1987). Investigations of eagle roosts have focused on the number of individuals using roosts (McClelland et al. 1982), temporal patterns of roost use (Steenhof 1983, Crenshaw and McClelland 1989, Curnutt 1992), physical characteristics of roost structures (Hansen et al. 1980, Keister and Anthony 1983, Chester et al. 1990, Stohlgren 1993, Dellasala et al. 1998), or landscape context of roost sites (Steenhof 1983, Stalmaster and Gessaman 1984, Keister et al. 1985, Buehler et al. 1991*a*, Stahlecker and Smith 1993). Despite eagles regularly moving among roost sites (Grubb et al. 1989, Buehler et al. 1991*b*,

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Watts and Mojica 2012), roosts have typically been both perceived and managed as stand-alone resources (Becker 2002, U.S. Fish and Wildlife Service 2007).

Regular roost-switching movements of bald eagles imply that, rather than existing in isolation, roosts may be part of an interactive network where roosts represent nodes linked by birds moving between them. Network analysis has been applied to a variety of biological systems ranging from proteins (Gardner et al. 2003, Hakes et al. 2008), metabolism (Jeong et al. 2000), and food webs (Montoya et al. 2009) to ecosystems (Patten et al. 1990, Manfred 2006), among others. Networks have both local and global properties that may be understood by a set of metrics describing the connectedness, closeness, and centrality of elements. Network analysis is not only a powerful descriptive tool, but also has the capability of evaluating the response of networks to perturbations (Rhodes et al. 2006, Chaverri 2010). Of particular interest to conservation is the use of network analysis to assess the role of individual nodes within their network and model the effect of node removal on network functioning and resilience. This aspect of network analysis has the potential to inform decisions about the management of bald eagle roosts.

The recognition that communal roosts are important elements within the life cycle of bald eagles led to their protection under the "disturb" clause of the Bald and Golden Eagle Protection Act of 1940 (16 U.S.C. 668-668d) and their management is incorporated into the National Bald Eagle Management Guidelines (U.S. Fish and Wildlife Service 2007). However, the role that roosts play in the use of the broader landscape by bald eagles remains understudied, leaving open questions about the expected effect of roost loss and little guidance for managers tasked with making permit decisions. This is particularly true in landscapes supporting large numbers of communal roosts. For example, what is the structure of bald eagle roost networks? Scale-free networks defined as having many nodes with few connections and few nodes with many connections (referred to as "hubs") tend to be robust against random attacks (all roosts with equal probability of removal) on nodes, but vulnerable to targeted attacks (well-connected roosts with high probability of removal) on hubs (Albert et al. 2000, Cohen et al. 2000, Newman 2003). For this network structure, differentiating hubs from other nodes is essential to conservation planning. For other network structures where connectivity is more uniformly distributed among nodes, information on specific nodes is less important to conservation decisions. Understanding the global structure of a network and the contribution of individual nodes to its basic functioning is a first step toward effective planning.

We used a network approach to analyze telemetry data from the upper Chesapeake Bay, USA, an area supporting a dense concentration of bald eagle roosts, to evaluate network structure and roost characteristics. We address 3 interrelated questions. 1) What is the structure or topology of the roost network? 2) Do basic network parameters (i.e., connectivity, betweenness, closeness) vary between roosts? And 3) to what extent is network function altered by the loss of roost sites?

STUDY AREA

Our study area (12,920 km^2) included the northern part of the Chesapeake Bay from the Bay Bridge at Annapolis, Maryland, USA, to just above the Conowingo Dam on the Susquehanna River (Watts and Mojica 2012, Watts et al. 2015). This area supported a significant number of eagles during the autumn and winter months and a large breeding population (Steenhof et al. 2008, Watts et al. 2014). The southwestern portion of the study area included urban expanses of Baltimore and Annapolis that were dominated by extensive residential and commercial development. These areas supported very little eagle activity (Buehler et al. 1991*c*, Watts et al. 2015). Remaining portions of the study area were primarily rural, with forest lands interspersed with agriculture. These areas supported an extensive network of communal roosts and many significant foraging areas (Buehler et al. 1991*b*, Watts and Mojica 2012, Watts et al. 2015).

The study area included the Upper Chesapeake Bay Bald Eagle Concentration Area, a relatively small area where 3 geographically distinct populations of bald eagles converge (Watts et al. 2007). The area supported a complex mixture of age classes from the resident Chesapeake Bay population. In late spring and early summer, eagles migrate north from Florida, USA, and other southeastern states to spend the summer months (Broley 1947, Wood et al. 1990, Mojica et al. 2008). In the late autumn, eagles migrate south from New England populations to spend the winter months (McCollough 1986). Eagles within the area feed primarily on fish during summer, but switch over to waterfowl and mammals during the autumn and winter when fish move to deeper water and waterbirds migrate into Chesapeake Bay (DeLong et al. 1989, Mersmann 1989).

METHODS

Eagle Trapping

We captured resident and migrant bald eagles, banded them, and fitted them with satellite transmitters between August 2007 and May 2009. Free-flying eagles were trapped on 3 sandy beaches using padded leg-hold traps, in 3 open fields using rocket nets baited with deer carcasses, and on open waters using floating fish traps (Grubb 1988, Cain and Hodges 1989, Jackman et al. 1993, King et al. 1998). We climbed nest trees to access broods (8–10 weeks of age) and deployed a transmitter on one nestling per brood. We conducted floating fish and leg-hold trapping during the summer months to target residents and migrants visiting from the southeastern United States. We conducted rocket-net trapping in the winter months to target residents and migrants from northeastern states and Canadian provinces. Eagle capture and handling methods were in compliance with Institutional Animal Care and Use Committee (IACUC) protocols at the College of William and Mary (IACUC-20051121-3).

Data Collection

We used solar-powered, 70-g, Global Positioning System–Platform Transmitter Terminal (GPS–PTT) satellite transmitters (Microwave Telemetry, Inc., Columbia, MD, USA) to track eagle movements. We attached transmitters using a backpack-style harness constructed of 0.64-cm Teflon® ribbon (Bally Ribbon Mills, Bally, PA, USA). We programmed transmitters to collect GPS locations (±18 m manufacturer estimated error) every daylight hour and one additional location at midnight. Locations were processed by Argos satellites (CLS America, Largo, MD, USA) and stored online by Satellite Tracking and Analysis Tool (Coyne and Godley 2005). We deployed transmitters over a period of several years and eventually they ceased transmitting data; therefore, the number of eagles we tracked varied each year from 2007 to present. We selected 2008–2013 as the study period for this investigation because this time frame had the greatest number of active transmitters within the study area. The final sample included 56 eagles (43 resident, 13 migrant). At the time of transmitter deployment, 11 birds were adults, 29 were subadults, and 16 were nestlings.

We used midnight locations (excluding breeding adults and young prior to dispersal) to delineate communal roosts (Watts and Mojica 2012). We delineated minimum convex polygons of roost boundaries using a nearest-neighbor clustering script in Crimestat III (Levine 2004). We used midnight locations (2008–2013) to quantify roost use and roost-switching movements between successive roost nights to quantify connections among roosts. We were interested in information relevant to roost management rather than ecological patterns, so we used locations from all individuals and across all years to evaluate network structure and patterns.

Network Analysis

For network analyses, we considered the universe of nodes to be the set of roost polygons previously delineated within the study area and the use of a node by a bird to be a midnight location that fell within the boundary of the roost polygon (Watts and Mojica 2012). We defined the total use of a node to be all midnight locations that fell within polygon boundaries (2008–2013) and assumed that this value provided an estimate of overall use by the eagle population. We considered edges (connections) to be movements between roosts on successive nights and the strength of connections between two roosts to be the sum of movements. We performed all network analyses in Program R v. 3.1.2 (R Core Team 2014).

Network topology.—We examined the overall topology (Table 1) or structure of the roost network by producing a frequency distribution of degrees (no. of edges or connections to other roosts) and qualitatively comparing the distribution to 2 well-known structures including random and scale-free (Bollobas 1979, Newman 2003). The degree distribution $P(k)$ gives the fraction of the nodes that have degree k and is obtained by counting the number of nodes $N(k)$ that have $k = 1, 2, 3\ldots$ edges and dividing it by the total number of nodes N. The degree distribution for a random network approximates a normal distribution, indicating that the majority of nodes have a degree close to the average (Bollobas 1985). The degree distribution of a scale-free network follows a power law of the form $P(k) = Ak^{-\gamma}$ where the exponent γ typically falls in the range $2 < \gamma < 3$ (Newman 2003). This function indicates that there is a high diversity of node degrees (few nodes with many connections and many nodes with very few connections) and no typical node in the network that is characteristic of most other nodes. The absence of a typical degree (or scale) is the reason these networks are described as "scale-free."

Network centrality.—We evaluated 4 metrics of network centrality at the node level—including degree, betweenness, closeness, and eigenvalue centrality—that quantify different aspects of the relative importance of a node within a network

Table 1. List of parameters, terminology, and definitions used in the evaluation of a network of bald eagle communal roosts ($n = 212$) within the upper Chesapeake Bay, USA. We assessed network structure using satellite telemetry data collected from 56 individuals (2008–2012).

Basic terms	Description
Network	A group or system of interconnected elements.
Scale-free network	A network with many nodes (roosts) that have few connections (edges) to other nodes and few nodes that have many connections to other nodes.
Random network	A network where all nodes (roosts) have an equal probability of being connected to all other nodes. The frequency distribution of connections is normal indicating that the majority of nodes have a no. of connections near the average.
Nodes	Element within a network representing an individual or vertex (in this case a roost).
Edges	Connection or relationship between 2 nodes (in this case a bird moving between 2 roosts).
Node-based metrics	
Degree	The no. of immediate neighbors or direct connections.
Betweenness	The no. of times a node acts as a bridge along the shortest path between 2 other nodes. Nodes with high betweenness are characterized as the "brokers" of the network.
Closeness	A measure of the degree to which a node is near all other nodes in a network. The inverse of the sum of the distances between a node and all other nodes in the network. Nodes with high closeness are capable of reaching all other nodes in the shortest period of time.
Eigenvalue centrality	An index reflecting the influence of a node on the entire network. The index is a weighted score based on the scores of neighbors and neighbors of neighbors. Nodes with high eigenvalue centrality have a large no. of neighbors that themselves have a large no. of neighbors.
Group-based metrics	
Network topology	Structure or patterns of interconnections between network components (nodes and edges).
Network resilience	The ability of a network to maintain similar topology or structure despite the removal of components.
Modularity	Modules are nonoverlapping groups of nodes (roosts) within networks and modularity is the extent of subdivision.
Clustering coefficient	A measure of how connected immediate neighbors are to each other relative to others in the network. A local measure of cliquishness or subgrouping.

(Table 1; Bonacich 1987, Borgatti and Everett 2006). Degree centrality is the number of connections that a node (roost) has with other nodes. Betweenness is the number of times a node (roost) acts as a bridge in the shortest path between 2 other nodes (Freeman 1977). Closeness is a measure of centrality and is the average, shortest path length between the node (roost) and all other nodes within the network (Bavelas 1950). Eigenvalue centrality is a measure of the "influence" of a node within a network (Newman 2010). The measure assigns relative scores to all nodes (roosts) in the network and assesses a node's importance based on the scores of connected nodes under the concept that connections to high-scoring nodes provide more importance than connections to low-scoring nodes. We explored the statistical relationships between centrality metrics using Spearman's rank correlation coefficients (Sokal and Rohlf 1981).

Network modularity.—Modules are nonoverlapping groups of nodes within networks (Hartwell et al. 1999, Newman 2010). We used a clustering coefficient C_i (where i is the focal node) to quantify the cohesiveness of the surrounding neighborhood of the node. C_i is defined as the ratio between the number of connections to adjacent nodes and the possible number of connections between them (Watts and Strogatz 1998). In other words, the clustering coefficient quantifies how close the local neighborhood of a node is to being part of a "clique," a region of the network where every node is connected to every other node. We explored the statistical relationships between the clustering coefficient and other network metrics using Spearman's rank correlation coefficients (Sokal and Rohlf 1981).

Network resiliency.—We evaluated the influence of node (roost) loss on network function by performing a simple remove-and-replace experiment and measuring the response on a network-wide metric (network centralization) to the removal. Network centralization is the average degree (no. of connections for each node) for all nodes in the network and provides a relative index of network function (Freeman 1979). We systematically removed each node (roost) from the network, reassessed network centralization, and compared the resulting value with a baseline value (entire network intact). We expressed the difference between the 2 values as a standardized deviation from the initial baseline. We plotted deviations from baseline function against the eigenvalue centrality of each node to examine the influence of node importance to the overall functioning of the network. We chose eigenvalue centrality because it is generally believed to be the best overall indicator of node importance (Newman 2003).

RESULTS

We collected midnight locations from 56 eagles during the 72-month study period. The cohort used 212 interconnected communal roosts or 1.3/10 km^2 within the study area. Use of roosts by tracked birds averaged 61.4 ± 9.04 (SE) roost nights per roost and a median of 20. We documented 2,634 edges or connections (movement of birds between roosts on successive roost nights) within the roost network. We used edges to evaluate network structure.

The overall topology or structure of the roost network approximated that of a scale-free network rather than a random network (Fig. 1). The degree distribution of a scale-free network follows a power law of the form $P(k) = Ak^{-\gamma}$ where the exponent γ typically falls in the range $2 < \gamma < 3$. The degree distribution of the roost network approximates that of a power function where $\gamma = 1.1$ ($R^2 = 0.87$, $F_{1,24} = 164.2$, $P < 0.001$). Degree (no. of direct connections)

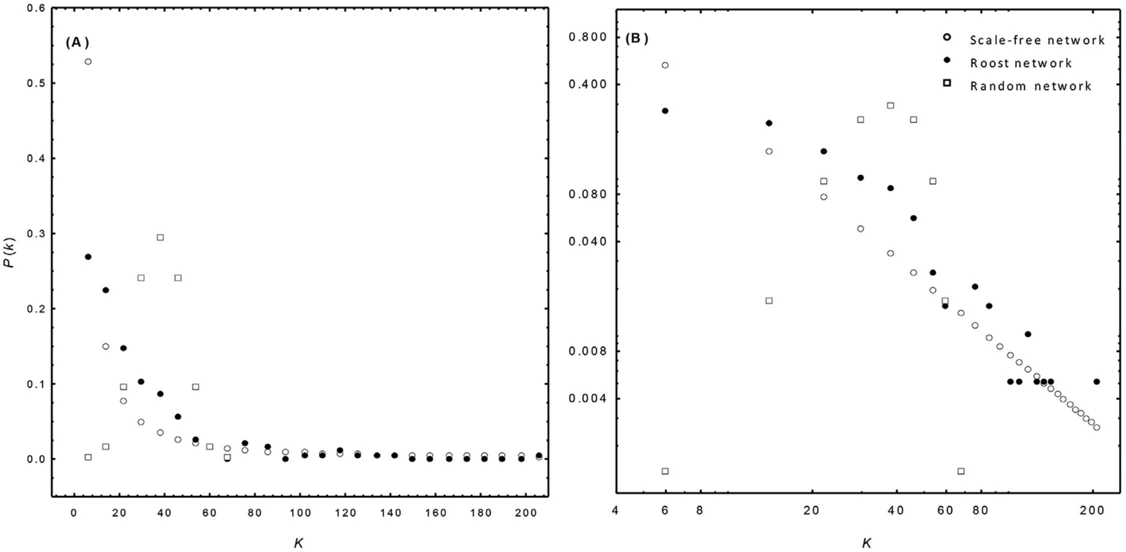

Figure 1. Comparison between the degree distribution of a scale-free network, the roost network (of nonbreeding bald eagles within the upper Chesapeake Bay, USA, 2008–2013), and a random network having the same number of nodes and edges. For clarity the same 2 distributions are plotted on a linear (A) and logarithmic (B) scale. The bell-shaped degree distribution of random networks peaks at the average degree and decreases rapidly for both smaller and larger degrees, indicating that these networks are statistically homogeneous. By contrast, the degree distribution of the scale-free network follows the power law $P(k) = Ak^{-\gamma}$, which appears as a straight line on a logarithmic plot. The continuously decreasing degree distribution indicates that low-degree nodes have the highest frequencies and high-degree nodes (hubs) are relatively rare. The roost network most closely resembles the scale-free network.

varied from 2 to 204. A characteristic of a scale-free network is that a large number of nodes have few edges and a small number of nodes have many edges. More than 50% ($n = 113$) of nodes within the study network had direct connections to <10% of the other roosts, while only 7 roosts had direct connections to >50% of the network. Incredibly, the Sod Run roost located near the center of the network had direct connections to 204 (96.7%) of the possible 211 other roosts and appears to serve as a central hub within the network.

Centrality Measures

Roosts within the network exhibited a great deal of heterogeneity in centrality measures (Table 2). Nine of the roosts had betweenness values of 0, indicating that they did not serve as bridges between other roost pairs. Betweenness of remaining roosts ranged from <0.1 to >4,000. Roosts within the upper end of this range served as connections or bridges between many pairs of other roosts. Eigenvalue centrality is bounded by 0 and 1 and likely the best generic indicator of the role or value of a roost within the overall network. This parameter varied dramatically among roosts (Fig. 2), allowing for the identification of roosts that appear to serve as global hubs (values >0.7), regional hubs (values >0.5, <0.7), or smaller local hubs. Roosts within the network also varied across a 4-fold range of closeness values, indicating that some roosts were positioned near the functional center of the network while others were not. Not surprisingly, roosts with the greatest closeness values were also those that appeared to serve as the largest activity hubs. All of the centrality measures examined within the roost network were correlated (all $r > 0.88$, $P < 0.001$). By comparison, centrality measures were less correlated with roost use (all $r < 0.6$, $P < 0.05$), a more traditional measure of roost importance.

Modularity

We found only weak evidence that the roost network was divided into subnetworks. The clustering coefficient was bounded by 0 and 1 and had a median value of 0.2 (Table 2). An inverse relationship between degree and the clustering coefficient is believed to suggest the occurrence of a hierarchical structure within some network types (Watts and Strogatz 1998). The suggestion reflects the tendency for nodes with high degree to be connected globally while the clustering coefficient highlights groups of nodes that exhibit high local connectivity. Within the roost network, degree and clustering were inversely related though the relationship was relatively week ($r_{200} = -0.39$, $P < 0.002$). Several roost clusters appear insular and consistent with a clique (modular) structure (Fig. 2).

Network Resiliency

We found that the magnitude of effect on overall network functioning was positively related to the eigenvalue centrality of the roost being removed, suggesting that the greater the connectivity of the node the larger the effect of its removal from the network (Fig. 3). As expected, the targeted removal of the majority (>90%) of roosts had very little effect on the network. Only when eigenvalue centrality rose above approximately 0.4 did the effect on overall network function accelerate. Less than 20 (8.5%) roosts had values above this threshold, suggesting that the targeted protection of these sites is essential to the maintenance of network integrity.

DISCUSSION

The large collection of roosts within the upper Chesapeake Bay is the most complex assemblage of bald eagle roosts described to date and first to be examined from a network perspective. Communal roosts used by eagles have been viewed as independent, stand-alone entities despite the fact that we have known for decades that birds regularly move from roost to roost (Grubb et al. 1989, Stahlecker and Smith 1993). This perspective reflects the difficulty of collecting movement data for such a wide-ranging species on the scale necessary to evaluate connectivity. Investigations of eagle roosts that have relied on direct observation or conventional telemetry techniques have often sensed movement patterns, but have lacked sample sizes to construct networks. The relatively recent appearance of GPS transmitters and other devices that have enabled the remote tracking of large samples of eagles has opened a new era of data collection with the potential to rapidly advance our understanding of roost networks. Investigations are needed within other study areas to extend our understanding of network structure.

The roost network examined here exhibits characteristics that approximate the well-known structure of scale-free networks (Newman 2003). Most communal roosts identified within the study area had relatively few connections to other roosts, whereas several roosts were highly connected throughout the network. Fifty percent of all connections were concentrated within only 11% of roosts, and 50% of roosts accounted for <20% of connections. This skewed distribution of connections is consistent with the pattern in

Table 2. Descriptive statistics for centrality parameters measured for a bald eagle roost network within the upper Chesapeake Bay, USA. We used bald eagles ($n = 212$) tracked with satellite transmitters (2008–2012) to estimate parameters.

Parameter	n[a]	Median	$\bar{x}$	(SE)[b]	Range
Degree	212	18	26.7	(2.1)	2.0–204.0
Betweenness	212	119.6	356.4	(42.8)	0.0–4,053.7
Closeness	212	0.0028	0.0028	(0.00002)	0.0014–0.0035
Eigenvalue centrality	212	0.12	0.17	(0.012)	0.004–1.000
Clustering coefficient	212	0.20	0.24	(0.013)	0.00–1.00

[a] Sample size of roosts.

[b] Standard error.

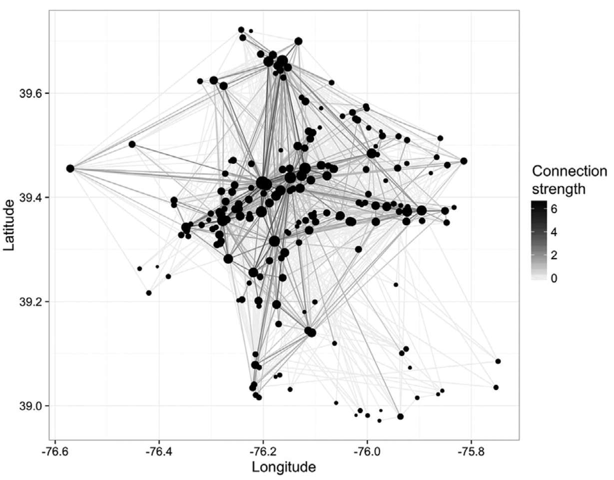

Figure 2. Bald eagle roost network within the upper Chesapeake Bay, USA, 2008–2013. Circles indicate nodes (roosts) where size is proportional to eigenvalue centrality. Lines indicate edges (connections) where the darkness value represents the strength (no. of eagle movements) of the connection between roosts. Connectivity of roosts varies over 3 orders of magnitude throughout the network.

roost use described within this system and other study areas. In an assessment of roost use within the study area (Watts and Mojica 2012), the number of roost nights, the number of calendar nights, and the number of different transmittered birds per roost were shown to be highly skewed. The result of variation in relative use was a "decelerating utility function" such that 10%, 30%, and 50% of roosts supported 52%, 78%, and 89% of roost nights, respectively. In similar observations, Keister and Anthony (1983) collected castings under 6 communal roosts in the Klamath Basin and showed that nearly 49% of the total castings were from a single roost and >80% were from the 2 largest roosts. Although the range of use was narrower, Isaacs et al. (1996) found that use of roosts by eagles wintering along the Upper John Day River in Oregon, USA, varied over an order of magnitude. Grubb et al. (1989), working with 28 roosts in the Coconino National Forest in Arizona, USA, found that use was highly skewed to a few large roosts. Although not subjected to network analyses, these observations suggest that roost networks in other areas may possess scale-free properties.

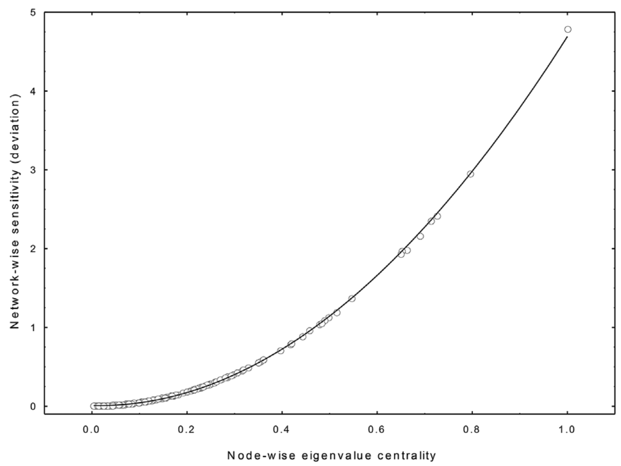

Figure 3. Relationship between eigenvalue centrality of nodes (roosts of bald eagles within the upper Chesapeake Bay, USA, 2008–2013) and the expected impact of node removal on overall network function. The positive relationship suggests that the greater the connectivity of the node the larger the impact of its removal from the network.

The relatively weak correspondence between the use of roosts and node-based network parameters (degree, betweenness, closeness, eigenvalue centrality) suggests that network metrics provide a dimension of roost importance not captured by use alone. Many roosts that received only moderate overall use had high centrality metrics, indicating a disproportionate influence on the flow of activity through the network. Centrality metrics were found to be highly correlated. Roosts that had large numbers of connections, serving as bridges for large numbers of roost pairs, had the shortest travel times to other roosts throughout the network and had the greatest influence on network functioning. These network hubs offer the greatest opportunities for information exchange. One of the proposed advantages of sociality in nonbreeding eagles is food finding through following behavior from communal roosts, which has been shown to support the hypothesis that some eagles gain an advantage from associating with roosts by increasing their likelihood of either finding or stealing food (Knight and Knight 1983, Stalmaster and Gessaman 1984). This benefit is believed to be particularly great for young, inexperienced eagles that have yet to master hunting skills and often resort to kleptoparasitism or scavenging to meet energetic demands (Stalmaster and Gessaman 1984, Elliott et al. 2006, Turrin et al. 2015). Hub roosts may represent concentrated information resources that may be visited periodically by eagles from throughout the network.

We found modest evidence of modularity within the roost network. Clustered networks are more typical within social systems where individuals naturally segregate into cliques and both the frequency and strength of interactions are stronger within rather than beyond the clique (Newman 2006). Examples include the social networks of leaf-roosting bats (*Thyroptera tricolor*) and Columbian ground squirrels (*Urocitellus columbianus*) that exhibit clustering coefficients of 0.86 and 0.81, respectively (Manno 2008, Chaverri 2010). By comparison, the mean clustering coefficient of the roost network was 0.24, which is similar to that reported for some marine mammals (Lusseau et al. 2006, Wiszniewski et al. 2009). Despite this low mean, a few roosts had large coefficients and inspection of the network reveals several areas of clustering. The benefit may be that activities within these subregions are somewhat insulated from disruptions elsewhere in the network. In other words, loss of a roost site in an area of the network outside of the module or clique may have little effect on the network functioning within the clique.

Scale-free networks are generally believed to be robust against random attacks (removal of a roost selected randomly) because the majority of nodes have few connections and the likelihood of hitting a hub by chance is low (Albert et al. 2000, Flack et al. 2005). In contrast, the targeted removal of well-connected hubs may have a marked effect on network connectivity. Removing any of the global hubs in the roost network may significantly alter the flow of activity, disaggregate the network into smaller roost clusters, and potentially reduce the access of information for a large number of individuals. This is similar to the western power grid when the loss of a central substation knocks out power to a large geographic area including a large number of customers. Other network configurations, such as random networks, are less vulnerable to targeted attacks because connectivity is more uniformly distributed throughout the network.

All of the management practices currently in use that pertain to eagle roosts are costly both from a regulatory (i.e., establishment, administration) and land use perspective. The recommended management includes the establishment of spatial buffers and time-of-year restrictions to reduce the effect of human disturbance and the physical protection of roost structures (Isaacs et al. 1993, U.S. Fish and Wildlife Service 2007). This approach may be coupled with the management of roost trees (Stohlgren and Farmer 1994), roost stands (Keister and Anthony 1983, Chester et al. 1990), surrounding forests (Dellasala et al. 1998), and the local prey base (Isaacs and Anthony 1987). Various costs are associated with roost management; therefore, decisions as to which roosts warrant protection and the policies governing these decisions are of paramount importance.

The findings presented here have implications for the selective management of roost sites. Network integrity was robust in the face of most roost losses. Small communal roosts were widespread, accounting for a relatively small portion of roosting activity, and contributing relatively little to network function. Benefits accrued to eagles for their protection relative to the burden imposed on landowners and managers appear to be small. Network sensitivity was high in responses to the loss of roosts within the highest 10% of connectivity. This small subset of roosts accounted for a large portion of eagle use and network function and their protection should be a stated objective with high priority. A conservative, risk-averse management strategy focused on their protection could follow one of 2 trajectories: 1) indiscriminately protect all known roosts so that significant roosts are protected somewhere in the mix; or 2) identify significant roosts and implement a targeted protection plan. The former blunt-force strategy requires minimal understanding of the roost network, but lays the greatest burden on landowners. The latter places the least burden on landowners but requires an upfront investment to identify sites of significant importance.

The topology of the bald eagle communal roost network within the upper Chesapeake Bay was found to approximate a scale-free network. Available evidence suggests that other eagle roost networks have a comparable topology. Scale-free networks are robust against stochastic events (e.g., loss of roost trees due to fire or disease) because the majority of nodes have few connections and a random event is most likely to impact one of these nodes. However, the loss of well-connected "hubs" would have a greater effect on connectivity by disaggregating the roost network into small and isolated clusters of roosts. Within the Chesapeake Bay example, highly connected roosts represent a small (<10%) portion of the network. These roosts are important for network function and accommodate the greatest percentage of both individual birds and collective roost nights. Managers should invest resources to identify hub roosts and prioritize them for long-term protection.

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