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Network analysis of a northern long-eared bat (*Myotis septentrionalis*) maternity colony in a suburban forest patch

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Abstract

Many bat species are highly social, forming groups of conspecifics, particularly during the maternity season. In temperate North America, these social groups are typically comprised of closely related individuals or individuals that share some common trait (i.e. reproductive state or shared hibernacula from the previous winter). In the summer, when bats use forests for day-roosts, these social groups often demonstrate nonrandom patterns of periodically associating in common roosts and disassociating using different roosts as a 'fission–fusion society'. As cave hibernating bat species in North America continue to decline due to the impacts of White-nose Syndrome, opportunities to describe these dynamics are becoming rare. Unfortunately, these patterns often are still poorly documented, yet understanding these behaviors is critical for species-specific habitat conservation and management. In our study, we tracked female northern long-eared bats (*Myotis septentrionalis*) to their day-roosts in a small, suburban forest fragment in coastal New York, USA, in the summers of 2018 and 2019. We confirmed that the bats shared roost sites and, using network analyses, analyzed social dynamics and space use. In contrast to previous research on this imperiled species in large, unfragmented core forests, we found a more dense, connected roost network that concentrated around forest patch edges. Unusual for this species, primary roosts were anthropogenic structures. Our findings suggest that northern long-eared bats can utilize small forest patches and that incorporation of specific types of anthropogenic roosts might be an effective strategy for long-term conservation in more urbanized landscapes where forest management actions to enhance day-roosting conditions are impractical and the risk of stochastic loss of roosts is high.

Key words: networks, *Myotis septentrionalis*, northern long-eared bat, coastal, white-nose syndrome

Introduction

Communal roosting is common among North American Vespertilionid bats throughout the year, with seasonal variation in social structures of those groups (Kerth 2008a). In the winter, many cave- and mine-hibernating bats cluster together in predominantly single-species aggregations (Davis 1970). In the

summer, reproductive females will often further subdivide into colonies that are sometimes related along matrilines (Kerth 2008b; Patriquin et al. 2013; Silvis et al. 2014b; but see Olivera-Hyde et al. 2019). Social roosting of bats allows allonursing and communal rearing of young, thermoregulatory benefits, and information transfer (Kerth 2008a; Silvis et al. 2014b). However, one major disadvantage to communal roosting is the greater potential for disease transmission among conspecifics (Kerth 2008a; Johnson, Ford, and Edwards 2012). In North America, this has contributed to the spread of White-nose Syndrome (WNS), a disease caused by the invasive fungal pathogen *Pseudogymnoascus destructans* (*Pd*; Cheng et al. 2021). The transport of *Pd* fungal spores between hibernacula has resulted in population declines of >90% of several temperate-zone, cave-hibernating bats species (Powers et al. 2015; Cheng et al. 2021).

During the summer months in North America, several species of bats form maternity colonies in which frequent roost switching is well documented (Silvis et al. 2014a): bats from a larger group will sporadically disassociate into smaller groups, such as mother/juvenile pairs, and use secondary roosts while intermittently returning to primary colonial roosts. This type of roost switching behavior is characteristic of fission–fusion societies. Fission–fusion dynamics are present in many bat species (Kerth and Konig 1999; Willis and Brigham 2004; Patriquin et al. 2010; Johnson, Ford, and Edwards 2012; Silvis et al. 2014b) and network analyses have been used to identify structural vulnerabilities of the colony, and to provide researchers and managers with a better understanding of how a colony uses and moves around the landscape (Kerth 2008b; Chaverri 2010; Patriquin et al. 2010; Johnson, Ford, and Edwards 2012; Silvis et al. 2014b).

Northern long-eared bats (*Myotis septentrionalis*) are a federally-endangered species in eastern North America that display a fission–fusion dynamic during the temperate summer maternity season (Garroway and Broders 2007; Patriquin et al. 2010; Silvis et al. 2014a). Using network analysis metrics to describe bat roost-switching patterns and inter-individual relationships, these studies have thus far been conducted in largely closed-canopy, contiguous forests that contained an abundance of available roosts across an expansive spatial extent (Silvis et al. 2015; Ford et al. 2016). Regardless of geographic locale, patterns emerged among most colonies: communal node trees were identified and bats preferred one to two roosting companions when they disassociated from the larger colony (ranging from 12 to 88 individuals; Owen et al. 2002; Garroway and Broders 2007; Patriquin et al. 2010; Johnson, Ford, and Edwards 2012; Silvis et al. 2014a; Lewis et al. 2022). Unfortunately, because northern long-eared bats have experienced substantial population declines due to WNS, continued opportunities to study day-roost ecology of the species are becoming limited (Gorman et al. 2022a).

In this study, we explored the social dynamics of a post-WNS maternity colony in a comparatively more developed, coastal landscape in the mid-Atlantic region of the United States. Due to their volant nature and high vagility, in theory bats may be less constrained by habitat extent and connectivity than other terrestrial species. However, the demonstrated importance of social and familial relationships coupled with multi-year roost fidelity of northern long-eared bats may negatively affect individual dispersal or fusion of multiple colonies. In recent years, researchers have been finding northern long-eared bats in more urban and fragmented landscapes than what has previously been recorded for the species (Deeley 2019;

Hoff et al., In review; Thorne et al. 2021). With northern long-eared bats maintaining social connectivity and reproductive success, even in areas with fragmented forests, understanding these populations could inform post-WNS adaptive management relative to varying landscape condition going forward (Rhodes et al. 2006; Snijders et al. 2017; Finch et al. 2022).

We hypothesized that a northern long-eared bat maternity colony in a highly-developed landscape would still display a general fission–fusion structure. However, given the more constrained, isolated nature of our study area's forest patch and reduced populations from WNS, we predicted that there would be stronger connections between bats, proportionally more use of primary (high-density) roosts, and less use of secondary roosts. Further, we hypothesized that, though constrained overall by the small residual forest patch size, bats in this post-WNS colony would have a larger roost-area spatial footprint than observed in previous studies because suitable roosts may be relatively diffuse in a spatially constrained forest patch.

Materials and methods

Study area

Our study was conducted at the William Floyd Estate (hereafter, the Estate), a 248-ha coastal park on the southern shore of eastern Long Island, New York, USA, managed by the National Park Service (Fig. 1). It is located approximately equidistant between the northernmost and southernmost portions of the northern long-eared bat's coastal distribution (Grider et al. 2016). Sixty-five percent of the Estate land is comprised of unmanaged, second- or third-growth oak (*Quercus* spp.)-dominated forest which is interspersed with open fields and salt marsh, fragmenting the forest habitat into several small patches (for a more detailed description see Klopfer et al. 2002 and Gorman et al. 2022a). Located approximately 100 km east of New York City, the Estate is surrounded by dense suburban neighborhoods to the north and west and the Atlantic Ocean to the south and east. Outside of the Estate, bats would need to fly a minimum of 3 km to reach additional forested habitat without having to cross open ocean, a distance greater than most observed mid-summer movements for northern long-eared bats (Henderson and Broders 2008). Long Island is frequently impacted by severe coastal weather events; overall, the climate is moderated by maritime influences, i.e. milder winters and cooler summers, than what interior New York State experiences (Gorman et al. 2021).

Field work

We caught bats from May–June 2018 and May–July 2019 using 4–12 m length, 38 mm bat mist-nets (Avinet Research Supplies, Portland, ME, USA) (any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government) in single-, double-, and triple-high configurations over wooded roads and trails throughout the Estate (Silvis et al. 2012; Deeley 2019; Gorman et al. 2022a). After recording sex, age class (based on epiphyseal gap; Brunet-Rossinni and Wilkinson 2009), and weight, we fitted all northern long-eared bats with a uniquely-numbered aluminum alloy band (Porzana Ltd., Icklesham, East Sussex, UK). For subsequent radio-tracking, we affixed Holohil LB-2X VHF radio transmitters (0.27 g, lifespan 8–15 days; Holohil Systems Ltd., Carp, Ontario, Canada) between the scapulae with surgical cement (Perma-Type Company Inc., Plainville, CT, USA) to all adult female
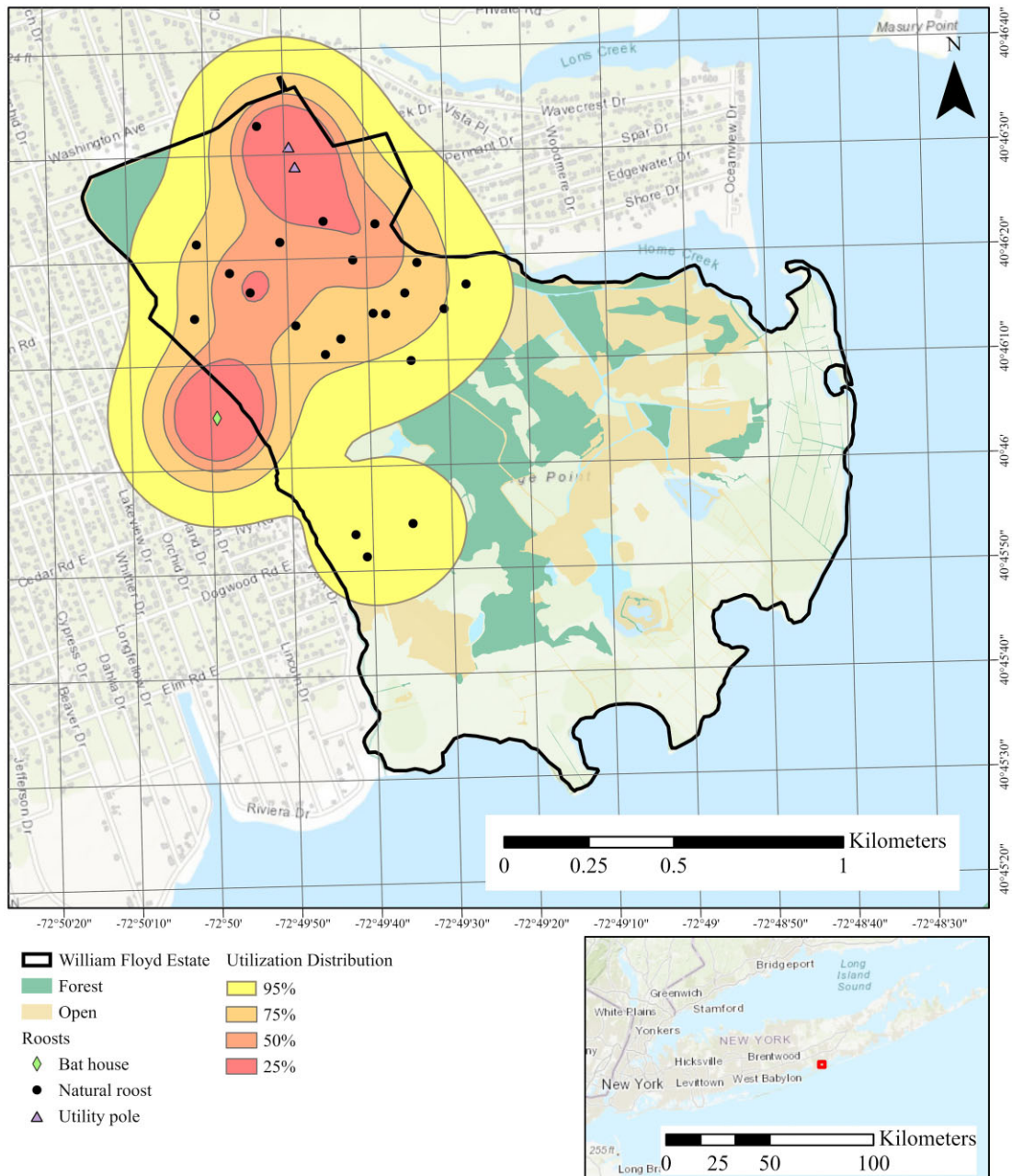
Figure 1: Utilization distribution for northern long-eared bat (*Myotis septentrionalis*) maternity colony at the William Floyd Estate, New York (2018–9). Contour lines show 25%, 50%, 75%, and 95% utilization distributions. Utility poles and the bat house are shown as triangles and a diamond, respectively. Natural (tree) roosts are shown as points. Map created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

northern long-eared bats and one juvenile male weighing 6.2 g (Silvis et al. 2014a; Gorman et al. 2022b), ensuring that transmitters did not exceed >5% of the bat's body mass (Aldridge and Brigham 1988). We tracked radio-tagged bats to their day-roosts using TRX-1000S receivers and folding three-element Yagi antennas (Wildlife Materials Inc., Carbondale, IL, USA) for the life of the transmitter, until it fell off, or until the bat could no longer be located three days in a row in the Estate or within 1.5 km of the boundary. When a roost was located, we georeferenced it with handheld GPS units (Garmin International Inc., Olathe, KS, USA). To maximize our potential of catching and radio-tagging bats within the same colony, we erected mist-nets around the located roost when cavities or loose bark were at or below the height of our triple-high net poles (approximately 7 m). Aberrant day-roosts such as utility poles were not netted for safety reasons. If weather permitted, we performed nightly emergence counts on each roost (Foster and Kurta 1999) to assess colony size. All handling of bats followed protocols approved by the Institutional Animal Care and Use Committee of the Virginia Polytechnic Institute and State University Protocol No. 19-227, and field work was conducted under the authority of permits issued by the New York Department of Environmental Conservation, National Park Service, and the U.S. Fish and Wildlife Service.

Network analysis

We calculated distance between subsequently used roosts using the *sp* and *adehabitatHR* packages (Pebesma and Bivand 2005; Calenge 2006) in R (version 4.0.3; R Core Team 2021). We created a utilization distribution using a fixed kernel method to approximate space use by the colony. To generate a more realistic representation of the space use area relative to the intensity and concentration of roost use, we weighted each roost location by the number of days the roost was used and added anonymous bats to reflect the emergence count numbers on those days (Popa-Lisseanu et al. 2008; Silvis et al. 2014b). We used base Program R to calculate summary statistics for day-roosts: mean number of tracking days per bat, mean number of roosts used by each bat, mean relocations, individual bat roost switching frequency, and the number of times each roost was used throughout the tracking periods.

To characterize colony structure at the individual and community levels despite our disparate tracking periods, we used the *igraph* (Csardi and Nepusz 2006) and *tnet* (Opsahl 2009) packages. We then projected the two-mode network (bat to roost) into two one-mode networks (bat to bat and roost to roost). To describe network coherence, we calculated the mean degree, the degree centralization index, and the betweenness centrality index. Degree describes the distance between the nodes based on the number of other nodes with which they are in direct contact by dividing the network into 'neighborhoods' rather than considering the network as one unit (Oliveira and Gama 2012). Degree is a measure of connectivity and centrality (Freeman 1978; Dong and Horvath 2007), and a high degree value indicates that many individuals have a large number of connections (Newman and Park 2003). The degree centralization index and betweenness index are methods that use the node-level centrality scores to measure the difference between the node(s) with the most connections (degree) and the number of nodes that fall between two others (betweenness) against the centrality scores of rest of the group; these indexes range in value from 0 (low) to 1 (high; Freeman 1978). We used the UCINET software (Borgatti, Everett, and Freeman 2002) to explore the same network measures exclusive of betweenness and to create visualizations. We assessed the structures of the networks by calculating network densities and clustering for the entire two-mode network. Density compares the number of connected nodes (in this case, either bats or roosts) to the number of possible connections within the network (Scott et al. 2005). Higher density values for the bat network would mean more direct interaction, and perhaps stronger relationships, between individuals, whereas higher density values for the roost network would indicate the *potential* for direct interaction if the bats were to inhabit the nodes at the same time (Scott et al. 2005; Donati, Zappalà, and González-Romá 2016). The clustering coefficient measures how densely-packed or 'cliquish' the connections and nodes are and the extent whereby individual bats are known to one another (Scott et al. 2005; Dong and Horvath 2007; Opsahl and Panzarasa 2009; Opsahl 2013). We calculated clustering as a scaled 0 (low) to 1 (high) value following Silvis et al. (2014b).

Results

Over both summers, we captured 20 individual northern long-eared bats ($n = 16$ total captures in 2018 and $n = 6$ total captures in 2019, including two recaptures from 2018; Table 1) over the course of 56 netting nights ($n = 17$ in 2018 and $n = 39$ in 2019). In

Table 1: Dates and sites of northern long-eared (*Myotis septentrionalis*) captures at the William Floyd Estate, New York (2018–9)

Bat	Capture date(s)	Capture site
72400	18 May 2018	WIFLTR08
	13 Jun 2018	WIFLTR08
72401	18 May 2018	West Gate
	12 Jun 2018	WIFLTR04
	13 Jun 2018	West Gate
72402	20 May 2018	West Gate
	13 Jun 2018	WIFLTR4
72403	20 May 2018	West Gate
	13 Jun 2018	WIFLTR04
72405	21 May 2018	West Gate
72406	13 Jun 2018	WIFLTR04
	16 Jun 2018	WIFLTR08
	22 Jun 2019	West Gate
72407	13 Jun 2018	WIFLTR04
72408	13 Jun 2018	WIFLTR04
72409	13 Jun 2018	WIFLTR04
72410	13 Jun 2018	WIFLTR04
72411	13 Jun 2018	WIFLTR04
	24 Jun 2019	Visitor parking lot
72412	13 Jun 2018	WIFLTR04
72413	16 Jun 2018	WIFLTR08
72414[a]	19 May 2019	West Gate
72418[a]	29 Jul 2019	West Gate
RRR034	29 Jun 2015	Unknown capture location
	16 Jun 2018	Red and yellow trail intersection

[a]Bats 72414 and 72418 were presumably part of the colony but we did not have direct evidence of this connection for this study. As a result, they were not included in the network analysis.
WIFLTR04 (bat house) and WIFLTR08 (black locust [*Robinia pseudoacacia*]) were roosts that were netted. West Gate and visitor parking lot were net sites over paved roads. Red and yellow trail intersection was a net site at a four-way dirt trail intersection.

2018, one captured adult female had been banded during earlier monitoring efforts from 2015 and two bats escaped before transmitters could be affixed. Captures were higher in 2018 because we were able to net the bat house rather than relying solely on mist-netting. In 2019, two adult females from 2018 were recaptured as was a new female, a juvenile male and a juvenile female, and one adult male that was not tracked. Of the juveniles, only the male was large enough to receive a transmitter. From the 16 individuals with transmitters (12 females in 2018 only, two females in 2018 and 2019, one female in 2019 only, and one juvenile male in 2019 only) we documented 30 unique day-roosts—one of which was a utility pole used in both years. Three of the recorded day-roosts were anthropogenic structures (one bat house and two utility poles; Fig. 2), the remaining were live trees or snags of eight species or snags unidentifiable to species (Gorman et al. 2022a). All day-roosts we located were within the Estate boundary, except for the bat house that was located at a private residence approximately 80 m west of the Estate boundary. Twenty-one (ca. 70%) of these day-roosts were snags or declining live trees (Gorman et al. 2022a), six trees were alive, and the three anthropogenic roosts were not assigned a decay stage. Twenty-two emergence counts accounted for 1–11 exiting bats per roost on any given night.

Our one-mode network visualizations initially revealed that two bats were not connected to the larger network (the juvenile male and one adult female from 2019), so the only tracked bats from 2019 retained in the network analysis were the recaptures

Figure 2: [Left] Nursery box used by northern long-eared bat (*Myotis septentrionalis*) maternity colony just outside the William Floyd Estate, New York (2018). [Right] Utility pole used by northern long-eared bat maternity colony within the William Floyd Estate, New York (2018–9).
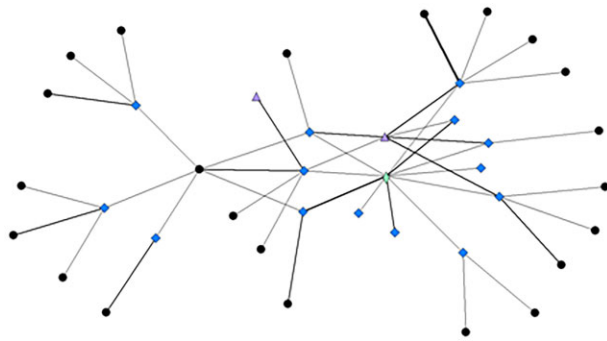

Figure 3: Scale-free two-mode network visualization for northern long-eared bat (*Myotis septentrionalis*) maternity colony at the William Floyd Estate, New York (2018–9). The narrow diamond node represents the bat house, triangle nodes represent utility poles, circle nodes are natural roosts (tree or snag), and larger diamonds are bats. Line weights represent the strength of the connection: the number of days the bat used that roost.

from 2018. Our final network for the analysis consisted therefore of 14 bats, 25 roosts, and 45 connections between bats and roosts (Fig. 3). The mean distance traveled between roosts was 228.3 m (SD ± 307 m, range 0–1233.09; Table 2) for all tracked bats; for bats restricted to the connected network, the mean distance travelled between roosts was 238.4 m (SD ± 311.6 m, range 0–1233.09). The utilization distribution displayed two noticeable core areas that were centered around the bat house and utility poles used as roosts for multiple bats over multiple days and an estimated 95% utilization distribution of 135.09 ha (Fig. 1).

On average, bats were tracked for 4.4 days each year (SD ± 2.3, range 1–10; for bats that were tracked both years, each year was treated as a separate tracking event in the calculations), regardless of whether they were connected to the colony. Over both years, bats in the connected network used a mean of 3.1 day-roosts (SD ± 1.6, range 1–6), had 2.6 (SD ± 1.2, range 1–5) relocations, and displayed a roost-switching frequency of 1.5 days (SD ± 0.5). Each roost was used, on average, 2.6 (SD ± 3.7, range 1–17) times. Mean degree of the bat network was 9.57, and the degree centralization index was 0.31 (no individual bats

were driving the connectivity). The betweenness index was 0.87 (many bats are connected through other bats), and density was 0.74 (signaling the potential of strong dyadic relationships, which is characteristic of northern long-eared bats, as opposed to larger subgroups; Friedkin 1981). The roost network mean degree was 4.88. The centralization and betweenness indices were 0.55 and 0.47, respectively (individual roosts were more important than individual bats to connectivity), and the network density was 0.20 (see Fig. 4 for one-mode network visualizations). Clustering over the entire network was 0.12 (low frequency of distinct cliques).

Discussion

Our study is among the first to describe multiyear roost and social network patterns of a northern long-eared bat maternity colony in a small, urbanized forest fragment following regional, WNS-related population declines (Sasse and Pekins 1996; Foster and Kurta 1999; Garroway and Broders 2008; Patriquin et al. 2010; Silvis et al. 2014a; Ford et al. 2016; Hyzy et al. 2020). We confirmed ongoing study site—and further, roost-specific—philopatry with recaptures of banded bats across years, similar to other northern long-eared bat maternity studies (Patriquin et al. 2010; Perry 2011; Olivera-Hyde et al. 2019). This continued pattern suggests that at least through 2019, despite disruptions to the overall population, northern long-eared bats were continuing to form colonies in their natal area *or* persisting northern long-eared bat females were joining existing colonies to cope with their own colonies' collapses as posited by Kalen et al. (2022).

Based on the total number of unique adult females we tracked over the two years, our minimum colony size (not including juveniles) was 15 bats. It is unlikely we were able to capture every bat in the colony, but our low emergence count numbers indicate a high likelihood that we captured most of the colony members. In large contiguous forest settings, prior to the advent of WNS, northern long-eared bat maternity colony research observed >80 bats in roosts (Owen et al. 2002). The colony at the Estate is considerably smaller, though colony sizes

Table 2: Number of days tracked (across both years), number of roosts used, and minimum, mean, and maximum distance (m) travelled between roosts used on subsequent days for northern long-eared bats (*Myotis septentrionalis*) at the William Floyd Estate, New York (2018–9)

Bat	Tracking days	Number of roosts	Minimum distance (m)	Mean distance (m)	Maximum distance (m)
72400	3	2	212.9	212.9	212.9
72401	3	3	98.04	420.09	742.95
72402	7	3	0	120.5	550.6
72403	1	1	–	–	–
72405	4	2	0	276.5	829.5
72406	8	6	0	318.29	829.48
72407	7	5	0	384.48	1233.09
72408	6	4	0	265.29	829.48
72409	5	3	0	345.4	829.5
72410	2	1	–	–	–
72411	14	6	0	128.3	829.5
72412	1	1	–	–	–
72413	5	4	0	272.52	650.08
72414[a]	4	2	0	221	663
72418[a]	4	3	0	43.89	81.06
RRR034	5	4	0	192.5	299.7

[a]Bats 72414 and 72418 were presumably part of the colony but we did not have direct evidence of this connection for this study. As a result, they were not included in the network analysis.
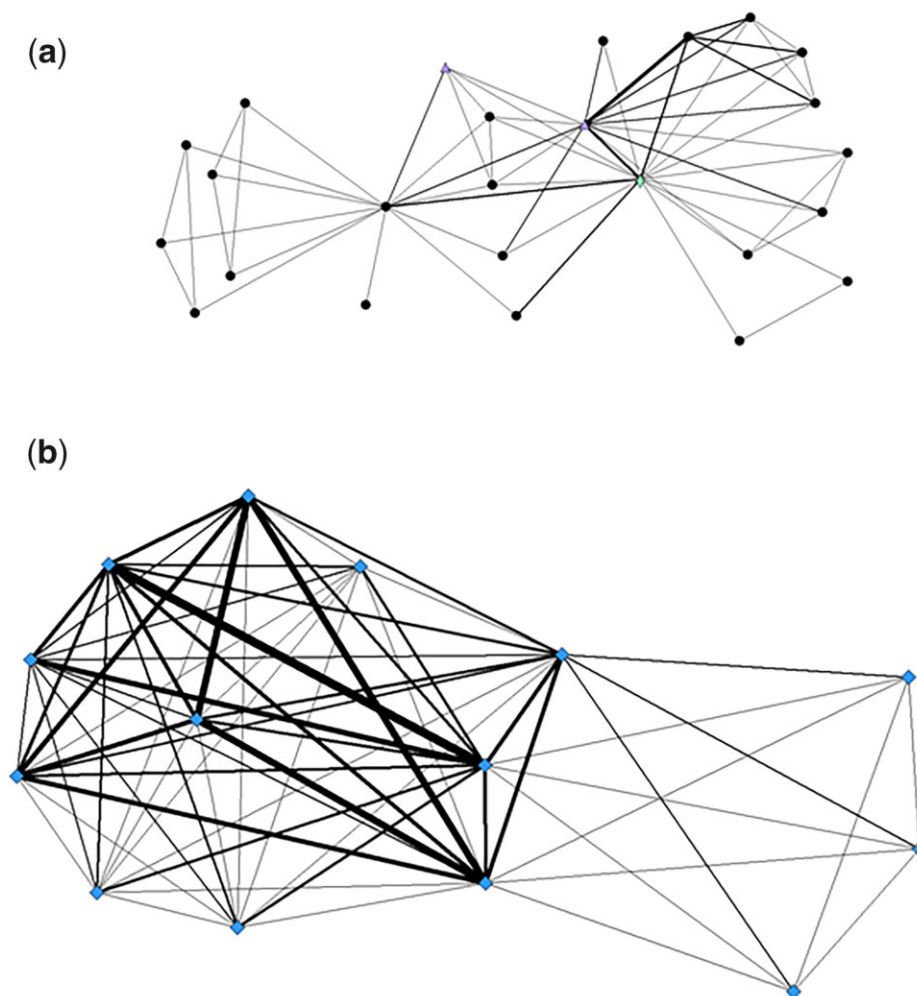

Figure 4: [Top] Roost network visualization for northern long-eared bat (*Myotis septentrionalis*) maternity colony at the William Floyd Estate, New York (2018–9). The narrow diamond node represents the bat house and the triangle nodes represent utility poles. One utility pole was used by bats both years. [Bottom] Bat social network visualization for northern long-eared bat maternity colony. Line weights represent the strength of the connection: the number of time bats went from one roost to the other, and the number of days the bats were in the same roost.

for northern long-eared bats in urban and suburban landscapes prior to WNS are unknown and we do not know when this colony was established (nor its historical social patterns or spatial footprint).

Despite being a small colony, bats in our study used a similar number of roosts throughout their tracking periods as with other studies (between 2.2 and 3.6 roosts per bat, with a maximum of 5–7; Sasse and Pekins 1996; Foster and Kurta 1999; Silvis et al. 2014a; Hyzy et al. 2020), suggesting that they are maintaining similar roost-switching patterns to pre-WNS and in other landscape and habitat types. The bats in this study, much like other study results, tended to switch roosts between every 1–2 days with little variation (Foster and Kurta 1999; Garroway and Broders 2007; Patriquin et al. 2010; Silvis et al. 2014a; Hyzy et al. 2020). Further, the distance the bats in this study travelled between subsequent roosts also was fairly consistent with the findings of others (333 m ± SD 88 m and 227 m ± SD 161 m; Foster and Kurta 1999; Henderson and Broders 2008, respectively), despite our study area being a spatially-constrained forest patch in the middle of suburbia. Similar to Henderson & Broders (2008), when bats were tracked to roosts outside of forested areas, we observed all were <80 m from the forest edge—well below their recorded average nightly movement between roosts.

In our previous work, a minimum convex polygon encompassing the roost area of this colony was 88.4 ha (Gorman et al. 2022a). Our utilization distribution highlighted that this colony made greater use of the forested edges of the Estate than the central forested portions of the Estate, indicating there were more suitable roost options along the edges of the property, i.e. snags or poor form trees with cavities and higher solar exposure (Burrell and Bergeson 2022; Gorman et al. 2022a). The middle of the Estate is comprised of grassy meadow that quickly transitions to a woody marsh in the southern portion of the property, which in theory would also provide many trees or snags with high solar exposure. However, these are salt marshes and forested areas which border the ocean; the lack of freshwater and higher wind exposure is presumably inferior quality habitat for northern long-eared bats. This leads us to question whether this colony is being forced into a concentrated, marginally more tolerable forest patch along the edges of the property due to lack of comparatively suitable, surrounding habitat throughout the rest of the Estate as well as surrounding neighborhoods. Although we do not know with certainty that these colony members were always staying within the Estate to day-roost, we have no evidence to suggest that they would be traversing through suburbia to other nearby forest patches based on concurrent bat capture and monitoring at Wertheim National Wildlife Refuge, 3 to 6 km away.

The locations of the primary roosts at the extreme north and west edges of the Estate boundaries (bordering neighborhoods) may point to a capacity to inhabit areas of high human-development rarely noted for this species in the past. This is contrary to Thorne et al.'s (2021) findings for an urban colony of northern long-eared bats in Toronto, Ontario, Canada, which exclusively used interior forest and natural roosts, but similar to the findings of Burrell and Bergeson (2022) in an exurban nature preserve in Indiana. One explanation for the unusual behavior in this study and that of Burrell and Bergeson (2022) is that the bats in these studies were adapting to habitat variation and/or resources that we did not measure, and that there are other underlying mechanisms influencing the roost selection and spatial extent resulting in more edge use.

Because of the small forest patch size of the Estate, our high mean degree values showed little distance between individual bats and roosts in this network. In other words, roosts that were not primary nodes were still being used by multiple bats, and there were frequent returns to communal roosts. Many connections emanating from the nodes indicate there was considerable movement within this colony, implying that different roosts were fulfilling the temporally changing needs of individuals. These needs may be thermoregulatory (driven by reproductive state or weather), related to foraging, or general communication between colony members. It is possible that our finding could be skewed by short tracking periods and the high number of captures at a primary roost, though the high number of captures at the bat house and dispersal thereafter serves as confirmation that the majority (or all) of the colony displayed this type of movement pattern. The higher degree centralization index for the roost network showed that the primary nodes (the bat house and one of the utility poles) were integral to driving the connectivity of the network. The degree centralization indices for bats within the network have varied by colony in other studies (range 0.19–0.99; Silvis et al. 2014a; Hyzy et al. 2020). Our results fall on the low end, indicating that all the bats in this colony were equally connected to one another and no specific individuals were driving the connectivity of the network. If individual bats from this colony were to enter hibernation and succumb to WNS (or another mortality event over the course of the year), the colony would likely not experience dissolution. The high betweenness ranking for the bat network reveals that bats had many connections *through* other bats, whereas the low betweenness ranking for the roost network means roosts were often *directly* connected to one another through few bats rather than being *indirectly* connected (e.g. hypothetical roosts A, B, and C are all connected to one another through single bats, rather than nodes A and C being connected *through* bats that also roost in B). Again, this indicates that even if bats were to lose the intermediary bat they would likely form new connections via shared roosts and perhaps slight adjustments in the timing of inhabiting the communal roosts so that they overlap with more colony members. We speculate that the juvenile male and adult female that were not connected to the larger network were likely part of the same colony considering the small and isolated area of the Estate. As such, if given longer tracking times (or earlier capture), we believe these two bats could have been connected to the larger group. Ultimately, these two bats were left out of the network analysis because we had no definitive proof of their inclusion in the colony, though based on our netting effort, we doubt there was another maternity colony on or near the Estate. Furthermore, colony fidelity among northern long-eared bats has been shown to be relatively high during summer maternity season (Johnson et al. 2015; Olivera-Hyde et al. 2019), and while immigration between colonies living in proximity does occur, the low degree of centralization indicates having one colony on the Estate.

The low clustering value, in comparison to other studies (range 0.57–0.86; Garroway and Broders 2007; Patriquin et al. 2010; Silvis et al. 2014a), reinforces the low degree centralization and high betweenness results, as it demonstrates a lack of preferential groups within the context of the whole study. In short, many individual bats are connected to many other individual bats through a larger number of shared roosts, rather than *only* being connected through the utility pole and bat house roosts that we considered primary roosts. Our bat network density was higher than typically reported in other studies (range 0.11–0.67; Silvis et al. 2014a; Hyzy et al. 2020), and our roost network

density was in the range of other findings. Although our short tracking periods could be contributory to this finding, it more likely reflects the concentration of comparatively better habitat of the Estate versus the surrounding suburban areas (Ford et al. 2016; Hyzy et al. 2020).

Taken together, all the network structural measurements we calculated point to a highly organized social network in which connections between bats and roosts are evenly distributed. The small forest patch size of this study may be functioning to elucidate patterns of connectivity between bats that is more difficult to ascertain in areas with more resources. Although some bats may have closer relationships with one another, as indicated by roosting patterns, they remain highly social with the entire colony. This mirrors the two-level society concept provided by Garroway & Broders (2007), whereby bats are categorized as 'constant companions' or 'casual acquaintances'. Given a longer tracking period throughout the maternity season, we might have seen these measurements change to reflect weaker relationships between cliques (the 'casual acquaintances' dissipating whereas the 'constant companions' remain as close associates) as colony disassociation begins at the end of the maternity season (Garroway and Broders 2007; Johnson, Ford, and Edwards 2012; Hyzy et al. 2020).

More important than any individual bat, the primary roosts (the bat house and one of the utility poles) were the critical loci of this colony during the period we tracked bats. Aside from meeting thermoregulatory needs during pregnancy, this could indicate that social rearing of offspring is especially valuable to this colony (Kerth 2008a; Johnson, Ford, and Edwards 2012), even outside the most-energetically costly period of lactation (Garroway and Broders 2007). However, as both of the primary nodes within the network were anthropogenic structures (not live trees or snags), we believe this could be an indication that the Estate mostly provides suitable foraging habitat for the colony and that roosting needs are not being sufficiently met by the current forest condition (Lewis et al. 2022). Disease and parasite transmission potentially could be higher in this type of network because of the tendency for several bats to congregate in the same place on the same days (Kerth 2008a; Johnson, Ford, and Edwards 2012; Ford et al. 2016). It is worth noting that all of the anthropogenic structures used by this colony were more analogous to trees than other humanmade roosts (attics, barns, bridges and cellars) used by other species within the same genus (Barclay 1982; Benedict, Benedict, and Howell 2017; Etchison and Weber 2020; Lewis et al. 2022), although roosting in those types of structures occasionally has been noted for northern long-eared bats (Henderson and Broders 2008; Geluso et al. 2018; Hoff et al., In review).

Ford et al. (2016) and Johnson, Ford, and Edwards (2012) noted that roost loss due to fire disturbance resulted in structurally different trees replacing the primary colonial roosts, adding that northern long-eared bats show adaptability (or tolerance) to sudden landscape alterations (provided the resulting forest retained heterogeneity). Additionally, these two studies as well as that of Silvis et al. (2014a) found that disruption to roost networks either strengthened bonds within maternity colonies or had minimal impacts on colonies with already-strong social bonds. Unlike our study, these efforts occurred in very large, forested landscapes with a great range in forest condition and a high number of potential day-roosts adjacent to disturbed patches, meaning it may not be entirely applicable to a study area such as the Estate.

With no known colonies nearby and several shared roosts, it is possible that a stochastic or intentional removal event of secondary roosts would not necessarily be overly deleterious if primary roosts remained (Rhodes et al. 2006), given the colony's overall social coherence. However, primary roost loss due to stochastic weather events or human intervention could be disruptive to the entire social structure of this colony. For a big brown bat (*Eptesicus fuscus*) maternity colony, Brigham (1991) found that reproductive success was negatively impacted when the bats lost access to a primary roost. In a small colony such as the one we tracked, reproductive failure could lead to a swift colony collapse as new colony members are generally the offspring of current or previous members (Olivera-Hyde et al. 2019). In this case, and in this particular setting, installation of additional artificial roost structures or forest management actions that would add additional roosts or improve current roost conditions could be a warranted conservation action (Johnson et al. 2010; De La Cruz, Ward, and Schroder 2018; Schroder and Ward 2022). As climate change continues, the risk of extreme weather events such as hurricanes or winter nor'-easters are threats that are unique to these coastal environments. Additionally, as urbanization expands, wildlife habitat can become more fragmented and wildlife contact with humans can increase. In the case of northern long-eared bats, this could result in an increased use of anthropogenic structures such as attics or cellars.

Our work demonstrates that even small patches of forest in areas surrounded by high human development can support reproductively successful maternity colonies of northern long-eared bats in the post-WNS environment. Like other studies, bats in this colony often segregated with one or two other bats that were presumably preferred over other colony members, but at the Estate no individual or subgroups of bats were necessarily driving the connectivity of the network more than others. Rather, the roosts as communal meeting areas or shared spaces were integral to the cohesion of the colony. In that case, the survival of this colony, and presumably others in similar urbanized settings (Deeley, Freeze, and Rohrbaugh 2021), could be precarious due to less alternative roost availability. There is evidence that focal points of similar networks of Indiana bats (*M. sodalis*) may shift across the landscape over time or in response to roost loss (Silvis et al. 2014b); such a shift would not be possible for the bats of this colony unless they left the Estate entirely. Although this colony may exhibit increased tolerance for fragmented or human-disturbed habitat, there may be an upper limit to how far the colony would or could move as a collective unit to reach other areas with sufficient roost options. Northern long-eared bats, over decadal periods, rely on a shifting mosaic of suitable forest conditions (Silvis et al. 2012); therefore, as forest succession and stand dynamics processes continue over time, a smaller forest patch such as the Estate may not provide enough structural heterogeneity suiting a bare minimum of northern long-eared bat needs (Oliver and Larson 1996). Accordingly, perpetuation of day-roost habitat in urbanized landscapes could require more management intervention such as placement of artificial roost structures or snag creation than in large, forested landscapes to retain local northern long-eared bat viability.

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Author contributions

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