Spatial environment drives land-based social associations in a central-place foraging seabird

Antoine Morel[1], Eric Vander Wal[2], Pierre-Paul Bitton[1,*]

[1] Department of Psychology, Cognitive and Behavioural Ecology, Memorial University of Newfoundland, St. John’s, NL, Canada

[2]Department of Biology, Cognitive and Behavioural Ecology, Memorial University of Newfoundland, St. John’s, NL, Canada

*Corresponding author: pbitton@mun.ca, Department of Psychology, Cognitive and Behavioural Ecology, Memorial University of Newfoundland and Labrador, 232 Elizabeth Avenue, St. John’s, NL, A1B 3X9, Canada

Abstract

1. Social and spatial environments shape the way individuals associate and thus impact their social network structure. However, nowhere are social and spatial mechanisms more likely to be simultaneously entangled and potentially misinterpreted than in central-place foragers.
2. We interrogated the spatial-social interface for a central-place forager in their colony. To do so we tested how the distance between individuals in a colony affected (i) their probability of association, (ii) their community structure, and (iii) and dyadic weight.
3. We used the Atlantic puffin (*Fratercula* arctica), a central-place forager that has limited movements on land, to determine the contribution of the social and spatial environments to the social network structure. We colour-banded 124 individuals, geo-localised their burrows and tracked their associations at the colony using focal observations during the breeding season.
4. We found that the spatial environment strongly influenced the social network structure of the Atlantic puffin. Individuals formed communities and associated significantly more than expected by chance with their close nesting neighbours, suggesting that the presence/absence of neighbours determined the association patterns. Additionally, we found evidence that distant associations with conspecifics were not all random, suggesting that individuals may seek each other out, if it provides mutual benefits, or have similar spatial and temporal requirements.
5. Our study demonstrates the importance of considering social and spatial environments in unison in studying social network structures and provides new evidence for the influence of these mechanisms on central-place foragers.

Keywords: Atlantic puffin, behavioural ecology, central-place forager, familiarity, social environment, social network, spatial environment.

Introduction

Social connections and the networks from which they emerge are often implicated as important to many populations and ecological processes (Snyder-Mackler et al., 2020). However, social networks, which intend to quantify sociality, by definition occur in some fixed geographic space; spaces that can themselves be linked to behavioural processes that affect animal fitness (Vander Wal et al., 2015). Thus, it is often unclear whether spatial or social mechanisms give rise to social network structure (Albery et al., 2021; Webber et al., 2023). We evaluated the contribution of spatial and social environments to the social network characteristics of a central-place forager, the Atlantic puffin (*Fratercula arctica*).

Environmental conditions (e.g., climate, resource distribution) and geography (e.g., distribution range, distance between territories) form the spatial environment that can affect social structures (Pinter-Wollman et al., 2014; He et al., 2019; Webber et al., 2023). The variability and the dynamic nature of the spatial arrangement of biotic and abiotic components such as habitat patches (Pinter-Wollman et al., 2014) induce uneven resource distribution (He et al., 2019) and directly affect individual uses of space (Newsome et al., 2013), potentially leading to cyclical and seasonal social patterns (Rabosky et al., 2012; Brent et al., 2013; Wolf et al., 2018). Caribou (*Rangifer tarandus*), for example, is a free-ranging species that has high interannual site fidelity in summer, when food resources are homogeneously distributed, and low in winter, when they rely on conspecific cues to access forage. The seasonal difference in activities leads to changes in social network structure, with a higher number of associations per individual during the winter (Peignier et al., 2019). Additionally, physical barriers generated by the spatial configuration of elements such as rivers and mountains (natural habitat) and roads and cities (anthropogenic structures) are likely to affect movement decisions that generate social opportunities (Strandburg-Peshkin et al., 2017; He et al., 2019).

Species that are strongly constrained in their use of the landscape, like central-place foragers, are potentially even more affected in their social structures by environmental conditions and geography than free-ranging species. For instance, central-place foragers are often constrained to spend much time at a specific location (e.g., nest, burrow, den). Seabirds, for example, are central-place foragers that nest at very high density (e.g., 1.37 burrows/m^2 in Atlantic puffin *Fratercula arctica*; Belenguer, 2023) and often travel great distances away from the colony to find food (e.g., 1086 km, for a four- to six-day trip for Leach's storm-petrels *Hydrobates leucorhous*; Pollet et al., 2014). Seabirds often use dual foraging strategies. The first covers long distances for self-maintenance. The second strategy adopts short trips for brood feeding (Welcker et al., 2009; Tyson et al., 2017). Between foraging trips, parents attend the colony. When at their nest, individuals can associate with near conspecifics nesting in proximity or move about the landscape to contact non-neighbours. However, it is unclear how the use of space by central-place foragers influences their social networks.

Elements upon which social networks are constructed, such as the frequency of association with specific individuals, are also influenced by the social environment. Specifically, group composition, size, density (Webber et al., 2023) and familiarity with specific individuals (Gokcekus et al., 2021) can influence social dynamics. Our understanding of the social environment can help predict behavioural mechanisms such as local enhancement (i.e., individuals attracting others to a foraging location; Buckley, 1997; Veit & Harrison, 2017), information exchange (Richner & Heeb, 1995), and risk dilution (Pulliam, 1973; Lehtonen & Jaatinen, 2016). Social environments also affect ecological processes, like migration (Young & Van Aarde, 2010), survival (Milner et al., 1999; Descamps et al., 2008) and reproduction (McKellar et al., 2014; Niemelä et al., 2021). Group composition is generally influenced by population structure (e.g., age, sex, hierarchy), and can lead to preferred associations (Almeling et al., 2016; Borgeaud et al., 2017). Social behavioural patterns can be observed among individuals of the same or different sex, especially during the breeding season (Fernandez et al., 2017), or between individuals of the same age (Franks et al., 2020), directly affecting learning or foraging activities. Large group sizes and greater population density offer more opportunities for social interactions than small scarce groups. Social connections can be greater in high density because individuals are not limited by their spatial environment in encountering conspecifics. Free-ranging male elk (*Cervus canadensis*) for example, associate more at higher density, suggesting the number of potential encounters increases in response to higher density (O'Brien et al., 2018; Webber & Vander Wal, 2020). However, the relationship between density and sociality may not be linear (e.g. female elk sociality peaks at intermediate density), suggesting that social benefit can reach a threshold (Cross et al., 2013). This emerging competition for resources can induce movement (Young & Van Aarde, 2010) and mechanically reduce connectivity in the network (Dubois, 2024). For example, the social plasticity in yellow-bellied marmots (*Marmota flaviventris*) decreases as group size increases, suggesting that the availability of conspecifics may be greater than the individual capacity to interact (Maldonado-Chaparro et al., 2015).

Familiarity with conspecifics, because it concerns repetitive interactions with the same individuals, directly affects patterns of association. Higher social connectivity with familiar individuals can be explained by the benefits gained in building a social network with long-lasting bonds (Griffiths & Magurran, 1999; Atton et al., 2014), particularly when moving to a new environment (Gomes et al., 2022; Baciadonna et al., 2024). However, familiarity can be complex to disentangle from matching temporal and spatial needs. For example, Australasian gannets (*Morus serrator*) mainly associate with individuals showing similar temporal and spatial patterns, but it is unclear if familiarity or matching needs are responsible for these groupings (Jones et al., 2020). In the case of central-place forager seabirds, individuals rely on socially collected information to optimize foraging. Often, individuals leading fishing parties are more experienced (Wakefield et al., 2019) and perform recruitment behaviour (e.g., call; Evans, 1982) giving them a central position in the network. While high-density nesting should constrain central-place foragers to mainly associate with near neighbours, it is unknown if species living in high-density colonies associate more often with specific individuals either because of familiarity or matching temporal and spatial needs.

We interrogate the spatial-social interface for a central-place foraging seabird, the Atlantic puffin, to disentangle the contribution of geography and social environment to social network structure. Because Atlantic puffins breed in close contact in a fixed geographic place and have limited terrestrial movements, we hypothesized that their land-based social network structure will be strongly limited by nesting distance. Therefore, we tested the influence of the distance between burrows on (i) the probability of association, (ii) cluster formation, and (iii) dyadic weight. However, Atlantic puffins have high breeding philopatry, a long lifespan, and nest in high density, leading to familiarity between individuals. Because familiar individuals associate more often, we hypothesized that individual preference should equally affect social network structure. Therefore, we tested if certain associations were more common than expected by chance after controlling for their spatial distribution.

Materials and methods

Study species and site

The Atlantic puffin is a monogamous colonial seabird with a maximum observed lifespan of over 33 years in the wild (Bird Banding Laboratory, 2023). Genomic analyses have revealed four distinct genetic clusters: The western Atlantic region, Norway and Iceland, the United Kingdom, and Spitsberg (Kersten et al., 2021). Those clusters can be explained by high natal philopatry and great distances between the main breeding areas. Puffins generally return to the same burrow every year to lay a single egg (Harris & Wanless, 2011). They form large breeding colonies with a broad range of burrow densities (e.g., 0.5 burrows/m² in St Kilda island Scotland, Harris, 1980; 0.6 burrows/m² in the Røst archipelago Norway, Anker-Nilssen & Røstad, 1993; 0.85 burrows/m² on Bakeapple Island and 1.37 burrows/m² on Gull Island Canada, Belenguer, 2023). Occupancy generally ranges from 75 % to 95 % but can drop to 65

% during poor breeding conditions (Harris & Wanless, 2011). Because of their high breeding philopatry, together with a long lifespan and high colony density, puffins would be expected to have good knowledge of their local environment and neighbouring conspecifics.

The data were collected on Great Island, located in the Witless Bay Ecological Reserve of Newfoundland and Labrador, Canada (47.1855N, 52.8121W). It is the only regularly surveyed population that is increasing: an estimated 350,000 Atlantic puffins bred in 2015 (Wilhelm et al., 2015) and 410,000 in 2023 (Wilhelm, unpublished data). Recent surveys found an average of 1.57 burrows/m^2 with 64.7 % laying success (Belenguer, 2023). We selected a plot of approximately 168 square metres (14 m X 12 m) with an estimated maximum of 170 active burrows (Wilhelm et al., 2015; Belenguer, 2023) that 1) minimised bird disturbance (e.g., for access and observation) and 2) minimised operational risks (e.g., avoiding cliffs and dangerous paths), but 3) maximised colony representation. We built a wooden semi-permanent blind as early as weather conditions would allow us, generally before puffins returned from their wintering grounds. The blind was set on a flat area at the foot of the slope with a direct view of the study population (Figure S1). At all times, birds exhibited normal behaviour and did not show signs of disturbance caused by the presence of the observation station or the researchers.

Field methods

To collect information about puffin social associations, we colour-banded 124 individuals over two years (50 in 2021, 74 in 2022). Atlantic puffins are prone to nest abandonment (Yorio & Boersma, 1994; Rodway et al., 1996; Blackmer et al., 2004) so adults were captured only after the chick had hatched. We minimised disturbances and maximised the capture rate by working with trained banders at night when the birds were usually in their burrow. In some cases (~10-20 %) both adults were found in the burrow at the same time. When this occurred, we only captured a single individual and targeted the other member of the pair no earlier than 48 hours later. Individuals were captured in their burrows by hand grubbing before being carried to the banding station set a few metres away. Banders equipped each bird with a unique combination of coloured leg bands to enable individual identification in the field. The bands were composed of three Darvic plain colour bands custom-made from Avian ID (9.53 mm internal diameter X 7.93 mm height, Black, White, Green, Grey, Red, Yellow, Dark blue and Light blue), and a Canadian Wildlife Service stainless steel band with a unique identifier. The whole procedure took no more than seven minutes before we released the individuals in their original burrows.

We defined an association as any individual entering within a two-metre radius of another, even if they did not physically interact or display. To document those associations, we performed 85 hours of focal observations on the 124 potential colour-banded individuals, distributed among 34 sessions from July 20th to August 09th, 2022. We conducted the observations independently of the weather conditions three to five days in a row, followed by a few days of rest. Over the data collection period, three trained observers (including A.M.) were involved in the annotation of interactions from the blind (Figure S1). Each session was conducted by two observers equipped with binoculars (Swarovski EL 10x42 WB), performing focal observations including the areas peripheral to the limits of the plot. The morning sessions lasted four hours and started at civil twilight when the colour bands began to be visible. The evening sessions started four hours before sunset and extended until the visibility was too low to identify colour bands correctly. The observers waited until birds had left the plot, generally at the start of astronomical twilight, before leaving the blind. To ensure all birds had the same probability of observation we scanned the area from top to bottom and right to left when the slope was crowded, or targeted specific groups of individuals when only a few were visible. At the time of observation, the observers recorded any known individual part of an event using their colour bands. We identified each event using an incrementing unique ID and noted the time at which they occurred. We created a new event for each banded individual every two minutes or every time a new individual entered the two-metre radius of a focal banded individual. The observers paid attention to quickly resume screening after identifying the bands to guarantee no birds were missed. The observers were trained on the first days of data collection using flags and natural features to ensure the accuracy of the detection radius and band identification.

At the beginning of the season, we marked each occupied nest with a permanent plastic peg holding a plain steel tag with unique numbers. At the end of the season, when birds had left the island and disturbance was minimal, we measured the burrow position for 76 individuals (63 burrows) using a Trimble Geo-7X GPS with an accuracy of 10 cm. Atlantic puffins tend to return to the same burrow over the years but in the absence of nest locations for individuals only captured in 2021, we did not assume they had returned to the same nest and excluded them from the spatially referenced analyses.

Data extraction

Burrow distance

To evaluate the effect of the spatial environment on social networks, we calculated the distance between burrows using GPS coordinates while accounting for the slope of the landscape. The GPS coordinates of each burrow were extracted, processed, and exported using GPS Pathfinder Office v. 5.6, which post-processed positions from the Trimble Geo7X GPS. To account for the slope (40 degrees measured by compass) we applied a correction to get a better estimate of the real distance between burrows. Slope correction was calculated in two steps. Using the GPS positions of each burrow, we first created a distribution map under the WGS_1984_Canada_Atlas_LCC (ESRI 102215) projection in the QGIS software v.3.34.3 (QGIS Geographic Information System, 2024). We then viewed the map in ImageJ software v.1.54 (Abràmoff et al., 2004), from which we calculated the number of pixels for one metre before extracting X and Y coordinates for each burrow. We calculated the distance between all pairwise burrows using basic trigonometric functions.

Community detection

For all data management and analyses performed, we used RStudio statistical Software v.4.2.3 (R core Team, 2023). Each association was digitally incremented following an undirected edge-list format by keeping the date and time but discarding the direction of the association as these were not applicable. To detect communities from the observed associations, we used two methods: (i) the original version of the algorithm developed by Clauset et al. (2004), and (ii) the most recent community analysis algorithm from Blondel et al. (2008). Both methods generated qualitatively similar results (see data and script available in Supplementary material); we only present the Blondel et al. (2008) version. To test the robustness of the community partition, we used the modularity metric based on a Laplacian algorithm (Lambiotte et al., 2014). The modularity metric compares the density of edges inside and outside the communities and returns a cluster assignment between -1 and 1. The robustness of our partition had a value of modularity of 0.443, indicating robust communities. To visualise the communities extracted from the modularity metric, we used Gephi software v.0.10.1 (Bastian et al., 2009).

Analysis

Spatial environment and probability of association

First, we evaluated the influence of burrow distribution on whether or not individuals were observed associating, by calculating the pairwise distance between all burrows (potential dyads) and dividing the number of observed dyads by the number of potential dyads in 14 bins of one metre. For this analysis, we kept all associations even when they occurred only once, but we excluded mate pairs because it would overrepresent the number of associations at null distance (same burrow). To best describe the relationship between burrow distance and probability of association, we compared the fit of an exponential decay model and an asymptotic model by using a maximum likelihood test.

To assess whether distances between burrows affected the frequency of association, we tested the average association distance in the observed network against a null model. When the data are collected using a ‘gambit of the group’ paradigm, a pre-network permutation is recommended (Farine & Carter, 2022). However, our data came from focal observations of associations within a two-metre radius on 76 individuals, for which we had a burrow location (n = 63), therefore we performed a randomization test following the method by Farine (2017) (Figure S2). To generate our null distribution, we assigned at the individual level a random distance, from the population of all pairwise burrow distances, for each observed dyadic association. These distances were weighted by the frequency of the dyadic association, before calculating the average random distance. To avoid over-representing null distances that would occur from pairs, the list of distances excluded mated individuals. The randomisation was performed on 10,000 replicates. The observed average weighted distance value was compared with the random distribution, calculating the proportion of values that were smaller than the observed value.

Spatial environment and communities

Second, to evaluate the influence of burrow distribution on whether or not individuals associate we investigated the role of burrow distance on community creation. To visualise the spatial distribution of the community structure, we produced a distribution map of the burrows, coloured by cluster indices, using the WGS_1984_Canada_Atlas_LCC (ESRI 102215) projection in the QGIS software v.3.34.3 (QGIS Geographic Information System, 2024). To test the influence of the distance between burrows on community structure, we used a randomisation test. The null model was built by randomly distributing all potential individuals within community clusters before calculating the mean distance between burrows of connected individuals over 10,000 replicates. We compared the original observed average distance repartition per cluster with the one obtained by randomisation for both partitions using the proportion of values smaller than the observed value.

Spatial environment and dyadic weight

Lastly, we evaluated the influence of burrow distribution on associations by testing if dyadic weights were a function of distance between burrows. We compared the average observed values to null distributions generated through randomisations at the edge level (the sum of the number of associations occurring for each dyad represented in the network; see Supplementary Methods for detail). For each individual, we first identified which individuals they associated with and the number of times they associated (dyad weight). The randomization test shuffled the distance between their burrows in consideration of their respective weight. Because permutation tests cannot be performed on less than two data points, individuals with 0 and 1 dyadic associations were removed from the analysis. Pairs were also removed as their distance was null. The average theoretical distances were then calculated for each dyadic interaction and were compared with the average observed values.

Social environment and dyadic weight

Because spatial environment alone may not explain the social network, we investigated the role of social environment at the edge level. Specifically, we looked at whether an individual was associated more often with some conspecifics than others within a specific distance. For this, we used two contingency table tests to compare the theoretical versus observed frequency of associations for each individual and dyad forming members for two distance intervals: 0-2 m and 2-16 m. The observed values for each individual were the dyadic weight of all associations, plus values of zero for all individuals they did not associate with. The theoretical values were calculated as the probability of an association based on the number of times individuals were observed on the plot (see mock example in Supplementary Methods). This method accounts for the effect of a high number of non-associating individuals with a low predictive value of association. To estimate how well the observed values were predicted by the theoretical values, we used a Goodman-Kruskal test (Pearson, 2020), which returns an effect size between zero and one with values of one being perfect predictions.

Ethical Note

This study was performed on a protected Atlantic puffin colony within the Witless Bay Ecological Reserve. Animal ethics were covered by an Animal Use Permit (22-01-PB) issued by Memorial University of Newfoundland's Animal Care Committee. All research activities including trapping, banding and the construction of a non-permanent structure were allowed under a Province of Newfoundland and Labrador scientific research permit (wepr2021-23atpucolouration), a Banding permit (10926) and a Migratory Bird Research permit (SC4061) issued by Environment and Climate Change Canada.

Results

Out of the 124 individuals marked (37 % of the estimated individuals) between 2021 and 2022, we detected 112 over 85 hours of focal observations. At the end of the breeding season, we located the burrows of 87 individuals (n = 69 burrows) with a median value of burrow distance calculated at 6.50 metres (Q1 = 4.07, Q3 = 8.68 metres). Not all burrow locations were known because not all individuals banded in 2021 could be trapped in 2022 to confirm their nest site. The clustering partition was calculated using 76 individuals (n = 63 burrows) for which we had sufficient observations. From July 19th to August 10th, we recorded 677 dyads and 1,843 associations.

Spatial environment and associations

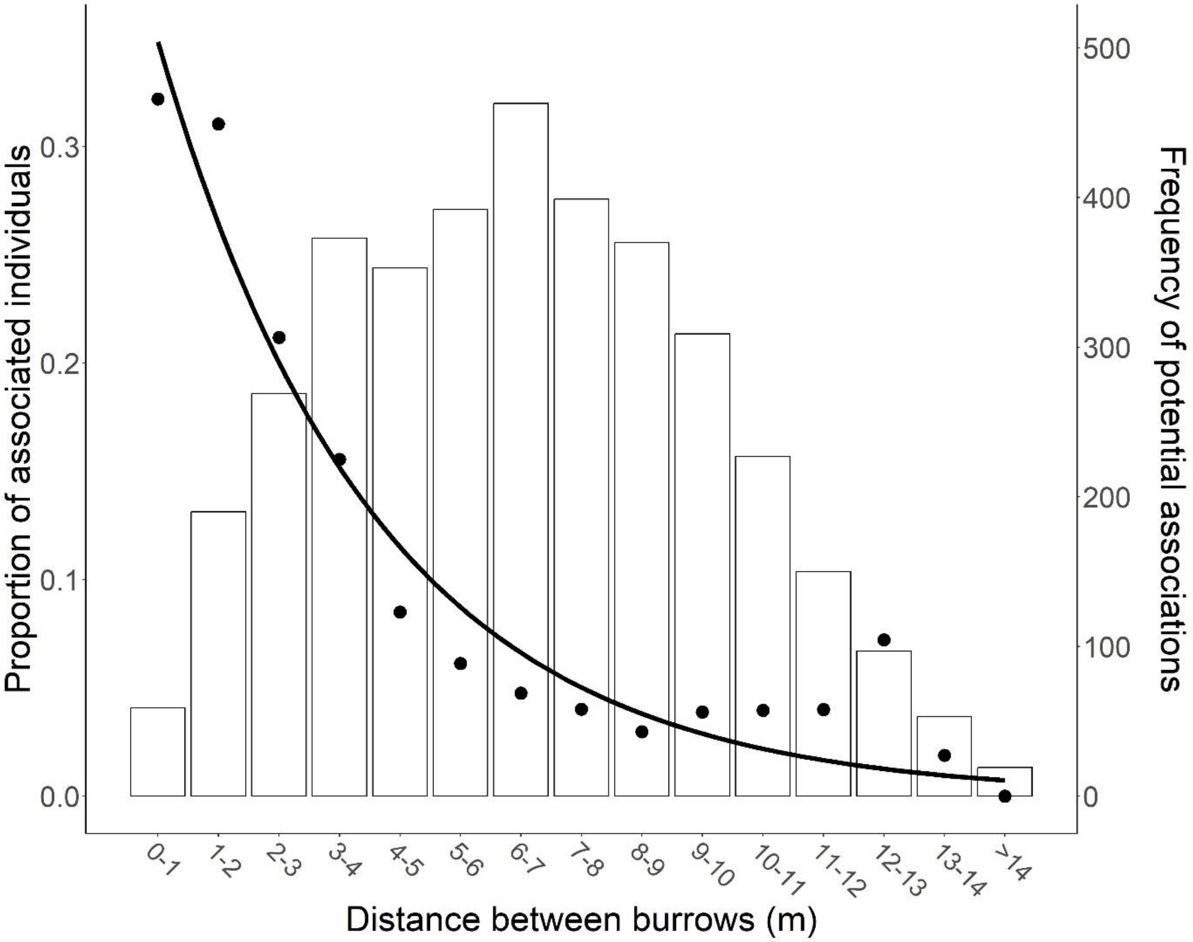

Figure 1. Relationship between the proportion of associated individuals and the distance between their burrows. The proportion was obtained by dividing real occurring associations by all pairwise theoretical associations from 87 individuals and binned according to their burrow distance, using 14 bins of equal distance. Weak ties (<=1) were preserved and associations between breeding partners were deleted to avoid the overrepresentation of null distances in the analysis. The white diagram represents the frequency of all potential associations. The trendline represents the exponential decay equation of the line of best fit.

From the 1,843 associations observed, we analysed the proportion of individuals associating in relation to their burrow's distance corrected for slope (Figure 1). Both models (exponential decay and asymptotic function) performed equally (delta AIC < 2), but the exponential decay function is presumed more biologically relevant to represent the declining probability of association over distance (eventually reaching near zero), we present it as the best model. Our results show that the proportion of individuals associating and nesting in close range (less than two metres) is equal to 30 % of the potential dyads. It gradually decreases to 20 % between 2-3 metres, and 10 % between 4-5 metres, until it stabilises around 5 % for 5 metres and above. The node permutation test strongly supported the higher proportion of associations at a short distance than expected by chance ($P < 0.001$ for 10,000 iterations; Figure S3a).

Spatial environment and communities

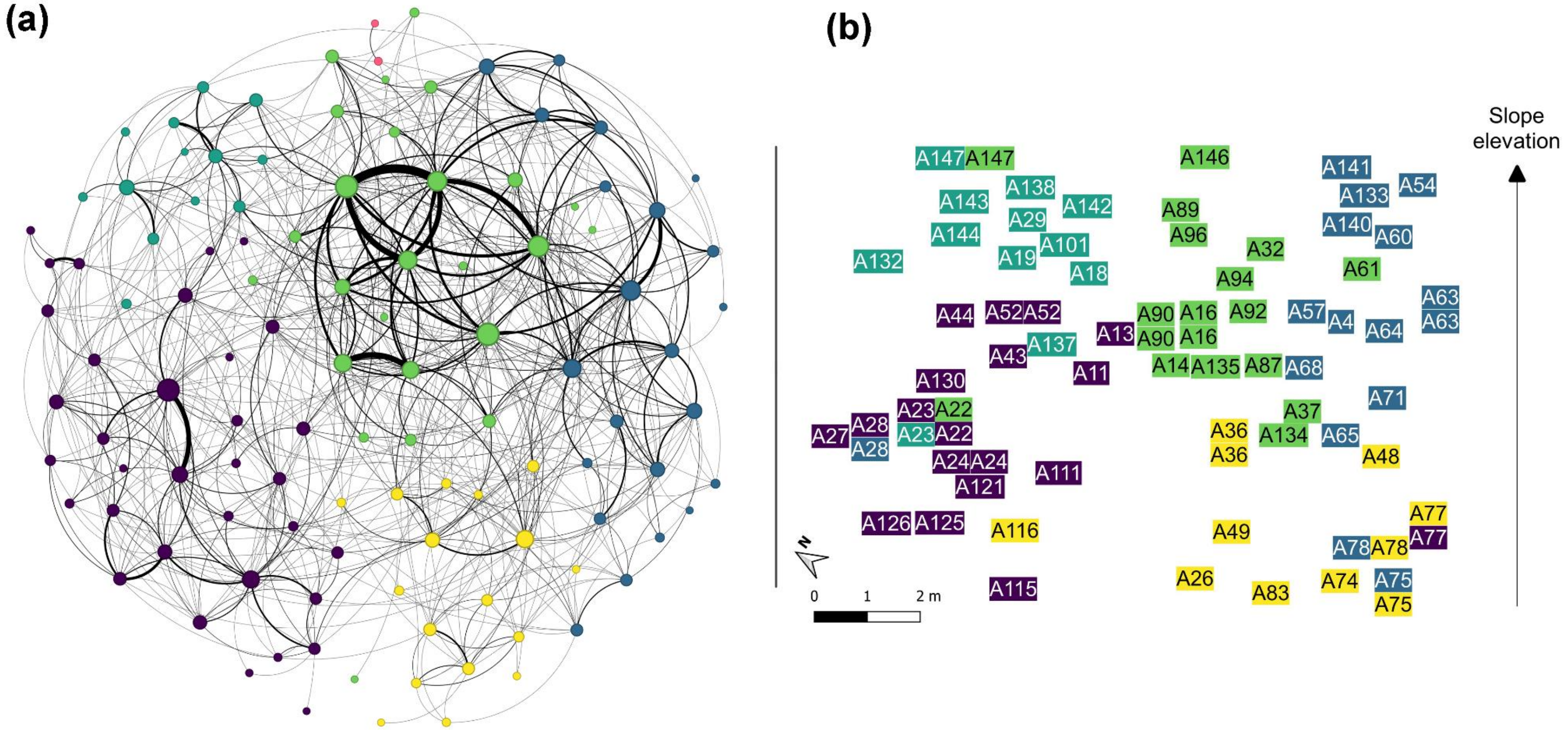

Figure 2. (a) *The social network graph, and (b) geographic distribution of 76 individuals nesting in 63 burrows on a 168 square metres sampling plot in Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada. On (a), node size is scaled on the value of degree, colours represent the six clusters calculated using modularity classes, and edge width is proportional to the weight of the association. On (b), individuals are mapped based on the geodetic coordinate of their burrows. Colours represent five of the six clusters calculated using modularity classes and identical alphanumeric code represents pairs living in the same burrow.*

The community analysis identified six clusters, one of which included only two individuals (Figure 2a). The clusters mapped well onto the spatial distribution of the burrows (Figure 2b). Seven mated pairs out of 13 were not in the same cluster (e.g., see A22 and A23 in Figure 2b). In all but one case, the female was not associated with the nearest cluster. The randomisation test revealed that the average distance between individuals within the same cluster (mean = 5.29 m) was shorter than expected by chance (mean = 6.44 m, one-tail test, P = 0.049; Figure S3b).

Spatial environment and dyadic weight

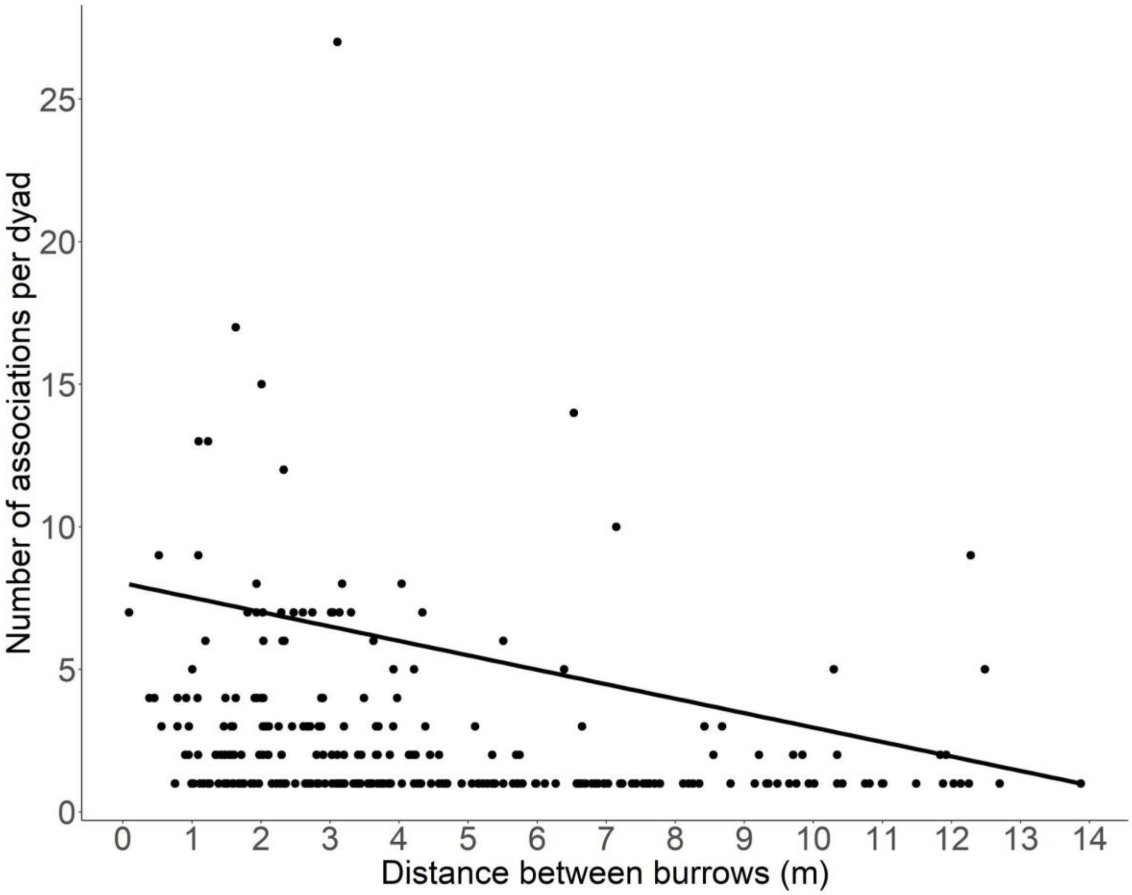

Figure 3. Dyadic strengths are a function of burrow distance for 74 Atlantic puffins. Each dot represents a dyad, with the trendline representing the linear regression.

To test whether dyadic weight was greater between physically close individuals, we compared them to a null model (Figure S3c), using a paired t-test. The model was run on the 74 individuals of known burrows observed at least once in a dyad. Individuals nesting at shorter distances were associated significantly more often than expected by chance (mean difference = 0.718 m, t(67) = -6.87, P < 0.0001) with a small effect size (-0.28).

Social environment and dyadic weight

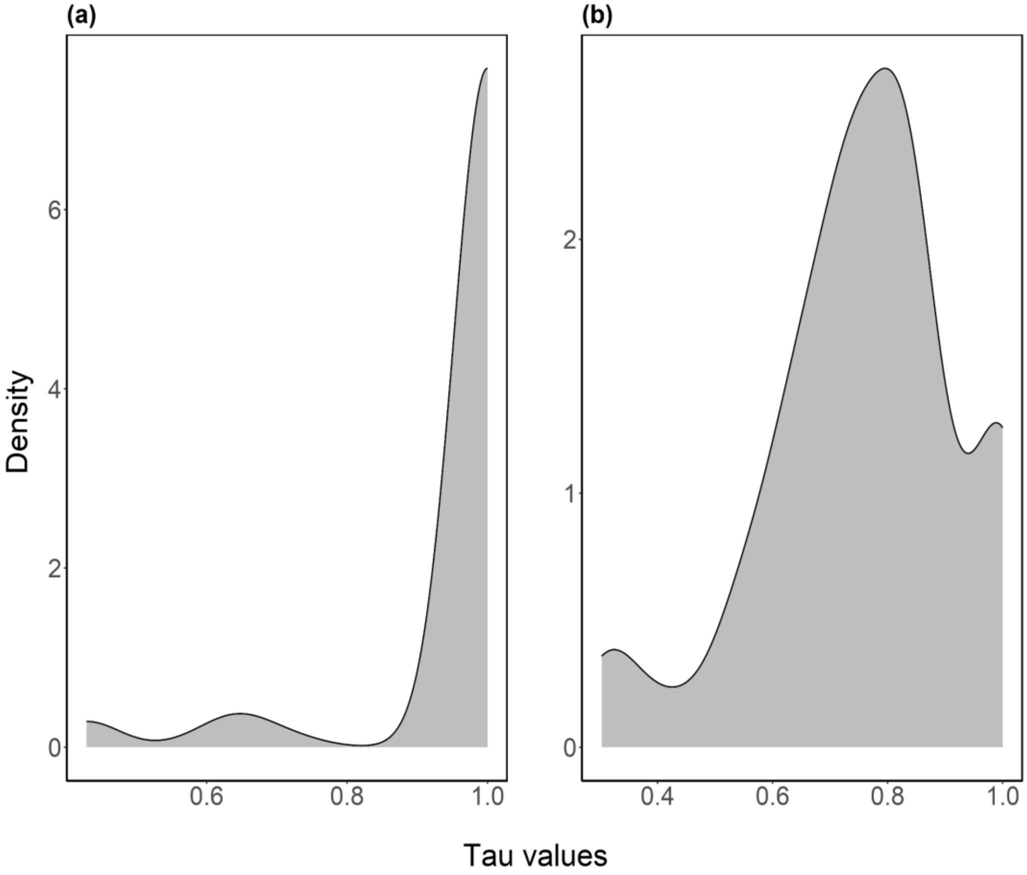

Figure 4. The probability of association between two individuals is almost entirely proportional to their frequency of colony attendance when their nests are within two meters of one another, but much less so when their burrow distance is greater than two meters. The figures represent the kernel density estimate of tau values for two distance ranges: (a) 0 to 2 metres and (b) 2 to 16 metres. Data were collected on 87 Atlantic puffins, and all individuals were preserved for this representation. A high tau value (close to one) reflects a strong match between the expected and observed proportion of associations (i.e., a random process). Lower tau values imply non-random associations.

To test how the social environment affects the social network, we compared the weight of observed and theoretical associations for each individual's dyad within two metres (Median = 1, Q1 = 1, Q3 = 1), and greater than two metres (Median = 0.764, Q1 = 0.659, Q3 = 0.853). The test identified a high proportion of observed values explained by theoretical values between 0 and 2 metres (Figure 4a; 91.80 % of the values are above 0.8) suggesting random associations between individuals (i.e., their frequency of associations was predicted by how often individuals were observed). From 2–16 metres, a greater number of lower tau values (Figure 4b; only 43.68 % of the values are above 0.8) suggested the presence of frequent non-random association (i.e., their frequency of associations was higher or lower than predicted by the individual's presence at the colony).

Discussion

Social and spatial mechanisms that contribute to social network structure remain entangled and potentially lead to misattributing which process affects structure. Nowhere is this more likely than in central-place foragers that live in high-density colonies. We examined the effect of the spatial-social interface on the land-based social network structure of the Atlantic puffin to disentangle the contribution of geography and social environment to the social network structure. Our findings demonstrate that the spatial environment consistently affects the expression of the Atlantic puffin's social phenotype, with individuals associating more with geographically close nesting neighbours. In contrast, we found only partial support for the influence of the social environment on social network structure: seemingly non-random associations were found between distant individuals.

We found evidence that the probability of puffins associating with conspecifics nesting between zero and two metres is much higher than with distantly nesting individuals. Additionally, we demonstrated that communities were spatially connected to the landscape, with close conspecifics more likely to form clusters, and found that dyadic weights were higher between individuals with short distances between their burrows. The findings highlight the influence of nest distribution on Atlantic puffin social associations and the constraints imposed by colonial breeding. Various other spatial structures have been demonstrated to influence social behaviours, but not to the same extent. Sleepy lizards (*Tiliqua rugosa*), for example, increase social connectivity when their territories are artificially limited by anthropological barriers, i.e., fences, because the habitat structure compels individuals to follow similar paths, increasing the probability of interaction (Leu et al., 2016). Individual three-spined stickleback (*Gasterosteus aculeatus*) exposed to an environment with physical limitations (e.g., barriers), rather than an open landscape, are more likely to explore in small groups using their immediate social network to spot food patches (Webster et al., 2013). Our results further suggest that central-place foragers living in high density have little choice with who they associate, at least while attending the colony. Indeed, our analyses revealed that the frequency of associations between individuals nesting within 2 meters was almost entirely predicted by their frequency of colony attendance, and it is likely to be the case for most seabirds as they spend most of their on-land time at their nest (Hatch & Hatch, 1988). Because social interactions are so strongly determined by burrow geography, puffins often attend alternate locations where they may be socializing. For example, boulders could serve as staging areas where social interactions are not affected by geography, thus providing puffins with more agency from whom they share and acquire information.

We found evidence for non-random association patterns between individuals nesting far away from each other. The probability of interactions was not a great predictor of the observed proportion of associations at distances greater than 2 metres (Figure 4b) suggesting that certain associations were favoured while others were avoided. Familiar individuals can seek each other out, even under high spatial constraints, because being with familiar individuals can provide benefits directly affecting adult survival (Croft et al., 2006), breeding success (Hansen et al., 2009; Kohn, 2017), or foraging success (Atton et al., 2014). For example, the Barnacle geese (*Branta leucopsis*) prefer to associate with familiar individuals when foraging but not for mate selection, probably because it returns indirect fitness benefits, suggesting that early life experiences can have consequences on foraging and mating social network structures later in life (Kurvers et al., 2013). Preferred associations in Atlantic puffins could come from individuals previously nesting close to each other. Atlantic puffin generally reuses the same burrow from one year to another (Harris & Wanless, 2011) but burrow relocation can happen following a catastrophic event or low breeding success. When relocating, the parents often move near their original burrow (Harris & Wanless, 2011). Thus, previously close individuals could still be in reach to associate with each other, keeping bonds despite the spatial constraints. To determine if these associations are resilient over time, and last after burrow relocation, we would need to test if non-random associations are the same over several years. We could also expect that young birds would have mostly random interactions at distances greater than two metres, while older birds, because of strengthening bonds over the years, would demonstrate non-random associations.

There is, however, an alternate hypothesis for non-random patterns of associations we detected tied to the topography of the environment. Individuals could regularly associate with each other due to matching spatial and temporal needs such as requirements to reduce energy expenses during flight initiation, and/or anti-predation behaviours. To decrease the energy required to take off, seabirds with high wing-loading often use environmental conditions such as wind or gravity (Clay et al., 2020). To initiate flight, Atlantic puffins need to be about 5-6 m above the water or flat land (Harris & Wanless, 2011). Our study plot consisted of a 40° angle slope characterized by a ridge found more than 5 m above the foot of the slope, where a flat section precluded low-nesting birds from taking flight straight out of their burrows. Before taking off, low-nesting birds climbed up the slope until they reached sufficient height or the top of the slope. Indeed, Atlantic puffins are regularly seen regrouping on higher ground, often the top of the nearest shoulder edge (Harris & Wanless, 2011). If the climbing behaviour is repeatable at the individual level, flight initiation requirements would regularly bring them in association with the specific individuals that breed at these locations (e.g., top of the slope directly above their own burrow). Different landscape features would lead to different patterns of associations making it unclear if social network characteristics are a function of spatial or social mechanisms.

Atlantic puffin social interactions near their burrows appear to be highly constrained by the spatial environment. Constraints are evidenced by the correlation with colony attendance and possibly even influenced by local environmental factors, like slope to reposition for flight. However, attending burrows represents only one of the several potential scenarios (e.g., aggregation sites, at sea resting areas, feeding grounds) where puffins interact and likely exchange information with conspecifics. For example, when not at their burrow entrance, puffins are likely to regroup in communal areas such as rafts, boulders or shoulder edges. Regrouping is more likely to remove the geographic constraints, increasing the agency puffins have to choose associates. Non-burrow communal areas are thought to dilute predation risk with the many-eyes effect (Lehtonen & Jaatinen, 2016). For example, Black-backed gulls (*Larus marinus*) and Bald eagles (*Haliaeetus leucocephalus*) directly prey on aggregations of puffins (Langlois Lopez et al., 2023). Non-burrow locations are superior predator escape habitats compared to burrows, where initiating flight can be challenged by the topography (Harris & Wanless, 2011). Puffins also experience kleptoparasitism but it is unlikely, however, to be a reason for land aggregation as only the flocks of returning adults are targeted (Merkel et al., 1998). It may be that individuals who have preferences for these same non-burrow locations would associate more often than expected by chance.

We demonstrated that spatial environments are key factors in social networks (Webber et al., 2023), and that central-place forager's sociality can be particularly affected by spatial limitations. Such social behaviour may affect how information flows within a breeding colony, which can affect foraging behaviour, predation, mate choice, habitat selection, or migration (Evans et al., 2015). For central-place foragers, our results suggest that burrow choice exhorts substantial spatial limits on social associations and that individuals likely require alternate spatial locations to express preferences in social associations that are not entangled with their local geography.

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