**Inter-nest distances drive most but not all social associations in a colonial 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

Antoine Morel: 0009-0003-0216-7365

Eric Vander Wal: 0000-0002-8534-4317

Pierre-Paul Bitton: 0000-0001-5984-2331

## Statements and Declarations

The authors declare having no conflict of interest.

## Author Contributions

Antoine Morel, Pierre-Paul Bitton and Eric Vander Wal conceived the ideas and designed the methodology; Antoine Morel led the collection, the analysis of the data and the writing of the manuscript; Pierre-Paul Bitton significantly contributed to the analysis and writing of the manuscript; All authors contributed to the drafts and gave final approval for publication.

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**Data availability statement**

Data are available in an open-access public repository, accessible here: https://osf.io/wkqyn/overview?view_only=75fb30bc030e42e4ab01caffd157d966

# Abstract

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 colonial species. The Atlantic puffin is a colonial seabird that nests in an underground burrow. Therefore, they are less limited in their land-based movements than open-nesting seabirds. We colour-banded 124 individuals, georeferenced their burrows and tracked their associations at the colony using a scan sampling approach during the breeding season to understand how the spatial distribution of the burrows constrained their associations.

We tested how the distance between nests in a colony affected (i) individual probability of association and dyadic weight, and (ii) their community structure. We also tested for the presence of non-random associations across different distances.

We found that the distance between burrows strongly influenced the social network structure of Atlantic puffins. Individuals associated more often with neighbours and did not seem to favour associations with specific adults attending adjacent nests. However, contrary to expectation, we found that groups of individuals formed communities and evidence that distant associations with conspecifics were not all random. We suggest that individuals may seek each other out, if it provides mutual benefits, or have similar spatial and temporal requirements. Our study demonstrates the importance of considering spatial constraints in studying social network structures and provides new evidence for their impact on colonial animals.


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

## Significance statement

The social networks of animals that breed in high-density colonies should be heavily constrained by the spatial distribution of their territories. Yet the limitations imposed by these constraints have rarely been assessed. Using observations of colour-banded Atlantic puffins, we demonstrate the extent to which network traits are impacted by the distance between nests, but also find that, in contrast to expectations, individuals form distinct communities and associate with some distant individuals more often than expected by chance. Our findings suggest that Atlantic puffins have some control over which individuals they associate with.

# Introduction

Social networks, and the social connections from which they emerge, are often implicated as important to many populations and ecological processes (reviewed in 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). In this study, we used a burrowing colonial seabird, the Atlantic puffin (*Fratercula arctica*), to evaluate how the constraints raised by spatial proximity between nests influence individual capability to associate and form communities. We also tested whether non-random associations emerged when controlling for this spatial constraint.

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 use 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 site fidelity 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).

Colonial species and central-place foragers are potentially even more affected in their social structures by environmental conditions and geography than free-ranging species, as they are constrained to spend much time at a specific location (e.g., territory, nest, burrow, den). Seabirds, for example, are central-place foragers that can nest in very high-density colonies (e.g., 1.37 burrows/m² in Atlantic puffin; 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). Colonial seabirds' social networks have been investigated in the context of information centres (Monier, 2024), mainly testing where and how individuals associate. For example, Australian gannets (*Morus serrator*) have been seen randomly associating at colony departure and return, when commuting and foraging (Jones et al., 2020) and Guanay cormorants (*Phalacrocorax bougainvillii*) are known to use social information mainly collected on rafting aggregations to select their bearing when departing the colony (Weimerskirch et al., 2010). However, little is known about social associations between foraging trips, when adults attend the colony. When at their nest, individuals can associate with nearby conspecifics nesting in immediate proximity or move about the landscape to contact non-neighbours. Most seabirds such as gannets, because of the exposed nature of their nests, rarely leave their nest unattended (Lewis et al., 2004) and will considerably limit their movement on land. These limitations on movement would set hard constraints on which individuals associate with one another. Other, such as Atlantic puffins, incubate and raise their chicks in a burrow, where they are naturally protected from the elements and natural predators. Thus, they can move about the landscape and have the potential to associate in ways that are not entirely driven by spatial limitations.

Animals can also have their association patterns induced by their social environment. Specifically, group composition, size, density (Webber et al., 2023) and familiarity with known 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). Large group sizes and greater population density offer more opportunities for social interactions than small, scarce groups. Free-ranging male elk (*Cervus canadensis*) for example, associate more (i.e., greater value of strength) at higher density, suggesting the number of potential encounters increases in response to higher density (O'Brien et al., 2018; Webber & Vander Wal, 2020).

We interrogate a subset of the influence of the spatial-social environment interface on the association network for a colonial seabird, the Atlantic puffin. Because Atlantic puffins breed in close contact in a fixed geographic place, we hypothesised that their network structure would be strongly constrained to the individuals nesting nearby. Furthermore, because we expect spatial homogeneity in the distribution of burrows, we would not expect communities to emerge (Leu et al., 2016; Webster et al., 2013). Therefore, we tested the influence of the distance between burrows on (i) the probability of association and dyadic weight, and (ii) community formation. However, Atlantic puffins have high breeding philopatry and a long lifespan, potentially leading to familiarity between individuals. Additionally, because they breed in burrows, they can leave their nest unattended, giving them the potential to move within the colony. We hypothesised that the influence of non-spatially driven factors should be visible in the social network structure. Therefore, we tested whether certain associations were more or less 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 at least 45 years old in the wild (Fransson et al., 2023). 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). Assuming a hexagonal array distribution, the average distance between burrow entrances can be estimated between 1.4 metres on Kilda Island and 0.85 metres on Gull Island. 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 may have good knowledge of neighbouring conspecifics. Atlantic puffin breeding season lasts three to four months and incubation can take up to 42 days (Harris & Wanless, 2011). Males seem to spend more time on land than females, probably defending the burrow entrance (Anker-Nilssen et al., 2024), and females may be more involved in incubation and chick provisioning (Creelman & Storey, 1991; Fitzsimmons, 2018). However, sexual differences have not been confirmed by other studies (Corkhill, 1973; Harris, 1986) and it remains unclear if parents should have similar opportunities for associations. Unlike seabird species with exposed nests where they must remain to protect the egg or chick, puffins are free to move about the landscape once out of the burrow. While they often remain present next to their burrow when engaged in territory defence (Anker-Nilssen et al., 2024), they can be seen gathering on slope edges and solitary rocks, moving toward incomers or crossing the slope looking for their burrows after landing (Harris & Wanless, 2011).

The data were collected on Great Island, located in the Witless Bay Ecological Reserve of Newfoundland and Labrador, Canada (47.1855N, 52.8121W). The population was estimated at 350,000 breeding adults in 2015 (Wilhelm et al., 2015) and 410,000 in 2023 (Wilhelm, unpublished data). Recent surveys found an average of 1.57 burrows/m² 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 (Fig 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 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 diametres 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. When more than two individuals were associated, they were considered as distinct dyads. This choice is justified to maximise scanning sampling effort and represent individual movement around their nest. To document those associations, we performed 85 hours of scan sampling on the 124 potential colour-banded individuals, distributed among 34 sessions from July 20$^{th}$ to August 09$^{th}$, 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 associations from the blind (Fig S1). Each session was conducted by two observers equipped with binoculars (Swarovski EL 10x42 WB), performing scan sampling 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. For this study, an event was defined as any association within a two-metre radius of an individual. An event was recorded if at least one bird was banded and identified, even if the other birds were unbanded or unidentified. All events were timestamped and given unique sequential record numbers. 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 we did not assume that the birds banded in 2021 returned to the same nest and unless they were recaptured in 2022, we excluded them from the spatially referenced analyses. Because our study involved individuals observed by scan sampling, recording the data blind to the specific individual associating was not possible.

## Data extraction

### Burrow distance

To evaluate the effect of burrow distribution on social networks, we calculated the distance between burrows using GPS coordinates (accuracy ~ 10 cm) 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 R statistical Software v.4.2.3 (R core Team, 2023). Each event was digitally incremented following an undirected edge-list format respecting dyadic associations and keeping the date and time. To detect communities from the observed associations, we used two methods: (i) the original version of the fast greedy algorithm developed by Clauset et al. (2004), and (ii) the most recent fast unfolding community analysis from Blondel et al. (2008). While these two methods have been developed for large networks with several million nodes, they still return very good results for smaller datasets (Ellis et al., 2017). 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. Values approaching one indicate very strong communities, values near zero suggest random assignment and values near minus one means weak communities. A value above 0.3 is a good indicator of significant community structure in a network (Clauset et al., 2004). To visualise the communities extracted from the modularity metric, henceforth called modules, we used Gephi software v.0.10.1 (Bastian et al., 2009).

## Analysis

### Distance and dyadic weight

To evaluate the effect of burrow distribution on associations, we used two approaches. First, the proportion of association was calculated using 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. We kept all associations even when they occurred only once, but we excluded mate pairs. To best describe the relationship between burrow distance and probability of association, we used an exponential decay function as it returns the best model fit (see section SM1 in the supplementary method).

Second, because the distribution of dyadic weights was heavily zero-inflated, we used a generalised linear mixed hurdle model (GLHM) implemented in the glmmTMB R package (McGillycuddy et al., 2025) to test the influence of burrow distance on whether individuals were observed associating, and on their corrected dyadic weight (*i.e.*, Simple Ratio Index; Hoppitt & Farine, 2018). GLHMs models evaluate two different processes: 1) they determine the factors that influence if an event occurred (the zero-inflated model - logistic regression with ‘0’ treated as ‘No’ and values > ‘0’ treated as ‘Yes’), and 2) they determine the factors that influence the non-zero values (the conditional model - generalised linear model). For this analysis, we kept all associations even when they occurred only once, but we excluded mated pairs because they would overrepresent the number of associations at null distance due to identical burrows. Our hurdle model included the number of associations as the dependent variable in both the zero-inflated and conditional model, burrow distance as the independent variable, dyad identity as the random term to control for non-independence structure in the data, and we used a Gamma distribution to model the residuals. Model assumptions were verified using the DHARMa package (Hartig, 2016). Because current methods do not permit isolating the marginal and conditional R-squared for both components of a hurdle model, we calculated the variance explained for the zero-inflation and conditional models separately, using two models: a binary (zero versus non-zero) and a continuous (positive values and dispersion). As a complement to the GLHM we also evaluated the frequency of association with distance using a randomisation test as an alternative method (see section SM2 in supplementary method).

## Distance between burrows and modules

We investigated the role of burrow distance on community structure using a randomisation test. The null model was built by randomly distributing all potential individuals within modules before calculating the mean distance of connected individuals over 10,000 replicates. We compared the original observed average distance between burrows per module with the one obtained by randomisation. The p-value was calculated using twice the proportion of randomised mean distances smaller than the observed value (two-tailed test). To visualise the spatial distribution of the modules, we produced a distribution map of the burrows, coloured by modules, using the WGS_1984_Canada_Atlas_LCC (ESRI 102215) projection in the QGIS software v.3.34.3 (*QGIS Geographic Information System*, 2024).

## Distance corrected dyadic weight

Because the distance between burrows alone may not explain all association patterns, we tested if individuals were associating more or less than expected by chance after controlling for constraints imposed by nesting proximity. We tested two distance intervals: 0-2 m (close neighbours) and 2-16 m (distant individuals). For this, we used a multinomial contingency table test to evaluate if observed associations between individuals were explained by how often they were detected on the plot. The observed values for each individual were the dyadic weight of all observed associations; when two individuals were not observed associating the dyadic weight was set to zero. The theoretical values were calculated as the probability of an association between a focal individual and each potential social partner based on how often individuals were observed on the plot. We performed a multinomial test for each individual using a Monte Carlo's procedure with one million permutations. The p-values for all tests (n = 87) were then adjusted using a Benjamini-Hochberg correction to control for the expected proportion of false positives among significant results (Benjamini & Hochberg, 1995; Nakagawa, 2004). We evaluated if significant results were mainly generated by the lack of associations between individuals present on the plot, or by high association rates between specific individuals by extracting the scaled (Pearson's) residuals of each multinomial test and looking at the sum of negative and positive values. We further evaluated the residuals for evidence of individuals associating much less than expected by chance (residuals with scores lower than -2.0), or much more than expected by chance (residuals with scores greater than 2.00; Agresti, 2008).

### 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 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 between 2021 and 2022 (37 % of the estimated individuals, greater than the 30 % considered sufficient for proper network models; Silk et al., 2015), we detected 112 over 85 hours of scan sampling. From July 19th to August 10th, we recorded 677 dyads and 1,843 associations. 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) and the average minimum distance between marked burrows of 1.43 metres (M= 1.43, SD = 1.24). 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).

## Distance and dyadic weight

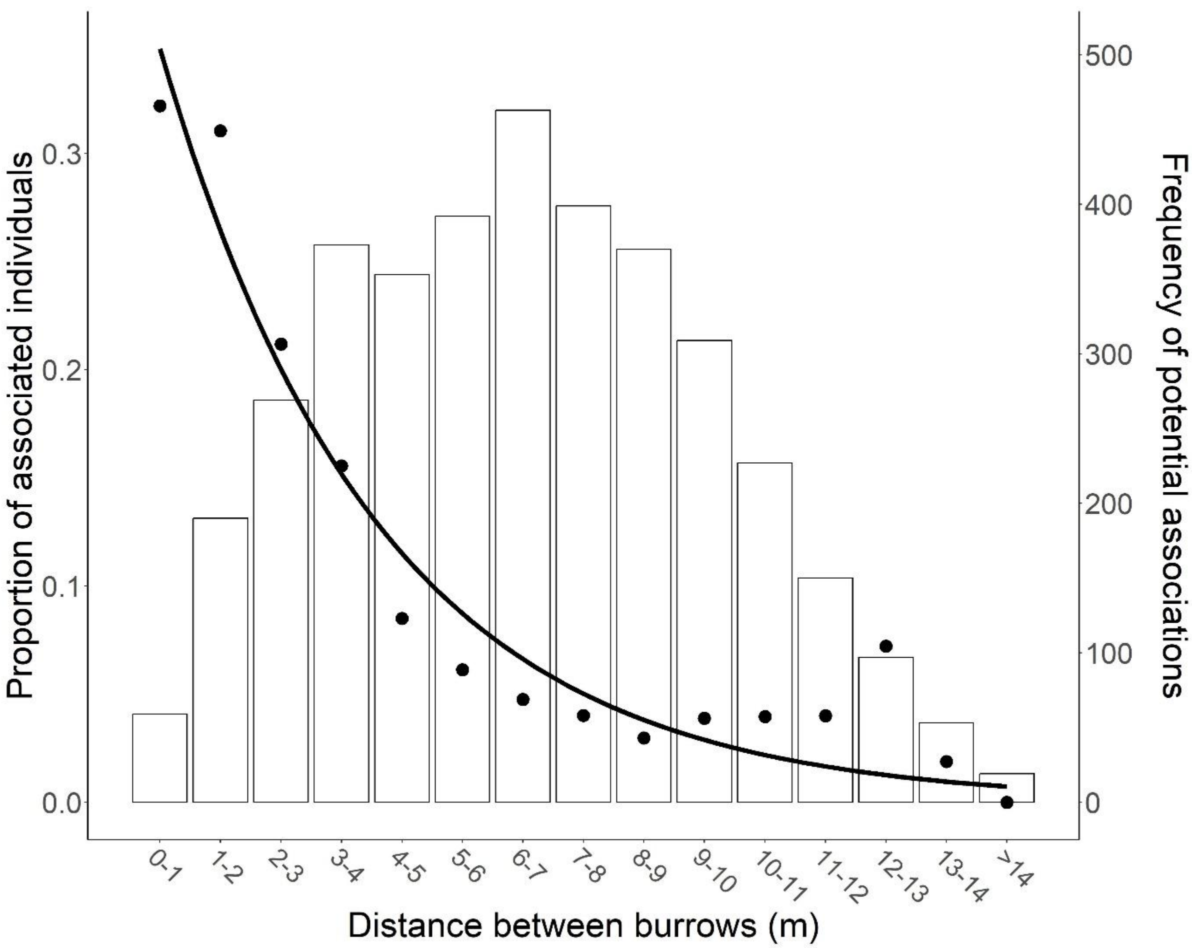


**Fig 1** *Relationship between the proportion of associated individuals and the distance between their burrows. The proportion was obtained by dividing real occurring associations by all pairwise potential associations from 87 individuals and binned according to their burrow distance, using 14 bins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

We compared the proportion of individuals associating in relation to their burrow's distance corrected for slope angle (Fig 1). The exponential decay model performed best in representing the declining probability of association over distance. 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. It also shows that despite a higher potential of association between 5 and 8 metres, the highest proportion of association happens between 0 and 3 metres. The GLHM (log-likelihood: 99.04) showed a strong significant effect of distance on dyadic weight in the zero-inflation (Est = 0.048, SE = 0.011, Z = 4.151, p < 0.0001, R2m = 0.0068, R2c = 0.0068) and conditional models (Est = 0.063, SE = 0.010, Z =6.10, p < 0.0001, R2m = 0.0290, R2c = 0.4608), implying that Atlantic puffins are highly constrained by burrow distance with who they associate, and how often. The randomisation test (See section SM2 in supplementary methods) concurred with this finding, with a higher proportion of associations at a short distance than expected by chance (P < 0.001 for 10,000 iterations; Fig S3a).

Distance between burrows and communities

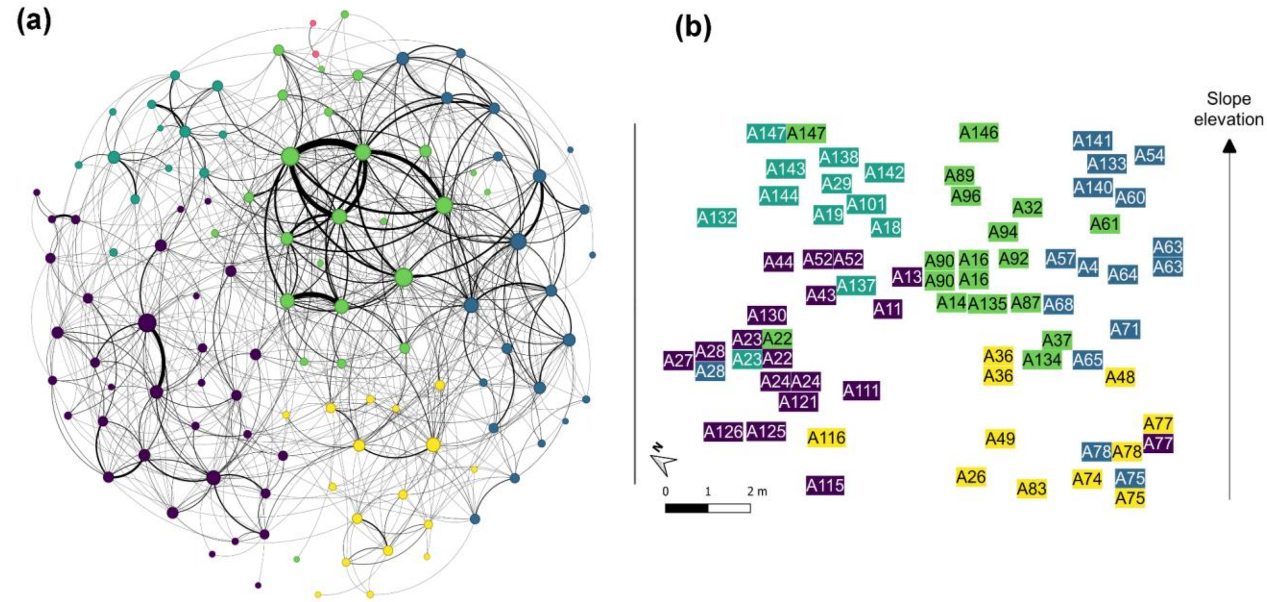


**Fig 2** (a) *The social network graph, and (b) geographic distribution of 76 Atlantic puffins nesting in 63 burrows on a 168 square* metres *sampling plot in Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada. On (a), node size is scaled on the value of degree, colours represent the six modules calculated using modularity classes, and edge width is proportional to the weight of the association. On (b), individuals are mapped based on the geodetic coordinates of their burrows. Colours represent five of the six modules calculated using modularity classes, and an identical alphanumeric code represents pairs living in the same burrow. The individuals in the sixth module (pink symbols) did not have their nests mapped out and are not included in (b)*

The community analysis identified six modules, one of which included only two individuals with unidentified burrows (orange colour; Fig 2a). The modules emerged with a significant modularity score of 0.443, indicating that individuals were not randomly distributed among communities (Clauset et al., 2004). The modules mapped well onto the spatial distribution of the burrows (Fig 2b). Seven mated pairs out of 13 were not in the same module (e.g., see A22 and A23 in Fig 2b). In all but one of these cases, the female was not associated with the nearest module. A randomisation test with a one-tailed hypothesis revealed that the average distance between individuals within the same module (mean = 5.29 m) was shorter than expected by chance (mean = 6.44 m, one-tailed test, p = 0.049; Fig S3b).

## Distance corrected dyadic weight

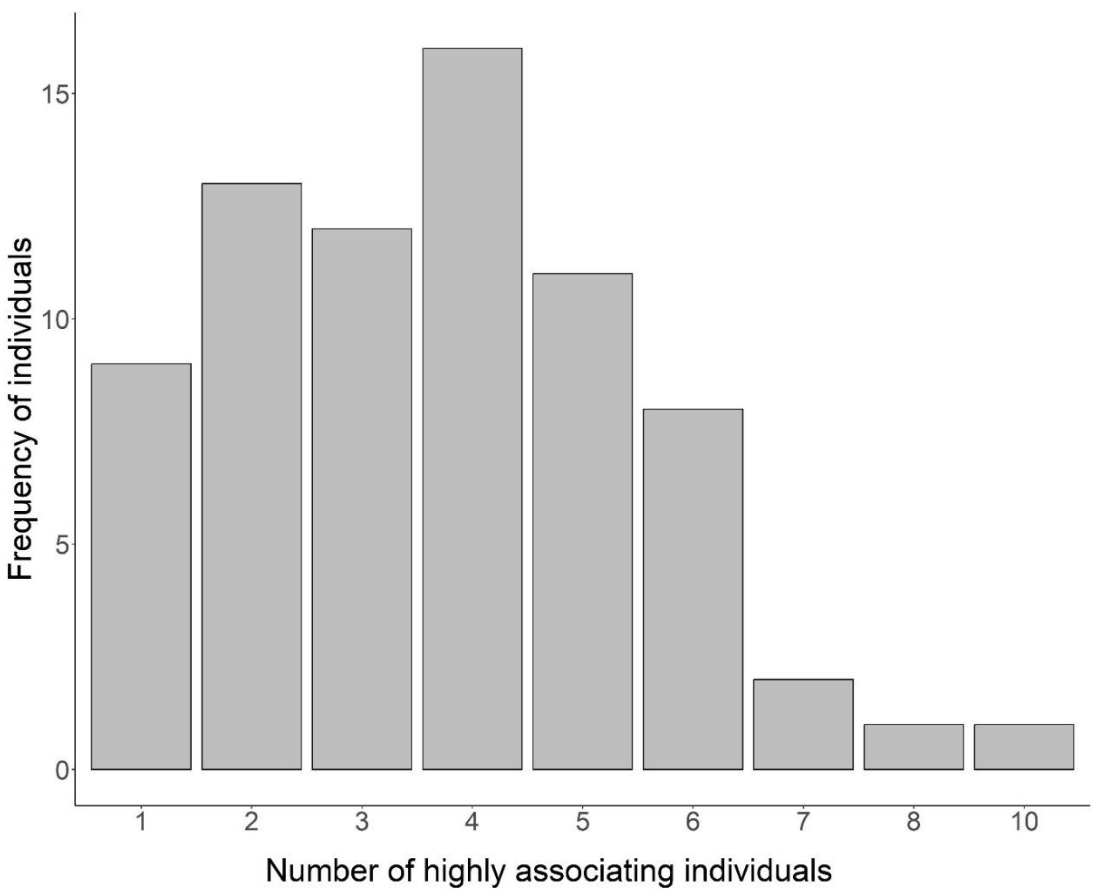


**Fig 3** *Frequency of associations with residual values from multinomial contingency table tests superior to or equal to 2.0 between 2 and 16 metres. These represent the number of associations observed more often than expected by the number of times individuals were observed on the study plot*

To identify patterns of associations at the individual level, we examined the distribution of the standardised residuals around zero from multinomial contingency tables. To evaluate the presence of non-random associations, we used the number of residuals greater or equal to 2.0 to identify individuals associating more than expected by chance, and less or equal to -2.0 to identify individuals associating less than expected by chance. Between zero and two metres, 96.5% of the individuals (84 out of 87 individuals) associated randomly. Of the three individuals with significant p-values, all were associated with at least one individual with a value of standardised residual higher than 2.0. Two out of three individuals had limited associations with another bird (standardised residual lower than -2.0). Between two and 16 metres, 61% of the individuals (53 out of 87) associated differently than expected by chance. Only one individual showed limited association with another bird (scaled residual values lower than -2.0), and all 53 individuals had evidence for high frequency associations with up to ten other individuals (standardised residual values higher than 2.0; Fig 3).

In both cases, p-values were mainly driven by a large proportion of standardised residuals with small negative values and few with high positive values (Fig S4a). This indicates that significant p-values were mostly driven by limited (or lack of) associations between distant individuals.

# Discussion

In their paper, Albery et al.(2021) describe the importance of incorporating the spatial component into social network analysis. This is because spatial environment and social behaviour interact, sometimes compete, in a way that is challenging to predict or disentangle. The understanding of the contribution of spatial mechanisms to social network structure was, in this study, made possible by the use of underground nesting colonial seabirds, leaving the adults free to move on the colony and express sociality. We examined the effect of burrow distance on the probability of association and dyadic weight, as well as in community formation in a colonial seabird that can move about the landscape. We also tested the presence of non-random associations while controlling spatial constraints to evaluate the potential role played by spatial and temporal parameters in the association patterns. Our findings demonstrate that the distance between burrows consistently affects the expression of the Atlantic puffin's sociality, with individuals associating more with geographically close (within two metres) nesting neighbours. In contrast to our predictions, modules were formed, mainly with close nesting neighbours. Finally, we found non-random associations between individuals nesting far from each other with several associations occurring more often than expected by chance.

We found that the proportion of associations between individuals decreases exponentially with distance. Furthermore, the dyadic weight and the probability of puffins associating with conspecifics nesting between zero and two metres was much higher than with distantly nesting individuals. These results suggest that colonial seabirds have little choice with whom they associate, at least while attending the colony, as they spend most of their on-land time at their nest (Hatch & Hatch, 1988). These 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 have implications for understanding the flow of information in colonial species (Evans et al., 2015), and provide useful parameters for disease modelling in these species (Silk et al, 2017).

We demonstrated that modules were spatially connected to the landscape, with close conspecifics more likely to form modules. However, in a social system driven by distance between individuals, modules should only form in the presence of environmental heterogeneity, created, for example, by physical barriers (Webster et al., 2013; Leu et al., 2016; He et al., 2019). In consideration of the relatively homogeneous environment in which this study was conducted, it is challenging to explain how modules could emerge. We suggest two hypotheses that might be responsible for this non-random association pattern. First, it is likely that individuals that nest close to one another also use loafing areas near their burrows, thus increasing the associations between a subset of individuals. For example, boulders and rocky outcrops are often used by puffins, where they are found in high density. By spending time in an area without nesting territories, individuals would gain the benefits of higher density aggregations, without the risk of aggressive behaviours (Beauchamp & Ruxton, 2012). These socialising structures could also be used as neutral areas, providing puffins with more agency with whom they share and acquire information. Because we did not note where individuals were seen associating on the landscape, we cannot directly address the mechanisms responsible for module formation. However, these findings provide us with a future opportunity to critically evaluate the value of loafing areas to Atlantic puffins. Second, the presence of obstacles that limit access to certain areas and encourage individuals to use specific paths could lead to module formation. Those barriers could be branches, rocks, vegetation, strong slope angles, and even the nest of other species that would generate real and perceived micro-barriers. Puffins are generally awkward on land and have limited ability to jump or fly to avoid obstacles. Literature on puffin movement at the colony in relation to fine-scale structures is lacking, and would require tracking individual movements in consideration of the three-dimensional structures of the landscape.

The multinomial test indicated that most individuals (96.5%) did not associate differently from expected by chance with near neighbours (between zero and two metres). In the few cases where the p-value was significant, evaluation of the residuals showed that small negative values, not large positive values, were more important. Overall, these results are in agreement with our previous results, indicating a strong influence of proximity on associations. For analyses of distantly nesting individuals (between two and 16 metres), we found that a large proportion of individuals (61%) associate in a non-random way.

In these cases, evaluation of the residuals showed a very large number of small negative values, suggesting that distant birds simply did not associate, even if present on the plot. However, we did not find evidence for individuals seemingly avoiding one another (residuals smaller than -2.0). In contrast, most individuals had large positive values of scaled residuals indicating that some distantly nesting individuals associate much more often than expected by chance. We suspect two non-mutually exclusive mechanisms could be responsible for this pattern. First, we suggest that individuals can seek each other out regardless of their inter-nest distance to benefit from interacting with individuals they know. Second, we argue that individuals could associate because of similar spatial and temporal requirements.

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). Familiar individuals can seek each other out, even under high spatial constraints, as it 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, 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 would also expect that young birds would have mostly random associations 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 characterised 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 would climb 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, as some real or perceived micro-level barriers might condition individuals in following a specific path, making it unclear if social network characteristics are a function of spatial or social mechanisms.

We demonstrated that spatial environments are key factors in social networks (Webber et al., 2023) and that colonial seabirds' 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). 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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