Body condition, but not reproductive success, is associated with sociality in a colonial seabird.

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Author Contributions

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

Supplementary materials

Data is available here:

https://osf.io/m7fcq/overview?view_only=e9208a508615407b9cf5856e53681900

Conflict of interest

The authors declare no conflict of interest.

Acknowledgement

We acknowledge Samuel Goguen, Jillian Taylor, Kathryn Collier, Chandler Anstey, Raul Zabala, Lily Bertolo, Jasmine Bridger, Fiona Le Taro, and Amy Wilson for their help in data collection and their assistance with banding. We also acknowledge the participation of Sittara Herat, Emma Wiseman, Jessica Vaters, Nazzin Dadashli, Hannah Stapleton, Rebecca Parsons and Amy Butler in the data entry. This work was supported by the Natural Sciences and Engineering Research Council of Canada Discovery Grant (RGPIN-2019-04984 to P-P. B.) and Discovery Launch Supplement (DGECR-2019-00029 to P-P. B.). Additional funding came from Memorial University of Newfoundland (MUN) Faculty of Science Start-up Funds, MUN School of Graduate Studies, the Canada Summer Jobs program, and Women in Science and Engineering Newfoundland and Labrador Student Summer Employment Program.

Abstract

Body condition, breeding habitat quality and access to socially acquired information are generally associated with higher fitness in social animals. In colonial species that breed in dense aggregations, such as seabirds, the combined effects of these factors on reproductive success have rarely been tested together.

In this study, we investigated the relationship between fledging success, body condition, nest site quality and sociality in Atlantic puffins (*Fratercula arctica*). We first tested how social network traits were related to individual body condition and nest position on a sloped breeding site. We further tested whether fledgling success was predicted by body condition, nest position and social network traits.

We found that social connectivity was positively associated with body condition, but not with social network eigenvector centrality or transitivity. However, nest distance from the bottom of the slope was not related to sociality. Fledgling success was not affected by body condition, nest position, social connectivity, or social network eigenvector or transitivity. We suggest that social benefits may be context-dependent and could become visible when individuals experience greater ecological stressors.

Keywords: Atlantic puffin, reproductive success, social network, fitness, body condition.

Introduction

Survival and reproductive success over the lifetime of an animal have been demonstrated to be valid proxies of an individual's fitness. Among others, reproductive performance is known to be influenced by body condition (McLeay et al., 2017; Kochvar & Bitton, 2025), habitat characteristics (Gilchrist & Gaston, 1997) and sociality. However, body condition, habitat characteristics, and sociality are unlikely to act independently. Habitat quality can influence individual body condition through resource availability (Johnson, 2007) and shape social interactions by affecting local density (Webber et al., 2023). Sociality also affects access to resources, influencing body condition (Monier, 2024). Together, those factors can drive reproductive performance, yet their combined effects remain poorly understood. Here, we interrogate the roles of parental body condition, habitat characteristics, and sociality in the reproductive success of a colonial seabird, the Atlantic puffin (*Fratercula arctica*).

Parental body condition in birds can be assessed with a variety of methods. This includes total body electric conductance (Castro et al., 1990) and other non-destructive methods to estimate fat reserves, but the most common one, the body condition index (Peig & Green, 2009), reflects body mass in relation to body size. This metric has been used to address important evolutionary and ecological questions relevant to natural selection (Gillooly & Baylis, 1999) and sexual selection (Rowe & Houle, 1996). Several studies have demonstrated, for example, that parents in better condition have chicks with greater growth rates, that fledge at a higher size and mass, and benefit from higher survival rates (Mota-Rojas et al., 2023). These benefits are conferred, in part, because parents in greater body conditions perform better during periods of poor resource availability (Houston & McNamara, 1993), and demonstrate greater behavioural plasticity in their food acquisition (Geary et al., 2019). The greater probability of survival can be further mediated through protective behaviours (Paredes & Insley, 2010); when predation at fledging is the main cause of reproductive failure (Gilchrist & Gaston, 1997), parents in better condition can invest more in territory defence and chick protection (Paredes & Insley, 2010). However, parental body condition is not only dependent on intrinsic qualities; it is also shaped by environmental conditions, particularly habitat quality (Johnson, 2007).

Habitat quality deriving from feature complexity and quality, along with distance between nesting and foraging resources are strong drivers of reproductive success (Vickery et al., 1992), and seabirds often select breeding sites accordingly (Gilchrist & Gaston, 1997; Regehr et al., 1998). In Black-legged Kittiwakes (*Rissa tridactyla*), for example, fledgling success is positively correlated with nesting in a central position and the presence of protective cliffs in the colony, as these features limit the risk of predation (Regehr et al., 1998). In Thick-billed Murres (*Uria lomvia*), it is the position of the nest toward the edges and the number of obstacles below them that influence chick survival (Gilchrist & Gaston, 1997). Those two examples reflect the importance of habitat characteristics by highlighting how nest position within the colony drives fledging success. Indeed, each species has a different criteria when evaluating habitat quality. Cliff breeders value inaccessibility to predation, while species breeding in burrows can be more attracted to locations on slopes, limiting flooding risks (Rodway et al., 1998). Preferences for slopes in species like Atlantic puffins could also be driven by their high wing loading (Shoji et al., 2015) resulting in limited ability to take off from flat nesting grounds. It would be expected that individuals would favour nest sites away from flat terrain and high enough on a slope to allow for easy flight take-off. Such nesting sites would be energetically beneficial compared to the efforts required by individuals nesting lower, who would have to move up to leave the colony, at least in days without wind. Such habitat structures not only shape the nesting distribution of individuals within the colony but also influence opportunities for social interactions.

The ability of individuals to establish and maintain social bonds, also called sociality, impacts reproduction (Silk et al., 2003; Cameron et al., 2009; Nuñez et al., 2015). In colonial seabirds, sociality can enhance opportunities to locate foraging patches otherwise inaccessible (Weimerskirch et al., 2010), and dilute predation and kleptoparasitism risks (Hammer et al., 2023). Overall, seabirds often aggregate to benefit from the protective mechanisms offered by the colony. In addition, sociality can generate learning opportunities through contact with conspecifics (van Schaik, 2010), and can improve chick survival through, for example, the capacity to match prey size to chick growth stage (Limmer & Becker, 2009). While the benefits of sociality, particularly on seabirds, are well documented, the mechanisms linking individual condition, habitat selection, sociality, and fitness remain poorly studied.

Parental body condition, habitat characteristics, and sociality are interconnected. Individuals in better body condition may have greater opportunities to engage in social interactions, such as territory protection or through increased social activity related to foraging (Giles et al., 2020). Habitat characteristics determine spatial proximity to conspecifics and influence their frequency of association (Krause et al., 2015). Individual body condition and habitat characteristics may shape social associations, which in turn can influence reproductive success. Social network analysis provides a powerful framework to investigate these relationships simultaneously. However, while sociality in seabirds and its advantages have been largely reviewed (Evans et al., 2015; Monier, 2024), studies using social network analysis to understand sociality in those taxa are much less common (but see Genovart et al., 2020). In this study, we co use a social network analysis framework on a colonial seabird, the Atlantic puffin, to understand how body condition, nest distance to the bottom of the slope (as a proxy of nest site quality) and sociality are related to chick fledging as a measure of fitness. We expect body condition and nest distance to the bottom of the slope to be related to sociality, as birds in better condition may engage more in social activities, whereas nest position on the slope influences which individuals repeatedly encounter one another. Additionally, individuals in better body condition with the highest nesting locations and greater social connectivity should have greater probability of fledging a young.

Methods

Study species and site

The Atlantic puffin is a colonial seabird that mates for life with a low divorce rate (Ens et al., 1996; Mercier et al., 2021), has a long lifespan (up to 45 years old in the wild; Fransson et al., 2023) and nests in dense breeding colonies (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). As in other species, densely populated colonies force high levels of social associations, and the position of an individual's nest dictates who they associate with (Morel *et al.* Under Review). Puffins lay a single egg from mid-May to mid-June, and the brood rearing period lasts ~39 days (Soriano, 2022). After fledging their young, from early to mid-August, adults leave the colony and migrate in September (Harris & Wanless, 2011). Body condition in adult Atlantic puffins is likely to be affected by their foraging strategy; the species they prey upon vary with their location, time of year, and oceanic conditions (Durant et al., 2003; Davoren et al., 2007). Additionally, they often alternate short foraging trips to provide chicks and long trips for self-feeding (Fayet et al., 2021). Atlantic puffins are social animals, forming communities and associating mostly with spatially close nesting conspecifics Morel *et al.* Under Review). While males and females exhibit similar social networks (Morel & Bitton, Under Review), it remains unclear whether they maintain distinct parental roles (Creelman & Storey, 1991; Fitzsimmons, 2018; but see Anker-Nilssen et al., 2024). Individuals nesting at the base of a slope must move up to take off, whereas those on flat land aggregate at the cliff’s edge, presumably to facilitate quick departure from the colony if needed. As in other species, breeding is energetically costly, as evidenced by body mass reduction over the breeding period, and parental condition and colouration are associated with chick growth and size at fledging (Kochvar et al., 2026).

This study was conducted on Great Island located in the Witless Bay Ecological Reserve of Newfoundland and Labrador, Canada (47.1855N, 52.8121W). The Reserve forms the largest Atlantic puffin colony in North America, with 350,000 breeding individuals (Wilhelm et al., 2015). The fledging success in the reserve was 76 % in 2021 and 2022, which is consistent with other breeding populations in the West Atlantic (e.g., Elliston 81 %, Puffin Island 90 %, Bakeapple Island 88 %; Belenguer, 2023) and twice that of the declining populations in Iceland (Hansen, 2021) and Norway (Anker-Nilssen et al., 2020). We selected a plot of ~168 square metres (14 m X 12 m) on the southern part of Great Island with a 40 % slope facing west. The slope face is about 20 m high, and its base is flat, so individuals nesting at the bottom must move up the slope to take off. Based on previous studies, we estimated this plot to support a maximum of 170 active burrows, with 76 % of them successfully producing fledglings (Wilhelm et al., 2015; Belenguer, 2023). The plot was selected to 1) minimise bird disturbance (e.g., for access and observation) and 2) minimise operational risks (e.g., avoiding cliffs and dangerous paths), but 3) maximise colony representation. To ensure data collection without disturbing the birds we built a semi-permanent blind/hide at the foot of the slope before the puffins returned from their wintering grounds, with a direct view on the plot (Figure S1).

Field method

Trapping and banding

We trapped 124 colour-banded individuals using the methods described in Morel & Bitton (2026). To evaluate the best capture period (mean hatching date with 80 % of hatched eggs), we regularly kept track of the egg-hatching status on the plot using burrowscopes with infrared illumination (EMS2021 Gopher Tortoise Camera System, Environmental Management Services, Canton, Georgia, USA). Experienced banders captured the birds by hand-grubbing in the nests. Nests were marked individually using a uniquely numbered tag secured by the burrow entrance with a plastic peg. We fitted each individual with a unique combination of three Darvic plain colour bands custom-made from Avian ID (9.53 mm ID X 7.93 mm HT), and a Canadian Wildlife Service stainless-steel band with a unique identifier. We weighed the birds to the nearest five grams with a Pesola spring scale and measured with a ruler the flattened wing chord to the nearest millimetre. Each bird was handled for no more than seven minutes before being released in its original burrow.

Social network

To collect information about puffins' social network, we used the same methods as presented in Morel & Bitton (2026) and monitored the 124 colour-banded individuals using a scan sampling method. This method consisted of scanning the plot and peripheral areas with binoculars, looking for associating banded individuals. We defined an association as any individual entering within a two-metre radius of another, even if they did not physically interact or display. For this study, we performed 85 hours of scan sampling distributed among 34 sessions from July 20th to August 09th, 2022.

Identification of fledgling success

To measure individual fledging success, we conducted two assessments of burrow contents from which we captured adults in 2022. The first assessment occurred during incubation, on June 16th 2022, to maximise occupancy detection and avoid late clutches while limiting the effect of early-stage failure. An active burrow was defined as any cavity containing an egg. For content detection, we used burrowscopes with infrared illumination (EMS2021 Gopher Tortoise Camera System, Environmental Management Services, Canton, Georgia, USA) as this method can perform better in content detection than handgrubbing (Belenguer, 2023). The fledging period is variable in puffins and can change from a few days to several weeks based on oceanic conditions (Rodway et al., 1998). Because we aimed to minimise bias by missing early-fledging chicks more than accurately finding the peak of fledging, we conducted the last burrow check as early as August 6th, 2022. A successful fledgling chick was defined as one that was still alive on this date.

Burrow distance from bottom of slope

We evaluated the nest distance to the bottom of the slope using burrow GPS coordinates while accounting for the slope of the landscape (40 °), using the method presented in Morel & Bitton (2026). We first projected each GPS position on a distribution map in the QGIS software v.3.34.3

(QGIS Development Team, 2022), before using ImageJ software v.1.54 (Abràmoff et al., 2004) to calculate the number of pixels for one metre and before extracting X and Y coordinates for each burrow. We then calculated the distance from burrows to the nearest slope edge using basic trigonometric functions.

Analyses

Calculation of body condition index

Body condition is often used as an indicative metric of health and fitness and was originally calculated from the residuals of an ordinary least squares (OLS) regression of body mass against length (Peig & Green, 2009). However, studies pointed out the risks of using OLS regression residuals with ecological predictor variables by highlighting potential important biases if the data have unequal variance or have heavy tails (Hayes & Scott Shonkwiler, 2006). In this study, we used the scale mass index, which is the most suited indicator of the relative size of energy reserves (Peig & Green, 2009). We calculated the scaled mass index (SMI) using the following function:

$$SMI_i = M_i \left[\frac{L_o}{L_i}\right]^{b_{SMA}}$$

Where M_i represents the mass of an individual, L_i is the wing length and L_o the mean wing length of the population b_{SMA} is the scaling component. The scaling component was calculated as the slope of the standardised major axis regression using the *lmodel2* package (Legendre & Oksanen, 2024) on the non-transformed values of mass on wing length (Peig & Green, 2009). The values were not transformed prior to calculating SMI, because they presented a linear relationship.

Calculation of social network parameters

For all data management and analyses performed, we used R statistical Software v.4.2.3 (R core Team, 2025). We calculated the values of betweenness, strength, closeness, degree, eigenvector and transitivity using the *igraph* package (Csardi, 2013). Because all variables but eigenvector and transitivity were highly correlated, we used a principal component analysis to reduce these traits to a single combined value. To validate the structure of the dataset for principal component analysis, we evaluated sampling adequacy and tested multicollinearity using a Kaiser-Meyer-Olkin test and a Bartlett's test of sphericity, respectively. The principal component analysis was performed using the '*prcomp*' function from R *stats* package, using scaled and centred values.

In social network analysis, community structure (henceforth called modules) represents sets of highly interconnected nodes. Different algorithms can be used, but optimisation methods that aim to maximise an objective function are among the most popular (Clauset et al., 2004; Pons & Latapy, 2006). Here, we used the most recent fast unfolding community analysis from Blondel et al. (2008), calculated by Gephi software v.0.10.1 (Bastian et al., 2009). This method was originally developed for large networks but still returns very good results for smaller datasets (Ellis et al., 2017). The modularity metric, to test the robustness of the module detection, was calculated using the Laplacian algorithm (Lambiotte et al., 2014). The modularity metric ranges from -1 and 1, with one reflecting a strong module attribution, and zero suggesting random assignment.

Models

We tested the relationship between social network parameters, body condition, distance to the bottom of the nearest slope edge and chick fledging success. Using the *glmmTMB* package, we tested how body condition and distance of the burrow to the bottom of the slope influenced social network terms using two models. In the first model, we tested an index including strength, betweenness centrality, degree of centrality and closeness as a dependent variable with body condition and distance of the burrow to the bottom of the slope as independent variables. In a second and third model, we tested eigenvector centrality and transitivity as outcome variables with the same predictors as in the first model. To avoid pseudo-replication when both members of a pair were captured in their burrow, the burrow identification number was included in the models as a categorical random term. We used the diagnostic plots from the *DHARMa* package (Hartig & Lohse, 2022) to validate the assumptions and found that the Gaussian family (for the values of social connectivity and transitivity) and the Gamma family (for eigenvector centrality) returned the best model fit. We reduced the full models using a stepwise approach, removing the non-significant interaction terms obtained from ANOVA tables. The final models only contained main effect terms that were significant.

Finally, we tested whether fledging success was a product of body condition, distance to the bottom of the slope and the three social network terms. We used generalised linear mixed models with a logistic regression (logit link function) to test fledging success as the binary (fledged/not fledged) dependent variable and the values of social connectivity, module identity, the values of eigenvector centrality, transitivity, body condition and distance to the bottom of the slope as the independent variables. Burrow identification number was again used as a categorical random term. We used the diagnostic plots from the *DHARMa* package to validate our assumptions. We reduced the full model using a stepwise approach.

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 and Labrador 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.

Result

To measure individual fledgling success, we conducted two burrow content assessments on 67 marked burrows from which 80 individuals were colour-banded. The 44 colour-banded individuals tracked but not assessed for fledging success included: nests where the content was uncertain because we were unable to see the burrow content, and individuals banded in 2021 for whom the burrow was not successfully relocated in 2022. We were not able to recapture all individuals from 2021, probably because puffins are known to dig deeper following disturbance (outside of grubber range, Harris & Wanless, 2011; Fitzsimmons, 2018). Three burrows had to be discarded at the last assessment as the fledgling success was uncertain, and two could not be found while assessing burrow location. Identifiers can be hard to find late in the season as the grass has often overgrown the markers and some markers can be pulled out by the birds. From the 62 remaining burrows, 23 failed, and 39 succeeded in bringing a chick to fledging (Figure 1). By using the fast-unfolding community analysis from Blondel et al. (2008), we found six modules. The modularity metric was significant (0.443), indicating that individuals were not randomly distributed in their modules. To reduce the correlated social network metrics to a composite measure, we conducted a PCA. The Kaiser-Meyer-Olkin tests ranged between 0.79 and 0.96, confirming high levels of correlations among variables, and Bartlett's test of sphericity ($\chi 2$ = 773.7932, df = 6, p < 0.001) demonstrated that the correlation matrix was different than an identity matrix. The first principal component explained 94 % of the variance and was approximately equally loaded by all four social network metrics (Table S1). High values of the principal component were associated with high values of degree, betweenness, strength and closeness, such that we interpret this component as a metric of social connectivity.

In the first series of models, we found that body condition ($\chi 2$ = 4.465, df = 1, p = 0.034, Figure 2, full model summaries available in Table S2) was positively related to social connectivity; high values of sociality were related to high values of body condition. Distance to the bottom of the plot was not a predictor of social connectivity. Body condition and distance to the bottom were also not significant predictors of either eigenvector or transitivity values.

We examined how fledging success was related to sociality, body condition, and distance from the bottom of the slope. In this model, only eigenvector centrality was negatively related to chick survival ($\chi2 = 6.2389$, df = 1, $p = 0.0125$). Burrow distance to the bottom of the slope, body condition nor any of the social network terms were significantly related to fledging success. The conditional R^2 of the final model explained a very high proportion of the variance in the model (conditional $R^2 = 0.998$, marginal $R^2 = 0.034$), because individuals from the same burrow have identical fledging success. Therefore, while the eigenvector term was statistically significant, it explained a very small proportion of the variance in the model.

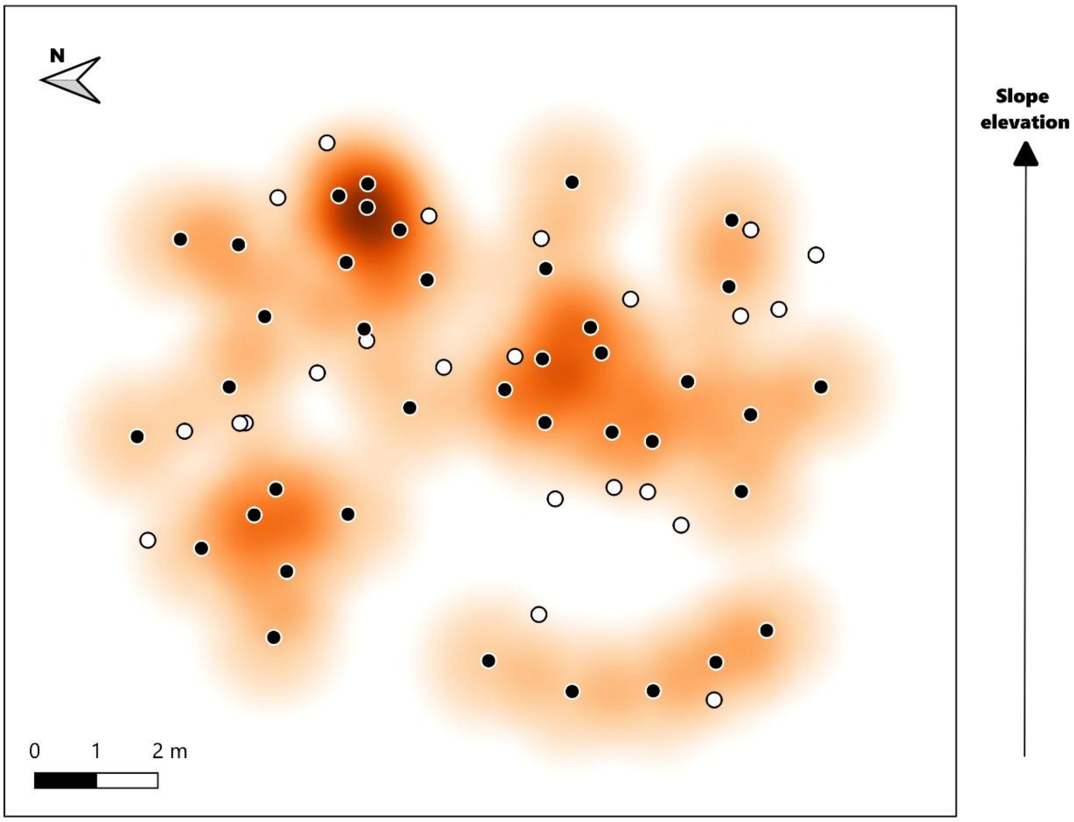

Figure 1. Kernel density map of 39 successful burrows in 2022 overlaid with burrow distribution, with black circle representing successful burrows (n= 39) and white circles representing burrows that failed to fledge a chick (n= 23). The details of the methodology are available in supplementary material.

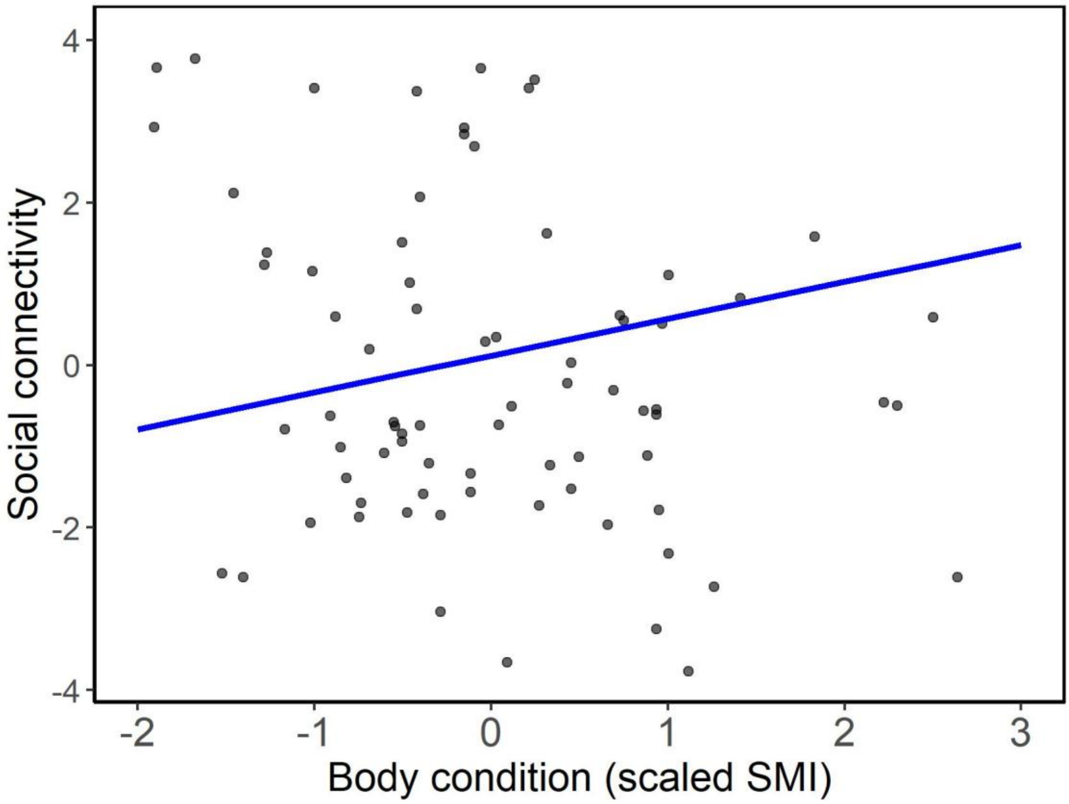

Figure 2. Relationships between body condition (expressed as the scaled mass index in grams) and social connectivity (expressed as the first dimension of a principal component analysis), based on model-predicted marginal effects from a generalised linear mixed-effects model.

Discussion

This study aimed to investigate whether body condition and/or distance to the bottom of the slope affected social network metrics in Atlantic puffins, and how these traits influenced fledging success. We found that individuals with greater body condition had greater social connectivity, a metric integrating betweenness, closeness, degree and strength, good indicators of social network structure (Freeman, 1978) and social behaviour patterns (Croft et al., 2008). Our results also showed that nest distance to the bottom of the slope was not related to any of the social terms tested. We did not find any strong evidence for the influence of body condition, nest position or sociality on fledging success.

Identifying traits that drive sociality is important for understanding colonial seabird systems, as they rely on social networks to obtain information about food resources, reduce predation risk, and locate mates (Monier, 2024). Body condition may influence an individual's ability to engage in social interaction, which can affect foraging performance, survival, and reproductive success. Birds in better condition (Öst et al., 2015), as in other taxa (Finn et al., 2025), are more capable of engaging in collective behaviours. Our results show a similar pattern: body condition was positively related to social connectivity. While birds in better condition are more capable of engaging in collective behaviours, the causal relationship is still unclear. Individuals who are more socially connected may gain information about profitable foraging opportunities, improving their body condition. In colonial seabirds that rely heavily on socially acquired information, we can expect birds in better condition to benefit from their conspecifics, by, for example, having greater access to foraging patch information or dilute risk of predation. Determining the causal relationship of our finding could be challenging, but at least partially resolved by evaluating the relationship between sociality and foraging proficiency (number of daily trips, duration of trips) among individuals.

Eigenvector centrality and transitivity, however, do not appear to be predicted by body condition, and this can be explained by the distinct social properties captured by these metrics. Social connectivity integrates four network metrics: strength, closeness, betweenness, and degree, which describe an individual’s own position within the network. Eigenvector and transitivity are metrics that depend on the connectivity of social partners. We found that a puffin in good condition is associated with many conspecifics, but those contacts are not necessarily the most well-connected individuals (eigenvector) or the most interconnected (transitivity) in the studied population. These results suggest that body condition can influence an individual’s position in the network, while having little effect on the social relationships of its conspecifics. Network metrics such as eigenvector centrality and transitivity may instead be shaped by environmental constraints, including habitat structure, which can determine access to social partners. Habitat structure could, for instance, limit or encourage movement and opportunities for association through physical barriers or mandatory passages. Furthermore, once individuals gain sufficient social benefits, fewer additional advantages to associating with particularly central individuals or highly interconnected groups would be expected. Thus, individuals may leverage social connectivity but may not seek particular individuals.

Nest position on the slope does not appear to constrain social associations in this population, contrary to our expectation. The high wing load of puffins prevents them from taking off without wind or a high position to jump from (Clay et al., 2020). To reduce the cost induced by taking off from a lower position, low-nesting puffins will climb up the slope until they reach a sufficient height. Individuals nesting high on the slope are likely to encounter the individuals climbing up to reach a better area to take off. Additionally, individuals at the bottom, since they are considered to have a lower quality nesting site due to a higher risk of flooding (Rodway et al., 1998) are likely to have fewer neighbours. One explanation is that animals in transit between the bottom of the slope and better flight-initiating locations do not slow down or pause when encountering other individuals, limiting our ability to detect these associations when they do take place. Video footage of colour-banded individuals and subsequent movement tracking would enable us to not only capture these associations but also explain this finding by placing them spatially on the landscape. Another reason why nest position on the slope may not be constrained by sociality is that nest position is generally fixed throughout the breeding season, whereas social associations can vary rapidly in response to breeding phases (Morel & Bitton, Under Review). Individuals can maintain non-random associations with individuals nesting far from them (Morel *et al.* Under Review), providing support against the idea that poor nesting sites will reduce social potential. Because during high winds, individuals nesting at the bottom of the slope may not have to climb up to take off, future studies should focus on comparing networks on windy and non-windy days to see whether wind can influence their social behaviours.

We had predicted higher probability of fledging success for individuals in better body condition, with higher nesting locations, and greater sociality; our results show that none of these factors has a large influence on fledging success. These findings contradict our expectations. While eigenvector centrality was considered a statistically significant predictor, inferences based on this finding should not be over-interpreted as the very small effect size (i.e., low marginal R^2) suggests limited biological relevance. Current literature on other taxa highlights higher offspring survival with higher body condition (Mota-Rojas et al., 2023), in better-located breeding areas (Gilchrist & Gaston, 1997; Regehr et al., 1998), and when parents are better connected (Silk et al., 2003; Cameron et al., 2009). However, this relationship appears to be particularly relevant after a catastrophic event reducing the population, or in periods of poor-quality forage (Nuñez et al., 2015). In certain species like puffins, ornamental colourations of fleshy ornaments have been demonstrated to reflect parental quality. Because their colours can change rapidly and are energetically costly (Rosenthal et al., 2012), they actively reflect individual quality. A study by Kochvar & Bitton (2025) found that individuals with higher parental quality (based on ornamental colouration) had offspring with greater growth rates and greater mass at fledging, indicators of future survival (Wanless et al., 2005; Cornioley et al., 2017). It is possible that body condition based on mass and wing length has a greater influence on chick growth trajectories, as opposed to fledging success, especially in years with high fledging rates.

While in many species, including puffins (Harris & Wanless, 2011), chick survival was found to be related to burrow position, our results did not find such a significant relationship. From a methodological perspective, our study was conducted within a relatively homogeneous plot selected to ensure colony representativeness and a high rate of associations. Although this design is appropriate for capturing social behaviours, it may limit the range of variation in burrow positions and associated risks such as flooding, erosion, or predation. This could explain in part why we did not find any effect of breeding position on reproductive success. Broader sampling across the full colony would capture a wider gradient of habitat conditions and by extending the study over a greater number of years, variance in environmental conditions and breeding success may shed light on the relationships between burrow position and reproductive success in this population.

We explain the absence of a relationship between sociality and chick survival because social advantages are expected to be expressed when food resources are limited or the level of predation is high. The relatively high fledging success observed in the study colony suggests that breeding conditions during 2022 may have been favourable, potentially reducing the difference in social benefits between individuals. Under low food availability, individuals with high body condition and with access to social information should be able to better track changing resources, maintain dynamic foraging strategies and bear increasing foraging costs (David et al., 2012; Dosmann et al., 2015). In such a situation, it would be expected that better-connected individuals should perform better, due to better access to social information. Finally, the benefits associated with predator dilution are likely shared by most individuals as birds often leave from and arrive to the colony in large groups, limiting the effect of individual social position.

This study highlights that individuals with higher body condition have higher social connectivity, suggesting a relationship between individual quality and social behaviour. However, we found no evidence that body condition, nest position toward the bottom of the slope or social network structure affected fledging success. We propose that theses finding suggests that some benefits from sociality are likely to emerge only under challenging environmental conditions.

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Supplementary material

Method kernel density map

Kernel density estimation (KDE) was used to visualise the spatial distribution of successful burrows. Geographic coordinates of all successful chicks were imported into QGIS (version 4.03). A kernel density raster was generated from the processing tool *Kernel Density Estimation* using a fixed bandwidth of 1.5 metres. Density values were displayed as relative density classes at 13 % intervals, with the lowest 13 % of values omitted from visualisation to emphasise areas of highest concentration. Locations of failed burrows were overlaid on the KDE map as reference points but were not included in the density estimation.

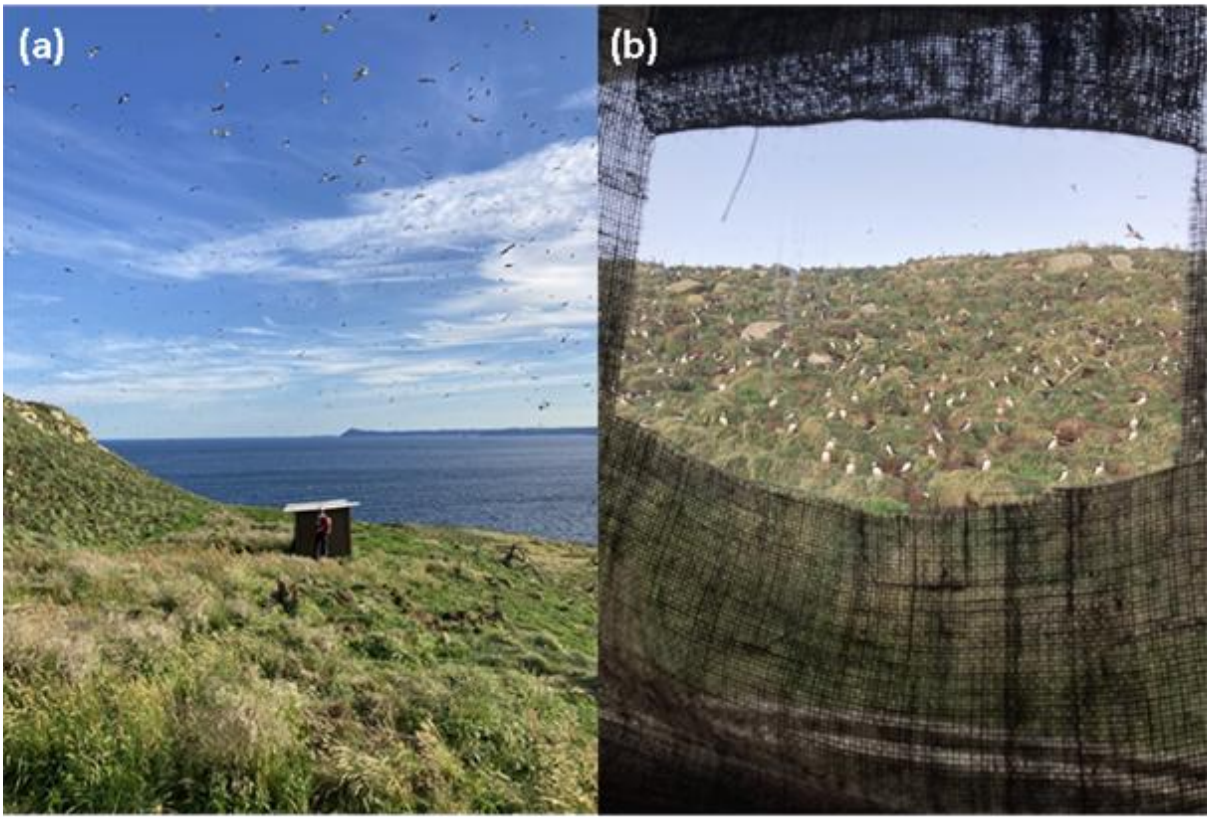

Figure S1. (a) Semi-permanent wooden blind with (b) a view of the sampling plot on Great Island in Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada. The structure is anchored to *the ground, slightly lifted and fully closed except for a front window. Two observers can simultaneously sit and have a view beyond the area of the plot while being hidden by a camouflage cover. The blind is reusable and removed between breeding seasons.*

Variables	Dim1	Dim2	Dim3	Dim4
Degree	25.70084	3.03363	21.26553	50.00000
Betweenness	23.96525	71.21962	4.815128	0.00000
Strength	25.70084	3.03363	21.26553	49.99999
Closeness	24.63307	22.71312	52.65380	0.00000

Table S1. Loading of the principal component analysis.

Model	Variables	Estimate	Std. Error	Z value	Pr (>|z|)
Transitivity ~ SMI + Distance_bottom	SMI	0.48087	0.21111	2.278	0.0227
	Distance_bottom	0.07953	0.21594	0.368	0.7126
Eigenvector ~ SMI + Distance_bottom	SMI	0.01075	0.01986	0.541	0.5882
	Distance_bottom	0.04042	0.01961	2.061	0.0393
Fledging_success ~ SMI + Distance_bottom + PC + Transitivity + Eigenvector+ Module	SMI	-4.973	3.919	-1.269	0.20443
	Distance_bottom	-2.759	3.932	-0.702	0.48293
	PC	3.583	7.693	0.466	0.64143
	Transitivity	-93.911	45.692	-2.055	0.03985 *
	Eigenvector	-124.955	61.812	-2.022	0.04322 *
	Module 1	-33.716	12.295	-2.742	0.00610 **
	Module 2	18.176	16.715	1.087	0.27686
	Module 3	-38.480	17.899	-2.150	0.03157 *
	Module 4	-19.080	10.870	-1.755	0.07922

Table S2. full model summaries.