Social network differences across the breeding season in a burrowing seabird with assumed similar sex-roles

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Conflict of Interest

The authors declare having no conflict of interest.

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; Pierre-Paul Bitton significantly contributed to the analysis and writing of the manuscript; Brendan Carswell significantly contributed to the analysis. All authors contributed to reviewing the manuscript and gave final approval for publication.

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Data availability statement

Data including analysis are available in an open-access public repository, accessible here:

Abstract

Changes in behaviours that follow seasonal cycles can affect social interactions, which in turn influence social network structures. Because such behaviours are often sex-related, their effect on social associations can impact males and females differently. While the effects of sex-related behaviours on the social network structure of species with distinct parental roles have been studied, their effects on species with seemingly similar parental tasks remain uncertain. We tested how social network trait values changed over the breeding season and whether they differ between males and females in Atlantic puffins (*Fratercula arctica*), for which parental roles are assumed to be very similar but perhaps non-identical. We studied associations between 120 colour-banded, sexed individuals and conducted scan sampling during the breeding season. We tested how social networks, built using a time-aggregated network method, changed over the breeding season. We found significant social network changes during the breeding season, with many of the traits changing during the peak hatching period. Social network traits followed similar trends for males and females during incubation but showed some evidence of divergence during the brood-rearing period. Our study demonstrates that Atlantic puffins have higher sociality during the chick-rearing period than during incubation and that males generally have greater network trait value rates of change, suggesting that they are more affected by shifts in parental behaviours than females. Because sex-related time budgets in the Atlantic puffin are unclear, we highlight the importance of having an accurate baseline of sex-related roles to interpret social structures.

Keywords: Atlantic puffin, behavioural ecology, sex-related behaviours, social network, time-aggregated network.

Significance statement

Studies on animal social behaviours suggest that changes in seasonal behaviours, because they directly affect associations with conspecifics, should influence social network traits. Using observations of identified Atlantic puffins in a colony, we demonstrated that social networks change during the different phases of the breeding season. Our results show that males and females increase their sociality when their young hatch, and that male sociality is more affected by changes in parental behaviours than females.

The activity time budget and roles of mated individuals change following seasonal cycles (Nelson et al., 1990), especially during the breeding season when requirements for the production of offspring result in sex-specific behaviours (Wojczulanis-Jakubas et al., 2014). Transitions in activity time budgets, in turn, can influence associations among individuals (Brent et al., 2013), but it is unclear what consequences they have on social network structures. In this study, we used social network analysis to investigate how changes in sex-related breeding behaviours affect the social network of a breeding colonial seabird, the Atlantic puffin (*Fratercula arctica*).

Seasonal changes affect behavioural processes such as reproduction (Brent et al., 2013; Wolf et al., 2018) and foraging strategy (Barrett et al., 2015; Durant et al., 2003), shaping social associations and subsequently forming social networks (Helm et al., 2006; Pinter-Wollman et al., 2014). The dynamic nature of behavioural processes over time (e.g., reproductive vs non-reproductive periods) induces uneven social environments (e.g., group composition and density), potentially leading to cyclical social structures (Brent et al., 2013; Wolf et al., 2018; Vilette et al., 2022). For example, individuals can form groups during winter and become territorial during the breeding season (e.g., Great tit *Parus major*; Aplin et al., 2013), or aggregate in the breeding season but not during the non-breeding season (e.g., Common guillemots *Uria aalge*; Buckingham et al., 2022). Associations forming social network structures are known to confer individual benefits, such as fitness (Snyder-Mackler et al., 2020; Philson & Blumstein, 2023). Indeed, more socially connected individuals can have better survival (e.g., Stanton & Mann, 2012; McFarland & Majolo, 2013). However, sociality can come with the increased probability of predation (Kelley et al., 2011; Hasenjager & Dugatkin, 2017) and disease transmission (Lucatelli et al., 2021).

Previous work has shown that social networks can differ between males and females (Spiegel et al., 2018), leading to sex-specific changes in social benefits (Silk et al., 2003; Cameron et al., 2009; Cheney et al., 2016). Activity patterns within many species are well known to differ between sexes, particularly in those that have pronounced dimorphism (Ginnett & Demment, 1997; Ruckstuhl & Neuhaus, 2002). Differential investment in gametes (anisogamy; Trivers, 1972) has been argued to lead to differences in sex-related roles during breeding attempts (Janicke et al., 2016; but see Kokko & Jennions, 2008). Sex-specific and transitions in time budget for activities such as territory defence, incubation, and foraging are bound to influence the availability for individuals to associate with others and, consequently, the resulting social network structures. For example, in species where females spend more time on parental care than males, females would be expected to associate less and with fewer adult conspecifics (lower values of degree and strength) because of a time budget directed toward parental care

(Vilette et al., 2022). Such lower female sociality has been shown in wild vervet monkeys (*Chlorocebus pygerythrus*), with females spending less time engaging in social behaviours than males during winter. Higher energy requirement during pregnancy explains these social differences, as increases in time spent foraging decreases socialising time (Canteloup et al., 2019). In contrast, social network attributes should be very similar among the sexes for species where sex-related roles are almost identical due to similar investment. Although sex-related behaviours affecting social networks have been broadly studied in species with distinct roles (Lavista Ferres et al., 2021; Spiegel et al., 2018; Vilette et al., 2022), social network structures of species with similar behaviours have received much less attention.

The Atlantic puffin is a monogamous colonial seabird with a maximum lifespan of over 45 years in the wild (Fransson et al., 2023). In Canada, Atlantic puffins spend every winter at sea and return to breeding sites in April. At breeding sites, puffins form large breeding colonies with high burrow densities (e.g., 1.37 burrows/m² on Gull Island Canada, Belenguer, 2023). Individuals generally mate with the same partner for life and return to the same burrow every year to lay a single egg (Harris & Wanless, 2011). Incubation starts in mid-May and lasts ~40 days with a mean hatching day of late June/early July (Belenguer, 2023), and the brood rearing period lasts between 38 and 44 days. After fledging, generally in mid-August, immature individuals spend the next five years (until sexual maturity) at sea. The adults leave the colony when their chick fledges and migrate back to sea in September (Harris & Wanless, 2011). Land-based activities for puffins are generally composed of incubating and chick feeding behaviours, as well as defending the burrow entrance against conspecifics and predators, and preventing the chicks from exiting the burrow too early (Creelman & Storey, 1991; Anker-Nilssen et al., 2024). Puffins are also often seen preening and resting sometimes on slope edges or exposed rocks and boulders, very often in high density. At sea, puffins form rafts and forage in groups (Harris & Wanless, 2011). Studies that have investigated sex-related roles in Atlantic puffin do not concur on which sex is more involved in specific behaviours (Harris & Wanless, 2011) or often have limited sample sizes (Wallace et al., 2025). The difficulty mainly comes from the complexity of quantifying nesting-related behaviours in this species. Atlantic puffins sex can only be accurately obtained molecularly (Friars & Diamond, 2011), making identification in the field possible only by colour bands. Furthermore, parents provision their chick a few times a day and enter their burrows quickly to avoid predators (Greater Black-backed Gull *Larus marinus*; Langlois Lopez et al., 2023) and kleptoparasites (e.g., Herring Gull *Larus argentatus*; Busniuk et al., 2020). In some studies, male puffins have been shown to spend more time on land than females, maybe to defend the burrow (Anker-Nilssen et al., 2024), whereas females are more involved in underground incubation and chick provisioning (Creelman & Storey, 1991; Fitzsimmons, 2018; Wallace et al., 2025). In this scenario, males would be more socially active than females in the two breeding phases because of more time spent on land, outside of their burrow. Other studies have found that females and males seem to share parental care equally and do not display a difference in time budget (Corkhill, 1973; Harris, 1986). In contrast to the previous scenario, males and females would have a similar social network structure that would change concurrently for both sexes with the transition between incubation and chick rearing.

In this study, we investigated a colour-banded population of Atlantic puffins to evaluate how social network trait values can change between (i) the two main breeding phases, incubation and chick rearing, and (ii) males and females. Current evidence shows that close nesting neighbours associate more than expected by chance, (Morel et al., 2025) and Atlantic puffin social associations on land are heavily influenced by the presence or absence of their neighbours at the colony. Thus, changes in land-based activities would be reflected by changes in social network characteristics.

Materials and methods

Study site

We selected an area on the south part of Great Island (47.1855N, 52.8121W), in the Witless Bay Ecological Reserve of Newfoundland and Labrador, Canada. The population of Atlantic puffin on the island was estimated at 350,000 breeding individuals in 2015 (Wilhelm et al., 2015) and 410,000 in 2023 (Wilhelm, unpublished data). Behavioural observations were conducted on a plot of ~168 square metres (14 m X 12 m), 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. We estimated a maximum of 170 active burrows (Wilhelm et al., 2015; Belenguer, 2023) present on the plot. To conduct the observations, we used the flat area at the foot of the slope to build a semi-permanent wooden blind 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 method

To collect information about puffin social network, we colour-banded 124 individuals over two years (50 in 2021, 74 in 2022). Atlantic puffins, like many seabirds, are more prone to abandonment during incubation than chick rearing (Yorio & Boersma, 1994; Rodway et al., 1996; Blackmer et al., 2004), so adults were captured only after their 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 at least 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 ID X 7.93 mm HT, Black, White, Green, Grey, Red, Yellow, Dark blue and Light blue), and a Canadian Wildlife Service stainless steel band with a unique identifier. At the time of capture, a blood sample was taken for each bird trapped. A volume of 0.1 mL of blood was taken from the brachial vein and stored on a Whatman® FTA (WB120210) card for molecular sexing. 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 in proximity (within a two-metre radius) to another, even if individuals did not physically interact or display. A radius of 2 metres was selected as a threshold for association, based on the average distance between marked burrows (~1.5 metres) to capture nearest neighbours and account for the influence of the spatial distribution of nests on social interactions. To document associations, we performed 210 hours of scan sampling on the 124 potential colour-banded individuals, distributed among 53 sessions from Jun 06th to August 07th, 2023. We conducted the observations regardless of the weather conditions three to five days in a row, followed by a few days of break. Over the data collection period, four trained observers were involved in the annotation of interactions from a blind. 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. Each session lasted four hours and consisted of visual observations performed by two observers equipped with binoculars (Swarovski EL 10x42 WB). The observers screened the plot and the areas peripheral to the limits of the plot for banded birds. A session was either in the morning or evening. The morning sessions always started at civil twilight when colour bands became visible. The evening sessions started four hours before sunset and extended until visibility was too low to identify colour bands correctly. To limit bird disturbance, the observers entered and left the blind at night, generally during astronomical twilight. To maximise detection, the observers used two strategies. When the slope was crowded, they scanned the area from top to bottom and right to left. When only a few birds were visible, observers targeted and followed specific groups of individuals. An event was created for each banded individual recorded with at least another individual within a two-metre radius. Each event was identified using time and an incrementing unique ID. A new event was generated every two minutes or every time a new individual entered the two-metre radius of a focal banded individual. The screening was resumed by the observers quickly after band identification to guarantee no birds were missed.

Data extraction

Molecular sexing

To identify the sex of the Atlantic puffins sampled, we followed the method described by Wages (2005). This method consisted of extracting the DNA from the blood before running a polymerase chain reaction (PCR) to amplify the chromo-helicase DNA 1 (CHD1) gene on the avian W and Z chromosomes. In short, we extracted DNA using the DNeasy® Blood & Tissue Kit (Qiagen Inc., Toronto, ON, CA) from a 1 cm^2 saturated blood card collected in the field. From 2 µl DNA, we added 12.5 µl Thermo Scientific™ PCR Master Mix, 2 µl of both primers 2550F and 2718R and 6.5 µl of nuclease-free water. We used an Eppendorf Mastercycler® ep gradient S to perform the PCR, which was then transferred to an electrophoresis gel made of RedSafe™ agarose gel. We used a Thermo Scientific™ EC 300 XL at 130 A to migrate samples and controls for 50 minutes. The results were read by Image Lab software.

Social network

For all data management and analyses performed, we used RStudio statistical Software v.4.2.3 (R core Team, 2025). To evaluate the influence of breeding phases and sexes, we evaluated the difference in network topology between the incubation and the rearing period as well as between males and females by using a time-aggregated network following the methods and R package netTS from Bonnell & Vilette (2021). The breeding season was divided into time windows, a series of periods for which social network terms can be calculated and compared. To assess the appropriate time window size, we compared the variation and the uncertainty between different time series of our parameters (e.g., strength, degree, and betweenness; closeness could not be calculated) using the ‘check.windowsize’ function of the netTS package (Bonnell & Vilette, 2021). We found low variation for a window size of 15 days and two fixed-day window shifts for strength, betweenness and degree (see Figure S2 in supplementary material). We confirmed this trend by testing the cosine similarity for three sample size series (100 %, 80 %, and 60 % of the data set) and four window sizes (10, 15, 20, and 25 days; Figure S3 in supplementary material). The measure of uncertainty revealed a very high similarity (0.9) at 15 and 20 days and a low response to sample size variation for strength and degree. The estimates for betweenness were not as robust as for the other parameters with higher similarity changes, but 15 days still appeared to be the best compromise between useful temporal aggregation and noise (see similar approach in Vilette et al. 2022). Together with the measure of window size variation, the uncertainty between time series and sample size validated our choice of a 15-day window and a 2-day window slide as being an appropriate parameter to detect social network’s change over time.

To evaluate the amplitude of social network changes between breeding phases, we used four centrality measures. 1) Strength: represents the number of associations per node (i.e., individual). A high value of strength can reflect an individual who associates often with a few conspecifics, or associates rarely with numerous conspecifics (Farine & Whitehead, 2015). 2) Closeness: the average of the shortest path length from the node to every other node in the network. It indicates how close an individual is to conspecifics and high values of closeness refer to individuals that can quickly have access to information from other individuals in the network (Croft et al., 2008). 3) Betweenness: represents the shorter path between two individuals. An individual with a high value of betweenness is more likely to connect distant sections of a network (Farine & Whitehead, 2015). 4) Degree: the number of nodes connected to an individual, which gives information about the number of partners a group member is connected with. A high value of degree indicates an individual connected with numerous partners (Farine & Whitehead, 2015). Additionally, we evaluated the similarity between each window using a cosine similarity metric. This index uses edge weight variation between networks to estimate their similarity and returns a value between 1 and 0. A high value reflects little difference in the edge weights between compared networks.

Analyses

Given the nature of the sampling method (four hours of observations every eight hours), we corrected for sampling effort by dividing the value of each term by the duration of the observation scan (first and last observation) using the ‘effort.time’ function of the ‘netTS’ package (Bonnell & Vilette, 2021). Missing observations can also heavily impact the network structure and can particularly occur while simultaneously observing a large number of individuals. To correct errors due to missing observations, we used the simple ratio index (Hoppitt & Farine, 2018; Bonnell & Vilette, 2021):

$$\text{SRI}=\frac{x}{(ya + yb + yab + x)}$$

with x the number of times individuals a and b were observed together, ya the number of times individual a was observed associating without b and yab the number of times individuals a and b were observed at the same time but not associating together.

To model within-breeding-season variation of the of social network terms, we used six generalised additive mixed models (GAMMs) implemented with the *mgcv* package (Wood, 2017; Wood 2025). We fitted a unique model for each of the social network trait values (i.e., strength, degree, betweenness, and closeness), and a unique model for each of the cosine similarity indices (i.e., similarity to first window, and similarity to previous window). All models were fitted with a Gaussian error distribution and by restricted maximum likelihood estimation. In addition, all models implemented a Gaussian process spline on Julian day, factorised by sex to allow for variable smoothing for males and females, and individual bird ID was implemented in a random intercept. We assessed the fit and variance inflation of splined terms using the '*gam.check*' and '*gam.vcomp'* functions.

For each model, we predicted social network trait values and cosine similarity indices across the observed range of Julian days for each sex. To determine the Julian days at which trait values were different between males and females, we identified days when the predicted 95% confidence intervals for each metric did not overlap. Finally, to assess how the rates of social network metrics and cosine similarity indices may change between sexes and across Julian day, we calculated the derivative between sequential Julian days in model predictions. Using the '*Deriv*' and '*signifD*' functions (Simpson 2014), we determined the Julian day for males and females where social network metrics and cosine similarity indices significantly increased or decreased relative to the previous Julian day. To compare social network structure across changes in breeding activities, we used the peak hatching period calculated by Benlenguer (2023) from previous years on the same island.

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 (23-01-PB and associated amendments) issued by the 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 in 2021 and 2022 (37% of the estimated individuals, greater than the 30% considered sufficient for proper network models; Silk et al., 2015), we detected 120 (57 females, 63 males) over 210 hours of observations in 2023. From June 06th to August 07th 2023, we recorded 842 dyads and 2,464 associations.

Most terms tested showed changes across the breeding period, especially around the peak hatching period. Strength (Table 1, Figure 1a) had greater value at the end of the peak hatching period (day 184) with an almost threefold score compared to pre-hatch and post-hatch values. Males and females had very similar values, following a non-linear distribution across the breeding season (Table 1, Figure 1a). However, the periods of rate of change were different between males and females (Figure 2a). Strength significantly increased for males and females between day 174 and day 182, and declined between day 186 and 192, but males also showed a period of decline between day 165 and 168 (Figure 2a).

The smoothed term for closeness was not statistically different from a linear relationship for either sex (Table 1, Figure 1b). Because the confidence interval from the model prediction did not overlap, females had generally higher but non-significantly different values than males. The rate of change for closeness did not significantly change for males and females at any time during the breeding season (Figure 2b).

Betweenness values increased throughout the breeding season and were significantly non-linear for males but linear for females (Table 1, Figure 1c). Based on the 95 % CI, male values of betweenness were significantly different from females from days 194 to 196 (July 13th to 15th). Betweenness significantly increased for males but not for females between day 175 and day 192 (Figure 2c).

The values for degree did not follow a linear trend (Table 1). They decreased until ~ day 170, around the time hatch would have started, but trended higher starting just before peak hatch period, reaching their highest point at day 190 (Figure 1d). The change of rate for degree significantly decreases for males and females, respectively from day 164 to day 170 and 163 to 169, and increases between days 183 and 190 (Figure 2d). Males also showed a period of increase between days 172 and 177, 183-190 and a decrease between days 198 and 202. While values of degree were generally the same between sexes, male values were significantly different from females from days 196 to 198 (July 15th to 17th).

The cosine similarity between the first and current window also did not follow a linear trend (Table 1). The values of cosine similarities were generally the same for males and females except between days 184 and 188 (July 3rd to 7th) for which the values of cosine similarity of the first window were higher for females than males (Figure 1e). The cosine similarity metrics displayed two shifting points during the breeding period. The first dramatic change was revealed by a drop in similarity (less than 12 % of similarity) for both males and females from day 158 to 171, matching the changes observed in strength and degree (Figure 1e, Figure 2e). The second shifting point occurred after the stabilisation of the cosine similarity value until it reached a relatively high value (~27 %) near the end of the peak hatching period. The change of rate for the cosine similarity for males and females increased between days 174 and 178 (Figure 2e). This change aligns with the differences observed around this date for strength and degree. The change of rate for females alone significantly decreases between days 188 and 194.

The cosine similarity with the previous window followed a nonlinear pattern, with no difference between sexes (Table 1, Figure 1f). The first drop to 12% mirrors the values observed in the cosine similarity between the first and current window and confirms that the social networks changed the most during incubation. For the rest of the breeding period, the similarity is very close for males and females and shows oscillations of lower amplitudes at relatively high cosine values. The change of rate for males and females decreases from days 158 to 166 and 198 to 202 (Figure 2f). The rate of change in cosine similarity increases between days 169 and 173, as well as 193 and 195.

Table 1 Summary of GAMM smooth term results for time-aggregated social network traits during the breeding season in Atlantic puffin.

Dependent variable	**Sex**	**F**	**Edf**	**p-value**
Strength	Males	12.489	7.175	< 0.001
Strength	Females	6.643	5.853	< 0.001
Closeness	Males	0.020	1.002	0.891
Closeness	Females	1.133	2.143	0.403
Degree	Males	59.25	8.079	< 0.001
Degree	Females	19.11	6.371	< 0.001
Betweenness	Males	15.757	3.434	< 0.001
Betweenness	Females	1.331	1.002	0.248
Cosine first	Males	132.060	7.795	< 0.001
Cosine first	Females	73.167	7.766	< 0.001
Cosine previous	Males	15.822	8.199	< 0.001
Cosine previous	Females	10.560	8.062	< 0.001

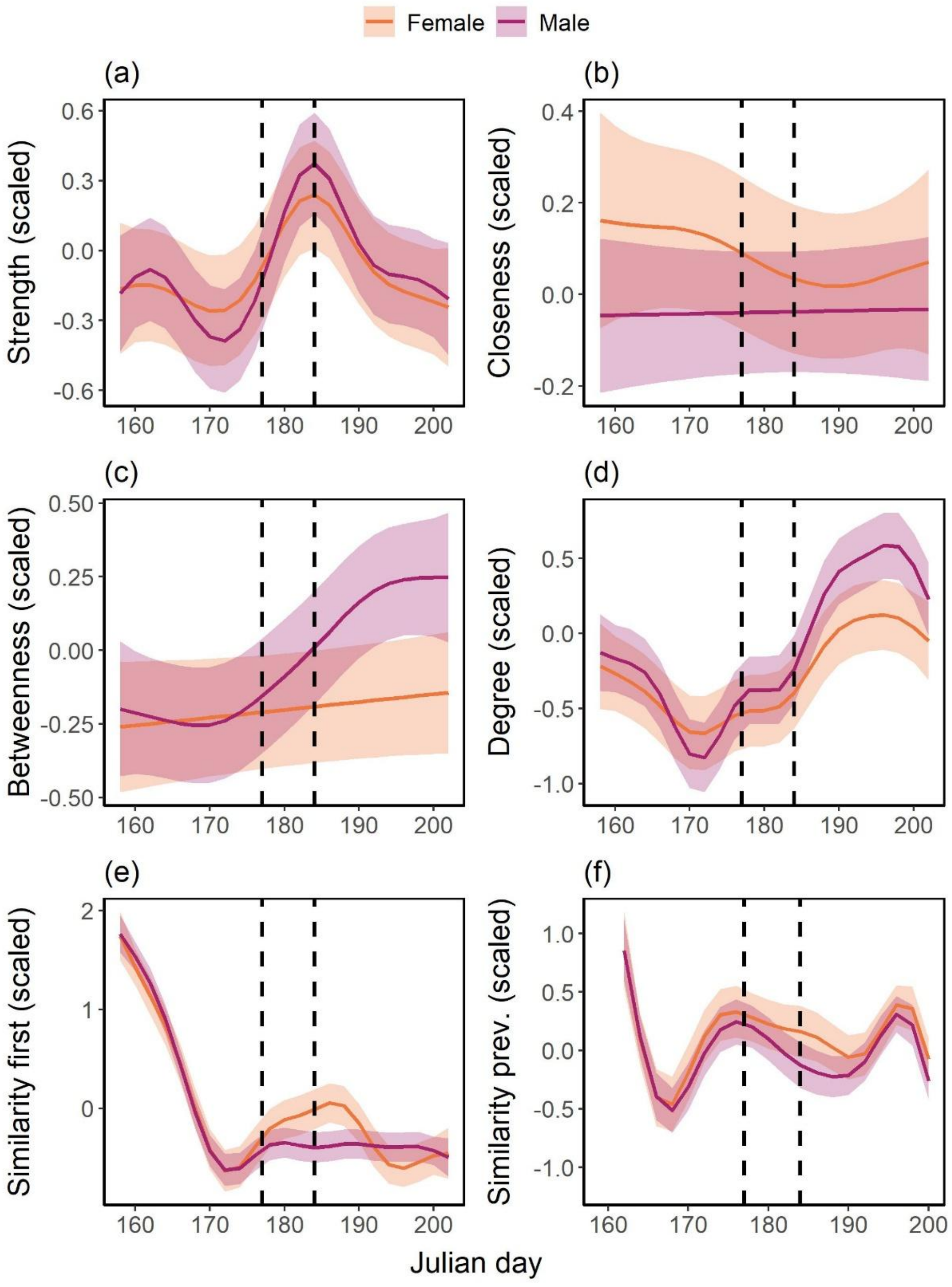

Figure 1. Seasonal changes for the values of (a) strength, (b) closeness, (c) betweenness and (d) degree in a social network of 120 Atlantic puffins (63 males, 57 females) during the breeding season after correcting for sampling effort. The cosine similarity is calculated from (e) the first-time window, and (f) the previous-time window. The orange and purple lines represent the relationship between Julian day, and social network values and their confidence interval obtained from Generalised Additive Mixed Models for males (purple) and females (orange). The two dashed line represents the peak hatching period (between Julian day 177 and 184).

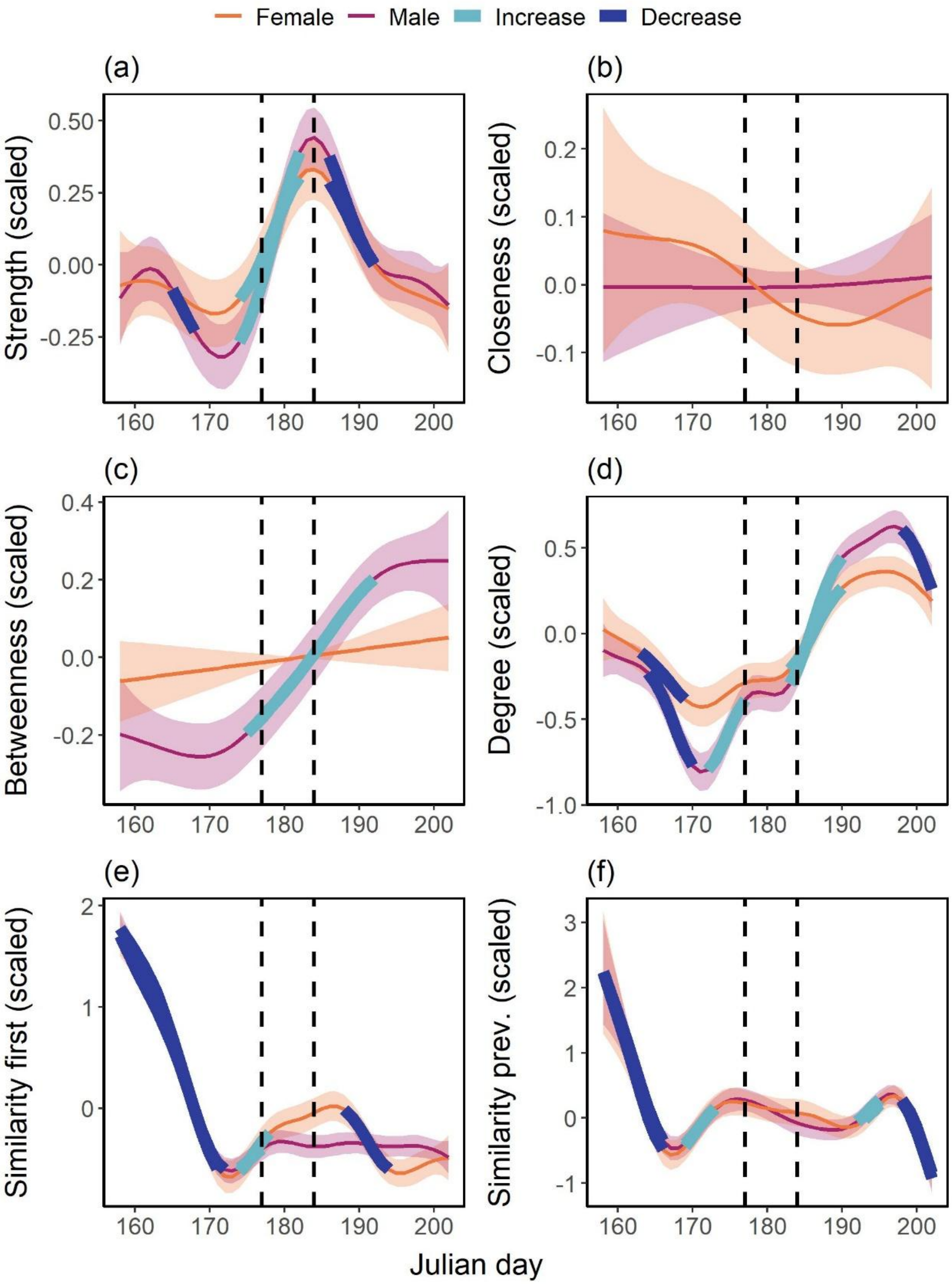

Figure 2 Rate of changes for the values of (a) strength, (b) closeness, (c) betweenness and (d) degree in a social network of 120 Atlantic puffins (63 males, 57 females) during the breeding season after correcting for sampling effort. The cosine similarity is calculated from (e) the first-time window, and (f) the previous-time window. The purple and orange lines represent the relationship between Julian day and changes in social network values, along with their confidence intervals, obtained from Generalised Additive Mixed Models for males (purple) and females (orange). Whether the rate of change increases or decreases is coloured respectively in light blue and dark blue. The dashed lines represent the peak hatching period (between Julian day 177 and 184).

Discussion

Cyclical patterns and sex-specific behaviours affect sociality in ways that are not well understood, particularly within a breeding season. Sociality on Atlantic puffin is dependent on their neighbouring individuals, with associations occurring more than expected by chance and individuals forming communities. Morel et al. (2025) suggest that associations on land are almost entirely dependent on the presence or absence of their neighbours at the colony. Because sociality in Atlantic puffins is closely related to colony attendance of neighbouring individuals, changes in breeding activity are likely to affect puffin social network structure. However, how mated individuals allocate parental behaviours among themselves is unclear in this species (Corkhill, 1973; Harris, 1986; Creelman & Storey, 1991; Fitzsimmons, 2018). By evaluating the changes in social network structure during different parental behaviours of the breeding season, we found strong temporal changes in sociality with fewer social associations during incubations than during chick rearing. We also found social network rate of change differences between males and females, at the beginning and end of the breeding season.

The seasonal change analyses showed that puffins associated rarely during the first part of incubation (until day 174 or June 23rd, low value of strength, Figure 1a) and were in contact with a low and decreasing number of conspecifics (low and decreasing values of degree, Figure 1d, Figure 2d). Additionally, we found that individuals had low connectivity between nodes (low value of betweenness and closeness, Figure 1b, c). The low values of social network terms could be explained by incubating adults being unavailable to associate with neighbours while spending most of their time underground, combined with generally low colony attendance of non-incubating adults. Indeed, if the egg is usually attended by one of the adults, only about half of the population could attend the surface, and many may be foraging for an extended period away from the colony. Opportunities to encounter neighbours would then be generally low, as individuals tend to spend less time on average at the colony if the density of conspecifics is low (Calvert & Robertson, 2002). A study from Anker-Nilssen et al (2024) supports this position, as the number of puffins observed at the colony during incubation was generally low.

We found no evidence for differences between male and female social network trait values during early incubation (until day 174 or June 23rd). These results suggest that males generally associated as much (strength, Figure 1a) and with as many conspecifics (degree, Figure 1d) as females and were as likely to connect distant sections of the network (betweenness, Figure 1c). However, male rates of change for betweenness and degree was significantly different from females during this period (Figure 2c, d). Starting on June 21st (day 172), the rate of change for each term, except for closeness, started to increase significantly independently of sex (figure 2a, c, d). Males and females gradually gained connectivity by associating more (degree, Figure 1d), more often with the same individuals (strength, Figure 1a), and by being more connected to the global social network (betweenness, Figure 1c). Around these dates, we expect eggs to start hatching (Belenguer, 2023), and adults to shift their foraging strategy toward predictable food patches (Pascalis et al., 2021), and shorter foraging trips (Alho et al., 2022) to maintain regular and frequent chick provisioning. Frequent provisioning (between 1.6 and 4.99 per day in average, Wallace et al., 2025) and associated colony attendance are likely to increase the frequency at which adults are present at their burrows and because puffins associate mainly with close nesting neighbours, it is likely to affect social opportunities (Morel et al., 2025).

In our study, the increasing values of social network terms were maintained until the mean hatching day (day 184, July 3rd) and beyond, except for strength, which reached its maximum value on that date before decreasing (Figure 1b, c, d). The cosine similarity of the previous window (Figure 1f) confirmed these changes by returning a higher similarity between time windows early hatching, probably because of a progressive change toward post-incubation network's values. The values of strength and its rate of change were non significantly different between males and females and followed the hatching pattern, perhaps because non-incubating individuals were visiting the nest more often as they got closer to the hatching date (Hatch & Hatch, 1989; Weidinger, 1996; Harding et al., 2005), to match their foraging activity shift as closely as possible to hatching. As the newborns grow and build thermal tolerance, parents gradually reduce their time in burrow and generally associate long foraging trips for self-maintenance with short trips to provide for the chick. The values of degree and betweenness increased and strength decreased, likely because individuals opportunistically associated with numerous conspecifics but for a short period (e.g., the time of a foraging rotation, or resting on the slope after foraging), probably to reduce predation risk.

We found very little difference in social network between males and females during the incubation period or the chick rearing period. We found that betweenness and degree were significantly different between females and males (Figure 1c, d) only during a short period during the chick-rearing. Particularly, males were in contact with more conspecifics (degree, Figure 1d) and had shorter paths (betweenness, Figure 1c) than females near chick fledging. The rate of change for males was also significantly higher than for females at this period for both betweenness and degree (Figure 2d, c). This difference could be a response to males spending more time gathering on the plot, particularly at the ridge of the slopes where they can associate with numerous conspecifics, while females could be spending more time away from the colony or brooding the chick (Anker-Nilssen et al., 2024; Wallace et al., 2025). The fact that the change of rate for betweenness and degree is overall greater for males than females suggests that they have different parental behaviours, or that changes in similar parental behaviours affect male social network more than females. The similarity metrics of the network confirmed this pattern (Figure 1e, 1f). Males had a significantly different similarity value to the first-time window, for a short time period (between day 180 and 190), suggesting their social behaviours probably did change more than females during peak hatching period, reinforcing the idea that this period is a turning point in puffin social behaviour.

Taken together, our results demonstrate that Atlantic puffins associated less when incubating than when taking care of chicks. This finding is supported by a significant increase in rate change and generally higher values for three out of four social network terms during peak hatching period. We also found that sex had little influence on social network, except for males having a higher value and rate of change for betweenness and degree toward the end of the breeding season. Because social associations in Atlantic puffins are highly influenced by the presence of their near-nesting neighbours (Morel et al., 2025), the absence of sex-related differences in social network trait values has to be related very similar sex-specific behaviours. Directed studies clarifying activity changes have been conducted for other species (Weimerskirch et al., 2006; Welcker et al., 2009; Paredes & Insley, 2010; García-Tarrasón et al., 2015; Thalinger et al., 2018; Scridel et al., 2023) and contributed to understanding social network patterns (Brent et al., 2013; Wolf et al., 2018; Vilette et al., 2022). However, sex-related activity in burrowing seabirds such as puffins has yet to be clarified as there is no clear consensus on whether males and females have different time budgets (Corkhill, 1973; Harris, 1986; Creelman & Storey, 1991; Fitzsimmons, 2018). The absence of consensus limits our interpretation of the social networks, highlighting the importance of having an accurate baseline of sex-related roles to interpret social structure.

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