Transition from incubation to brood-rearing activities influences dyadic associations differently between the sexes in a central-place foraging seabird.

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Abstract

1. Changes in activities following seasonal cycles can affect social interactions, which in turn influence social network structures. Because such activities are often sex-related, their effect on the social environment can affect males and females differently, particularly during periods of high activity such as the breeding season. While the effects of sex-related activities on the social network structure of species with distinct roles have been studied, their effects on species with similar roles remain unexplored.
2. We interrogated the role played by sex differences in breeding activities across the reproductive season on the expression of social network structure in a colonial seabird.
3. We studied associations between Atlantic puffins (*Fratercula arctica*) by colour-banding 120 sexed individuals and conducting focal observations during the breeding season. We tested how different networks, built on consecutive time series, changed from each other.
4. We found that the social network structure changed during the breeding season differently between males and females. The mean hatching date marked the turning point between two phases with distinctive social network structures: one during incubation and one during chick rearing. During incubation, social network traits changed similarly for males and females. During chick rearing, sociality increased, with males gaining higher values of degrees and betweenness than females. Network strength increased during the hatching period until the peak hatching date when it suddenly dropped back to its baseline value.
5. Our study demonstrates that Atlantic puffins have higher sociality during the chick-rearing period than during incubation and are associated more often with fewer conspecifics at hatching. Because sex-related activities 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 activities, social network, time-aggregated network.

Introduction

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 induce sex-specific activities (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 activities 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 the social networks that rise from them (Helm et al., 2006; Pinter-Wollman et al., 2014). The dynamic nature of behavioural processes (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). 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 in contrast to the non-breeding season (e.g., Common guillemots *Uria aalge*; Buckingham et al., 2022). Differences in activity are not only visible between species but between individuals of different sexes, particularly when they 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 conspecifics (lower values of degree and strength), because of a time budget directed toward parental care (Vilette et al., 2022). This 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 activities 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.

In this study, we investigate the role played by changes in sex-related activity patterns induced by the breeding cycle on the social network structure of a central-place forager, the Atlantic puffin. We tested the changes in social network structure between (i) two main breeding phases, incubation and chick rearing, and (ii) males and females. Atlantic puffin social associations on land are almost entirely dependent on the presence or absence of their neighbours at the colony (Morel et al., 2025). Thus, changes in land-based activities would be reflected by changes in social network characteristics. Studies that have investigated sex-related roles in Atlantic puffin do not concur on which sex is more involved in specific activities (Harris & Wanless, 2011). The difficulty mainly comes from the complexity of quantifying nesting-related behaviours in this species. Atlantic puffins are monomorphic and 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, males 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). In this scenario, males would be more socially active than females in the two breeding phases, because of more time spent on land. 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.

Materials and methods

Study species and site

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 their breeding site in April. There, they form large breeding colonies with high burrow densities (e.g., 1.37 burrows/m² on Gull Island Canada, Belenguer, 2023). Individuals generally mate for life and return to the same burrow every year to lay a single egg (Harris & Wanless, 2011). Incubation starts in mid-May for ~40 days with a mean hatching date 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 leaves the nest, and migrate in September (Harris & Wanless, 2011).

For this study, 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). The observations were conducted on a plot of ~168 square meters (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 calculate the mean hatching date, we regularly assessed the content of burrows during the incubation period using burrowscopes with infrared illumination (EMS2021 Gopher Tortoise Camera System, Environmental Management Services, Canton, Georgia, USA; Belenguer 2023) and visited each burrow within the plot to attribute a content (empty, egg, chick). We estimated the mean hatching date from the proportion of nests with eggs and hatched chicks following Belenguer (2023).

To collect information about puffins' social network, we colour-banded 124 individuals over two years (50 in 2021, 74 in 2022). Atlantic puffins, like many seabirds, are prone to abandonment (Yorio & Boersma, 1994; Rodway et al., 1996; Blackmer et al., 2004), so adults were captured only after the chick had hatched. We minimised disturbances and maximised the capture rate by working with trained banders at night when the birds were usually in their burrow. In some cases (~10-20 %), both adults were found in the burrow at the same time. When this occurred, we only captured a single individual and targeted the other member of the pair no earlier than 48 hours later. Individuals were captured in their burrows by hand grubbing before being carried to the banding station set a few meters 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 entering within a two-meter radius of another, even if they did not physically interact or display. To document those associations, we performed 210 hours of focal observations on the 124 potential colour-banded individuals, distributed among 53 sessions from Jun 06th to August 07th, 2023. We conducted the observations independently 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 focal 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 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. 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, they targeted and followed specific groups of individuals. Each event was identified using time and an incrementing unique ID. An event was created for each banded individual recorded with at least another individual within a two-meter radius. A new event was generated every two minutes or every time a new individual entered the two-meter 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, 2023). 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 (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 fixedday 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. 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

To measure the differences in social networks between breeding phases, we plotted the average values of the four social network terms and cosine similarity for different time windows in a time-aggregated network framework. To assess the variation between males and females, we projected those values by sex and included a 95 % confidence interval to address their variation.

Given the nature of the sampling method (four hours of observations every eight hours), it was important to consider the effect of the sampling effort. We corrected for sample size 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 without b and yab the number of times individuals a and b were observed at the same time but not associating.

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

Based on the proportion of hatched chicks on various days, we estimated the mean hatching date as the 3rd of July (Belenguer, 2023). Out of the 124 individuals marked in 2021 and 2022, we detected 120 (57 females, 63 males) over 210 hours of focal observations in 2023. From June 06th to August 07th 2023, we recorded 842 dyads and 2,464 associations. All terms tested showed changes across the breeding period, especially around mid-incubation (June 15th; Closeness and both measures of similarity) and mean hatching date (July 03rd; Strength, Betweenness, Degree).

Strength (Figure 1a) peaked exactly at the mean hatching date with an almost threefold score compared to pre-hatch and post-hatch values. Both males and females had very similar values across the breeding season. The pattern for closeness was not so consistent. The values of this metric remained relatively the same for males across the breeding season, with some fluctuations, reaching near zero several times (Figure 1b). Females, however, experienced a large increase in the mid-incubation period. For about ten days (~June 15th to June 25th), the values for females were much higher than for males (little or no overlap in 95 % confidence interval). In the days leading up to the mean hatching date, the values dropped back to near zero with no differences between males and females. Betweenness (Figure 1c), on average, increased throughout the breeding season. Around the 25th of June, the male values started separating themselves from those of females, with near-significant differences towards the end of the hatching period (~ July 10th). The values for females showed a fairly large drop at the mean hatching date. The values for degree showed large differences before and after the mean hatch date

(Figure 1c). Before hatch, male and female values were nearly identical and decreased during the mid-incubation period. After hatch, the values of degree increased suddenly, especially for males, to the point that male and female values were significantly different post-hatch (no overlap in 95 % confidence interval). The cosine similarity between the first and current window (Figure 1e) was generally the same for males and females but highlights the presence of two shifting points during the breeding period. The first dramatic change is revealed by a drop in similarity (less than 12 % of similarity) for both males and females (Figure 1e) during mid-incubation, matching with the changes observed in closeness and degree. The second shifting point occurs after the stabilisation of the cosine similarity value until it reaches a peak (~27 %) near the mean hatching date. This change aligns with differences observed around this date for strength, betweenness, and degree. The cosine similarity of the previous window (Figure 1f) follows a cyclical pattern of peaks and drops. 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.

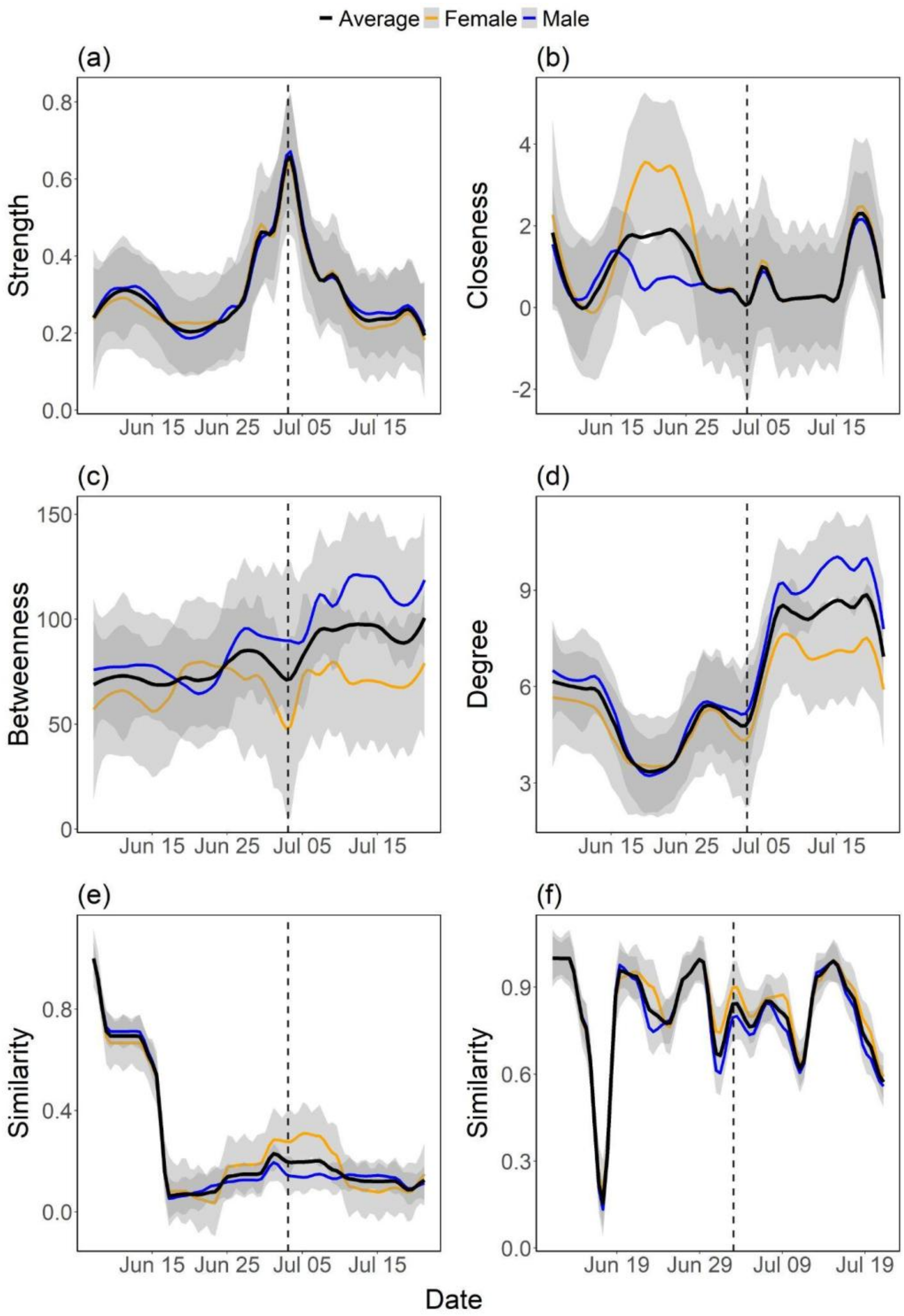

Figure 1. Seasonal changes for the values of (a) strength, (b) closeness, (c) betweenness and (d) degree in a social network of 120 Atlantic puffins (63 males, 57 females) during the breeding season after correcting for sampling effort. The black, blue, and orange lines represent the locally estimated scatterplot smoothing for the average values with their 95 % confidence interval. The dashed line represents the mean hatching date. The cosine similarity is calculated from (e) the first-time window, and (f) the previous-time window.

Discussion

Cyclical patterns and sex-specific activities affect sociality in ways that are still not well understood, particularly within a breeding season. Because sociality in Atlantic puffins is closely related to colony attendance of neighbouring individuals (Morel et al., 2025), a change in breeding activity is likely to be detected through their social network structure. However, how mated individuals allocate tasks among themselves is unclear in this species (Corkhill, 1973; Harris, 1986; Creelman & Storey, 1991; Fitzsimmons, 2018). Here, we interrogated the role played by seasonal changes in the breeding cycle on their social network structure. We found strong evidence of changes in the network structure within the course of the breeding season. We also found that some but not all the changes in the network were linked to sex, with males and females having different social network structures mostly during the chick-rearing period.

Independently of sex differences, the results showed that puffins associated rarely during the first part of incubation (until June 20th, low value of strength, Figure 1a), and were in contact with a low number of conspecifics (low value of degree, Figure 1d). Additionally, we found that they 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, individuals tend to spend less time on average at the colony if the density of conspecifics is low (Calvert & Robertson, 2002). 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. 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.

During the first part of the incubation period (until June 20th), the shorter path between two nodes (betweenness, Figure 1c) was generally stable, but the trends were irregular for strength (Figure 1a), degree (Figure 1d) and average connectivity (closeness, Figure 1b). These changes in network trait values were reflected by the succession of low and high social network similarity scores, resulting in consecutive drastic changes compared to the previous time window (Figure 1f). The proximate mechanisms leading to variation in these traits are unclear and could be related to environmental factors not considered in this study. For example, unseasonably warm temperatures and food availability are known to influence colony attendance (Anker-Nilssen et al., 2024) and could affect social network structures.

During this same period, we found relatively few differences between male and female social network trait values. Particularly, we found that only closeness differed significantly between males and females (Figure 1a, b, c, d), and only for a short period. 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). One explanation for females having higher values of closeness during part of the incubation is that they may be more mobile than males. Males in this species generally spend more time near the burrow entrance (Creelman & Storey, 1991; Anker-Nilssen et al., 2024), and there is evidence for females associating with more distant individuals than males (Morel et al. 2025). A better understanding of the difference in colony attendance and movement patterns by sex, like in other seabird species (Huffeldt & Merkel, 2016) would help to interpret the reasons why females become such a central component of the network during this period. Starting around June 20th to June 25th, the average trend of each term, except for closeness, started increasing (figure 1a, c, d). Individuals 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 and associated colony attendance are likely to increase the frequency at which adults are present at their burrows and thus affect social opportunities. Previous works on primates have shown that changes in females' behaviour at birth (e.g., increasing grooming) increased protection from the group resulting to higher newborn survival (Silk et al., 2003) and were visible in social network analysis through an increase in degree and strength at this time (Brent et al., 2013; Vilette et al., 2022, 2025). In our study, the increasing values of social network terms were maintained until the mean hatching date (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 after than before the period June 20th to June 25th, probably because the changes are progressive. The values of strength 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 activities change as closely as possible to hatching. During chick rearing, parents rarely stay in the burrow for an extended period 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 from the network for a short period (e.g., the time of a foraging rotation, or resting on the slope after foraging), probably to reduce predation risk.

In contrast with incubation, we found that betweenness and degree were significantly different between females and males (Figure 1c, d) during the chick-rearing period. Particularly, males were in contact with more conspecifics (degree, Figure 1d) and had shorter paths (betweenness, Figure 1c) than females. This difference could be a response to males spending more time on the plot, defending the burrow, while females could be spending more time brooding the chick (Anker-Nilssen et al., 2024). The similarity metrics of the network confirmed this pattern as they returned very close similarity for males and females except at the mean hatching date (Figure 1e, 1f). Males had a slightly lower similarity value, suggesting their social behaviours changed more than females during this period.

Taken together, our results demonstrate that Atlantic puffins associated less when incubating than when taking care of chicks. We also found that males had higher sociality than females during the chick rearing period but not the incubation period, with the mean hatching date representing the shifting point where those differences occur. Because social associations in Atlantic puffins are highly influenced by the presence of their near-nesting neighbours (Morel et al., 2025), sex-related differences in social network trait values have to be related to sex-specific differences in activities. Specific 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 puffin is 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). Our findings suggest that males and females have different roles during chick rearing, roles that influence their social network and thus the access to social information.

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