The Role of Pace of Life in Animal Social Network Structures

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Abstract

Pace of life history is a key axis of variation in life history strategies that captures the evolutionary trade-off between investing in lifespan versus reproduction. It has been suggested that social behaviour, and therefore network structure, may vary with pace of life, but formal theory remains scarce. We develop a novel mathematical model to examine how differences in demographic turnover may constrain emergent social network structures in natural populations. We additionally consider variation in social preferences and social inheritance mechanisms. Our key finding is that rapid demographic turnover, associated with faster pace of life, can substantially constrain the structure of dynamic social networks. For slow pace of life, network structures are primarily determined by social preferences, while for fast pace of life they are primarily determined by mechanisms of social inheritance. By considering how demographic turnover can constrain social network organisation, our work provides important insights into social evolutionary ecology.

Introduction

Life history strategies are defined by trade-offs between survival, development and behaviour, which are in turn subject to natural constraints imposed by resource availability, environmental conditions, and allometry (Wang *et al.* 2021; Stearns 2000; Healy *et al.* 2019). A well-known trade-off that shapes life history strategies is the *fast-slow continuum* (Stott *et al.* 2024; Healy *et al.* 2019), which describes the relative investment in lifespan and reproduction, termed *pace of life* (Silk & Hodgson 2021; Stott *et al.* 2024; Healy *et al.* 2019; Zipple *et al.* 2024). Species with a slow pace of life are characterised by long lifespans but low reproductive rates. Such species tend to have greater levels of maternal investment and improved juvenile survival rates, well exemplified by the life history strategies of killer whales (*Orcinus orca*) or African elephants (*Loxodonta africana*) (Zipple *et al.* 2024; Paniw *et al.* 2018; Weiss *et al.* 2023; Hoerner *et al.* 2023; Allen 2006). Conversely, species with a fast pace of life have a high reproductive rate but a short lifespan, and often exhibit higher metabolic rates than slow species (which may have behavioural consequences (Biro & Stamps 2010)). As the fast-slow continuum is a key axis of variation in life history strategies, it is important to understand how it is associated with other characteristics that impact fitness, such as social behaviour. However, few studies have explicitly tested how social behaviour and pace of life are interlinked (Salguero-Gómez 2024).

Individual social behaviours collectively define the social network structure of a group or population (Krause *et al.* 2014; Sumpter 2005), and this structure can be shaped over time by demographic processes such as birth or death (Shizuka & Johnson 2020). The impact of demographic processes can be both direct, through the removal and addition of possible social partners, and indirect, by inducing behavioural changes in other individuals that shape social network dynamics and modify the structure of the network as a whole (Shizuka & Johnson 2020; Ilany & Akçay 2016; Firth *et al.* 2017). The demographic rates of birth and death may also shape social network structure by altering the selective advantage of different social behaviours. For example, if the initial costs of forming a particular social relationship are high or the benefits are gained gradually over time, then forming such relationships would be expected to be selected for more often in species with longer lifespans (Silk & Hodgson 2021). Since pace of life is closely linked to the demographic rates of birth and death, a species' position on the fast-slow continuum might be expected to influence their social network structure and dynamics (Silk & Hodgson 2021). However, covariation between pace of life and social network structure could be a direct outcome of demography, or related to evolutionary relationships between social behaviour and life history. As a result, how and why social network structure varies predictably across the fast-slow continuum remains an open question (Silk & Hodgson 2021).

Despite the clear links between demography and social structure, demographic processes are rarely incorporated in social network models (Shizuka & Johnson 2020;

Pellis *et al.* 2015), with network representations typically either static in both size and structure (Ferreri *et al.* 2014; Gallos & Fefferman 2015, or including network dynamics but with a constant size (Li *et al.* 2011; Fefferman & Ng 2007). This restricts the relevance of such studies over longer timescales, where the influence of demography on network structure cannot be neglected (Shizuka & Johnson 2020). Theoretical network modelling approaches that incorporate more realistic demographic dynamics could be effective tools to better understand the relationship between pace of life history and social structure.

Social network structures and their temporal dynamics can also be linked to individual-level social preferences (Croft *et al.* 2016). A wide diversity of preferential behaviours are observed in nature. These behaviours may be realised as preferences for social connections with particular traits, for example larger physical size in greater kudu (*Tragelaphus strepsiceros*) (Owen-Smith 1993) or greater maturity in African elephants (McComb *et al.* 2001). Preferences for phenotypic similarity (homophily) drive social organisation in a variety of systems and through a variety of phenotypes (Massen & Koski 2014; Ebenau *et al.* 2019; Seyfarth *et al.* 2012; McPherson *et al.* 2001; Bizzozzero *et al.* 2019; Croft *et al.* 2009). Therefore, theoretical models of social structure and dynamics can benefit from incorporating such preferential behaviour (Brask *et al.* 2024). Such an implementation was introduced in the dynamic social network model of Fefferman & Ng 2007. Here, each individual is assigned a social preference and frequently reevaluates their social bonds with respect to their preference, altering their own social network accordingly. In this model social preferences are implemented in the form of network centrality measures, describing the position of individuals within the network (Freeman 1978; Sosa *et al.* 2021), with the use of different measures able to capture a wide range of natural preferential behaviours (Fefferman & Ng 2007). This showed that variation in social preferences drives differences in emergent group-level social network structures, with simple individual-level mechanisms able to drive complexity in the group or population network structure. The model has also been extended to address other ecological (Hock *et al.* 2010; Hock & Fefferman 2011) and epidemiological (Hock & Fefferman 2012; Gallos & Fefferman 2015) questions. However, the ecological and evolutionary conclusions which can be drawn from these model frameworks are limited since they do not account for the impact of demographic processes, which can be important over longer timescales.

A fundamental consideration when integrating demographic processes into models of social network dynamics is *social inheritance*: if and how social relationships are passed from a parent to its offspring (Shizuka & Johnson 2020; Ilany & Akçay 2016; Ilany *et al.* 2021). A model of social inheritance developed by Ilany & Akçay 2016 suggested that network stability is achieved through individuals interacting with the social circle of their parents, with this model able to replicate some aspects of the observed social network structure of four mammal species. On the other hand, parent and offspring social relationships may be disjoint, such as in species which exhibit abandonment

behaviour (Davenport *et al.* 2019). Therefore, different forms or extents of social inheritance may also play a vital role in long-term animal social network dynamics. The role of social inheritance may be especially significant for fast-lived species, if social network dynamics are indeed strongly governed by demographic processes due to the more rapid individual replacement of individuals (Shizuka & Johnson 2020; Ilany & Akçay 2016). It is therefore important to consider social inheritance when assessing how demography may constrain the emergence of complex social network structures (Ilany & Akçay 2016; Shizuka & Johnson 2020).

Here we extend the dynamic social network model of Fefferman & Ng 2007 to include demographic turnover and different social inheritance strategies. We consider popularity and closeness social affiliation preferences (as in Fefferman & Ng 2007), but also consider homophilic social preferences, to broaden the range of natural animal behaviours which are captured by the model (Fu *et al.* 2012). Our central aim is to determine if there are demographic constraints on the formation of highly structured social networks, and to assess whether these constraints differ according to pace of life history, the nature of social inheritance, and the type of social preference. Our key finding is that pace of life can constrain social network structure, determining the extent to which particular individual preferences shape the social organisation. Further, for faster paces of life social inheritance becomes more important in determining social network organisation. The resulting relationship between social network structure and pace of life yields insights into how demography may constrain and shape co-evolution of life history and sociality.

Methods

Initialisation

We model the social network of a population as a directed graph $G = (V, E)$. Here, V is the set of nodes, each representing an individual of the population, and E is the set of directed edges representing (not necessarily mutual) social relationships between individuals. The graph is initialised with $N = 100$ nodes, with each node having five outward edges assigned from a uniform distribution across the population. No duplicated edges are allowed, nor edges which connect a given node to itself. Additionally, in order to consider homophilous social dynamics, all nodes are assigned a (non-social) phenotype value (or 'trait value'), T, taken from a truncated normal distribution, $\mathcal{N}(0.5, 0.1)$, restricted to the interval $[0, 1]$.

Demography

The demographic process is modelled using a continuous-time Markov chain process, where individuals can give birth at rate $b - qN$, and die naturally at rate d. Here, b is the maximum birth rate, N is the current total population, and $q = (b - d)/K$ is the populations' susceptibility to crowding, with K denoting the population carrying capacity. As such, each individual has a probability of giving birth, P_{birth}, and a probability of death, P_{death}, which increases and decreases the population size, respectively (see equations 1-2).

$$P_{\text{birth}}(N) = \frac{b - qN}{R(N)}, \qquad (N \to N + 1) \tag{1}$$

$$P_{\text{death}}(N) = \frac{d}{R(N)}, \qquad (N \to N - 1) \tag{2}$$

Here, $R(N) = N(b - qN) + dN$ is the sum of the transition rates of the Markov chain at the current state N. The time between events is drawn from an exponential distribution with parameter $\lambda = R(N)$. Note, if $P_{\text{birth}} < 0$ it is set to zero. This is an application of the Doob-Gillespie algorithm (Doob 1942; Gillespie 1977) for sampling from continuous-time discrete-space Markov chains.

We capture pace of life by scaling the birth and death parameters. We define the 'fastest' demographic parameters as $(b_f, d_f) = (10, 1)$. Then, by considering a scaling by $c \in [0, 1]$, we use the fastest parameters to obtain slower paces of life $(b, d) = (cb_f, cd_f)$. A higher value of c therefore corresponds to a faster pace of life. For further mathematical details on how c acts as the control parameter to vary pace of life see supporting information S1.1, and for a discussion of the choice of values for b_f and d_f see S1.2.

Social Inheritance

To integrate birth processes into the network structure requires a consideration of social inheritance. Upon the birth of a new individual, we consider three different social inheritance strategies: (i) *Zero-inheritance*, where no edges are assigned to the newborn at birth, (ii) *Full-inheritance*, where newborns are assigned the same outward edges as their parent, and (iii) *Parental-inheritance*, where newborns are given an outward edge to their parent only. Whenever an individual dies, their corresponding node is removed from the graph, along with all of their inward and outward edges.

We also include trait inheritance. The new node (individual) is assigned the trait value of their parent, T_p, plus a mutation, z, drawn from a Normal distribution, $z \sim N(0, m)$, where $m = 0.25$. Trait values are fixed to the range $[0, 1]$ using reflective boundary conditions. The value of $m = 0.25$ was chosen as a relatively small value for which genetic drift does not lead to the distribution of trait values becoming narrower during the simulation time.

Social Dynamics

To model social dynamics we follow the methodology of (Fefferman & Ng 2007). The dynamics are composed of multiple *social updates*, occurring at fixed timesteps. These are driven by preferential behaviour, assuming that individuals act selfishly to maximise the quality of their own connections according to one of three social rules. Prior to the social update step, each node in the graph can have between 0 and 5 outward edges. Nodes with greater than 3 edges may improve the quality of their connections by dropping their worst scoring connections, based on a particular rule (their social preference type), until exactly 3 connections remain. Then, all nodes form new outward edges to other nodes, chosen uniformly from V but excluding their current and recently removed connections, until each individual has 5 out edges. We assume that the frequency of social updates is independent of pace of life.

Individuals are scored using the individual-level scores given in Table 1, with each measure corresponding to a given social preference. We consider three distinct social preferences: (i) Popularity, where a social relationship is preferred if it has a high in-degree, (ii) Closeness, where a social relationship is preferred if that individual has high closeness centrality (i.e. is well integrated in the network with a strong ability to reach others within the network), and (iii) Homophily, where a social relationship is preferred if it is with an individual of a similar trait value. In each simulation, all individuals in the network have the same social preference. For homophily, we additionally consider the scenario where the new edges added to the graph are those that are the most preferred from the remaining population (including individuals removed when dropping the lowest scoring connections), to consider a scenario where social preferences are

based on an easily observed and assessed phenotype. We refer to this extra case as 'complete knowledge', and the other cases as 'incomplete knowledge'.

Model Overview and Simulation

After initialisation, we run the demographic process for a duration of $t = t_D$. Within the demographic process if the birth of a new individual occurs, we implement the social inheritance strategies. If a death occurs, all social contacts for that individual are removed. We then perform a 'social update', and the demographic processes continue for another duration of $t = t_d$. This process is repeated for a sufficient period of time such that the properties of the social network structure converge to a quasi-stable state (until $t = 500$). Each component of the full model is visualised in Figure 1.

We quantify the differences in social structure with pace of life by recording three network-level measures (Table 1) after each social update. These network-level measures indicate the extent to which the social organisation of our group or population is achieved according to one of three social preference rules: popularity, closeness and homophily. We perform 100 simulations for each social inheritance type, each preference type, and for variation in pace of life (100 different values of c), to analyse how the network-level scores change with time, totalling 120000 simulations. The recorded network-level measures are then taken as the mean (over the 100 simulations) of the final 100 iterations. Further details of the simulation process are provided in S1.3.

Table 1: The individual-level and network-level measures considered in this study. Notation: V is the set of nodes (individuals), E is the set of edges, $T(i)$ is the trait value of individual i, $\deg_{\text{in}}(i)$ is the in-degree of individual i (meaning the number of edges going *into* this individual), $N = |V|$ is the total number of individuals, $P_{\max}$ is the maximum individual-level popularity score in the network and $v(i,j)$ is the length of the shortest path from individual i to individual j (where $v(i,j) = N$ if no path exists). The popularity and closeness measures here are as defined in (Fefferman & Ng 2007. Individual measures drive social updates and global measures evaluate organisational success and describe structural properties of the network.

Measure	**Formula**	**Description**
	Individual-level scores	
Popularity	$P(i) = \dfrac{\deg_{\text{in}}(i)}{N-1}$	Measures the proportion of other individuals in the population choosing to affiliate with a given individual.
Closeness	$C(i) = \sum_{j \neq i} \dfrac{N-1}{v(i,j)}$	Average path length from one individual to all others in the network relative to network size.
Trait Difference	$D(i,j) = \lvert T(i) - T(j) \rvert$	Measures the dissimilarity of a pair of individuals, using the Euclidean distance between their trait values
	Network-level measures	
Popularity	$P(G) = \sum_{i \in V} \dfrac{(P_{\max} - P(i))}{(N-2)}$	Measures the average divergence from the most popular individual, and therefore how centralised the network is.
Closeness	$C(G) = \sum_{i \in V} \dfrac{C(i)}{(N-1)(N-2)}$	Average closeness score across all nodes in the network, and therefore the level of network cohesiveness.
Average Trait Difference	$D(G) = 1 - \dfrac{1}{\lvert E \rvert} \sum_{(i,j) \in E} D(i,j)$	Average trait difference across all edges in the network, scaled so a higher score means greater average assortativity or homophily.

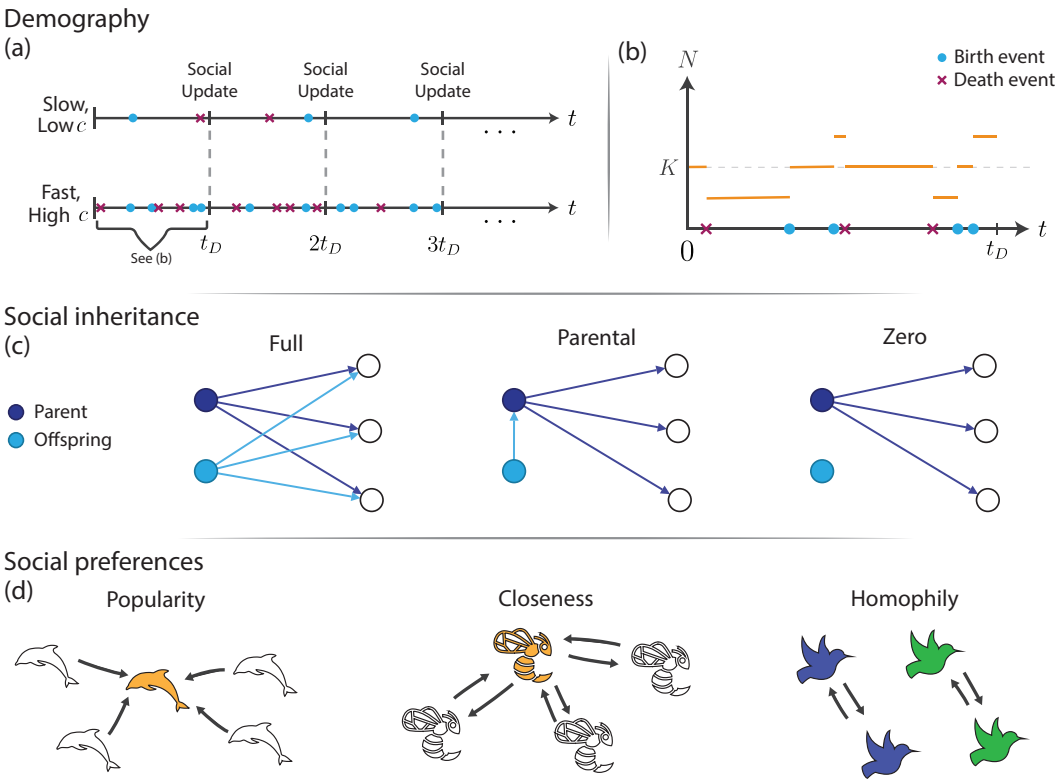

Figure 1: Graphical representation of the model components. (a) Timeline of the model, highlighting the position of the social updates alongside birth (blue dots) and death (purple crosses) events, with (top) slow pace of life and (bottom) fast pace of life. (b) The changing population size between one social update, as a realisation of a continuous-time Markov Chain model. (c) The different social inheritance schemes, with a parent (dark blue), individuals they are connected to (white) and their offspring (light blue) alongside the connections given at birth. (d) The different social preferences, with high scoring individuals highlighted in orange. For homophily preferences, individuals of similar traits aim to connect with each other (dark blue with dark blue, and green with green).

Results

Our model simulations showed that changes in pace of life can have a significant impact on the network structure of dynamic social networks. Furthermore, the relationship between pace of life and network structure depended on both social inheritance and the social preferences that individuals use to update their networks. The results for incomplete knowledge demonstrated that for slow pace of life, emergent social network structures are primarily determined by the social preferences, while at a fast pace of life social inheritance played a more substantial role. This is because demographic turnover is more rapid in fast species, providing fewer opportunities for individuals to update their networks based on their social preferences. When individuals are equipped with full knowledge, the social dynamics were more robust to changes in the pace of life.

Popularity Preferences

When the social dynamics were driven by popularity preferences, there was substantial variation in network structure across the fast-slow continuum. In absence of demographic turnover ($c = 0$), our model returned a highly centralised social network structure with three 'central hubs' (Figure 2a), as observed in Fefferman & Ng 2007. However, with an increased rate of demographic turnover the networks became less centralised (Figure 2). This effect is quantified by the network-level popularity scores, which rapidly decayed as the pace of life becomes faster (Figure 3a(i)), and by the network-level closeness scores, which increased and saturated with faster paces of life, indicating a more cohesive social structure (Figure 3a(ii)). This dramatic variation was due to the more frequent deaths of central hubs in the networks, ultimately resulting in networks being stuck in an unstable state that is attempting to converge towards the structure shown in Figure 2a. Faster death rates resulted in networks being stuck in an earlier phase of convergence, on average, when the centralisation is lower. The trait assortativity scores of the observed networks varied little with pace of life, except in the absence of demography ($c = 0$), where the score is anomalously dependent upon initial conditions (Figure 3a(iii)).

The mechanism of social inheritance affected the strength of the relationship between pace of life and the network scores by mitigating the impact of the death of central hubs upon the network centralisation. With full-inheritance, the magnitude of the changes in the structural properties of the network were smaller than with zero or parental-inheritance. This is because the full-inheritance strategy led to the more rapid replacement of central hubs (should one be removed due to a death event). For the zero and parental-inheritance schemes, the network-level popularity and closeness scores were the same. However, the parental scheme lead to slightly higher levels of assortativity by trait value, since, offspring typically shared similar trait values to their

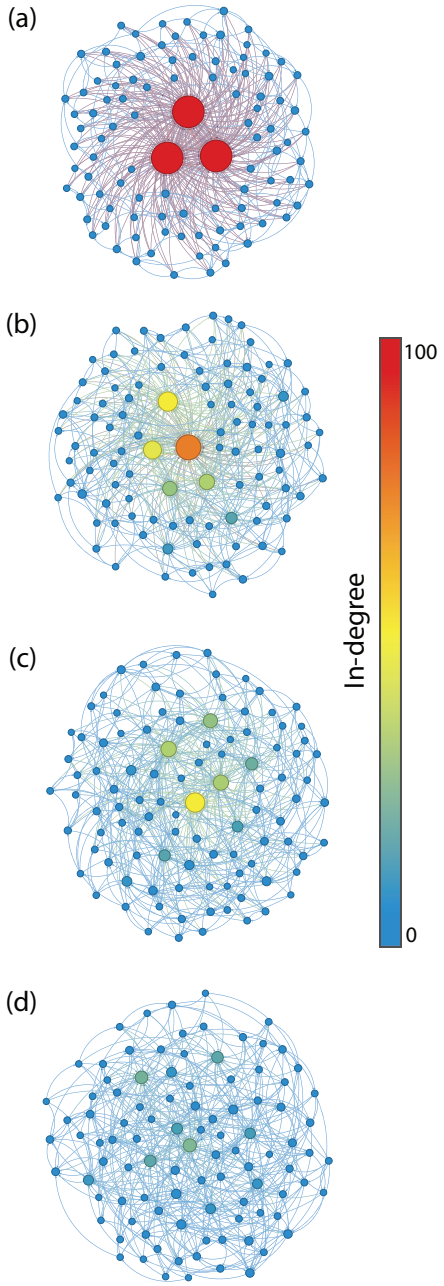

Figure 2: Example social networks obtained as an output of the model for a group with popularity preferences, full social inheritance and paces of life (a) $c = 0$, (b) $c = 0.01$, (c), $c = 0.1$ and (d) $c = 0.2$. Nodes are sized and coloured according to their indegree.

parent and individuals started life with a connection to their parent (Figure 3a(iii)).

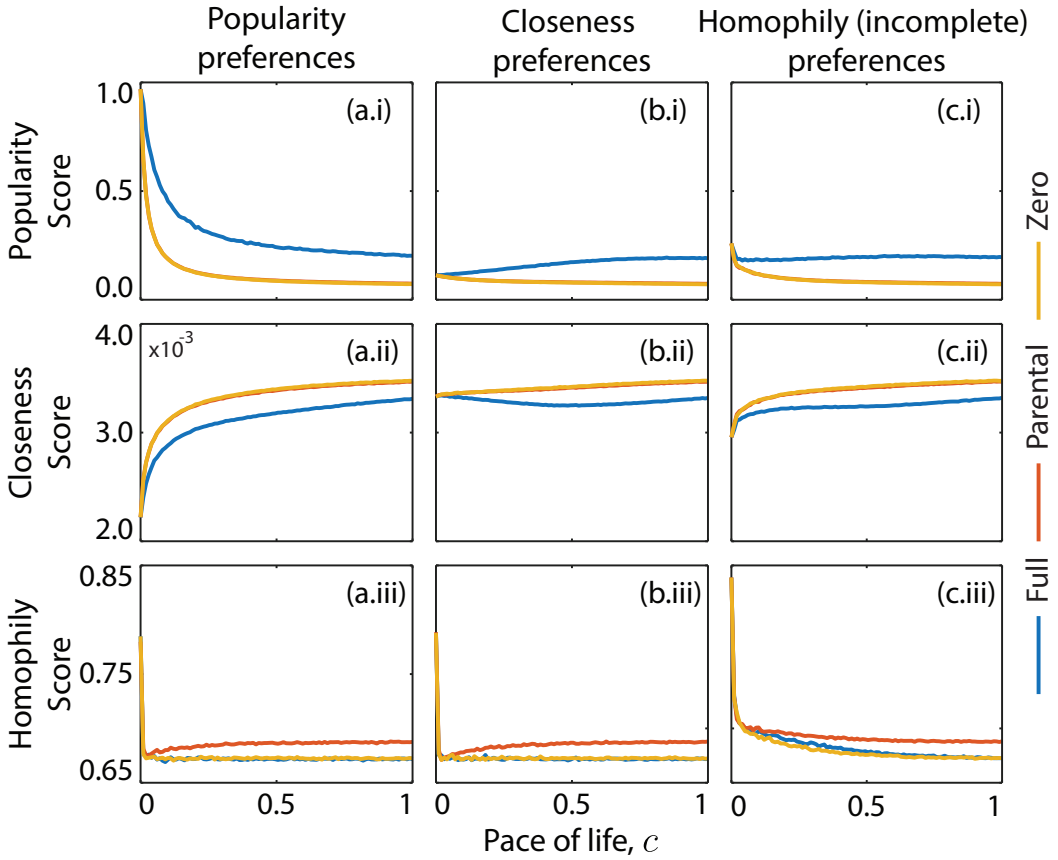

Figure 3: Variation of the average network-level measures with pace of life, c. Social preferences are: (a) popularity, (b) *closeness*, and (c) trait (incomplete knowledge). Network-level scores are: (i) popularity, (ii) closeness, and (iii) homophily. Social inheritance strategies are: full (blue), parental (red) and zero (yellow). Whenever the parental (red) curve does not appear in a subplot, it had a negligible difference from the zero (yellow) curve.

Closeness Preferences

When the social dynamics are driven by closeness preferences, changes in the rate of demographic turnover lead to only small changes in the properties of the network structure (Figure 3b). This invariance is due to the sensitivity of the closeness measure. In particular, the rewiring of a single connection can dramatically change an individual's closeness score, making the search for optimal connections difficult. Therefore, the social dynamics are suboptimal under a closeness affiliation preference (Hock *et al.* 2010; Fefferman & Ng 2007) and are less affected by demographic processes. As with popularity preferences, the full-inheritance scheme led to higher centralisation and lower cohesiveness than the other two inheritance schemes, and the parental-inheritance scheme led to slightly higher trait assortativity.

The centralisation of networks slightly increased with pace of life for the full-inheritance

scheme only. Here, full-inheritance super-additively makes popular individuals more popular, increasing the group-level popularity score. This tendency for full-inheritance to lead to higher popularity scores at faster pace of life was consistently observed across the other social preferences (Figures 3b-d(i)).

Trait-based Preferences (Incomplete Knowledge)

When the social dynamics were driven by trait-based preferences, and knowledge was incomplete, the effect of pace of life on the network properties was limited (Figure 3c). As in popularity-driven networks, the change in the network-level popularity and closeness scores with pace of life were initially rapid, but then saturated. However, the magnitude of the decline was smaller, and there were less significant differences between the network structures of fast and slow species under trait preferences (compared with popularity preferences). The key difference with trait-based preferences is that a very slow pace of life led to a slight increase in network assortativity over the other social preferences (Figure 3c(iii)). Nevertheless, this increase in assortativity score rapidly declined as pace of life increased, as shown in S2.1

Trait-based Preferences (Complete Knowledge)

When individuals had complete knowledge of other individual's trait value, the resulting network dynamics and emergent structure were dramatically different to those with incomplete knowledge and, in some circumstances, the emergent social structure was highly organised (Figures 4a-c).

For trait-based preferences with complete knowledge, the popularity and closeness scores were much lower than with any other social preference with incomplete knowledge (compare Figure 4d(i) & (ii) with Figures 3a-c(i) & 3a-c(ii)). However, complete knowledge lead to much higher assortativity scores (compare Figure 4d(iii) to Figures 3a-c(iii)) across the entire fast-slow continuum and social inheritance mechanisms. In particular, higher social knowledge lead to social dynamics being significantly more robust to the impact of demographic processes.

Increasing the rate of demographic turnover did, however, still impact network dynamics, although only by increasing the proportion of social bonds formed through inheritance. This is evidenced by pace of life having no impact on network structure (by any measure considered) when there is zero social inheritance (Figures 4d(i)-(iii)). With full-knowledge, the social dynamics can only add optimal (assortative) connections, while inherited connections may be suboptimal (due to mutations in trait value). Therefore, without social inheritance there is always an optimal (highly assortative) network structure. Such 'optimal' structures (shown in Figure 4a) have low centralisa-

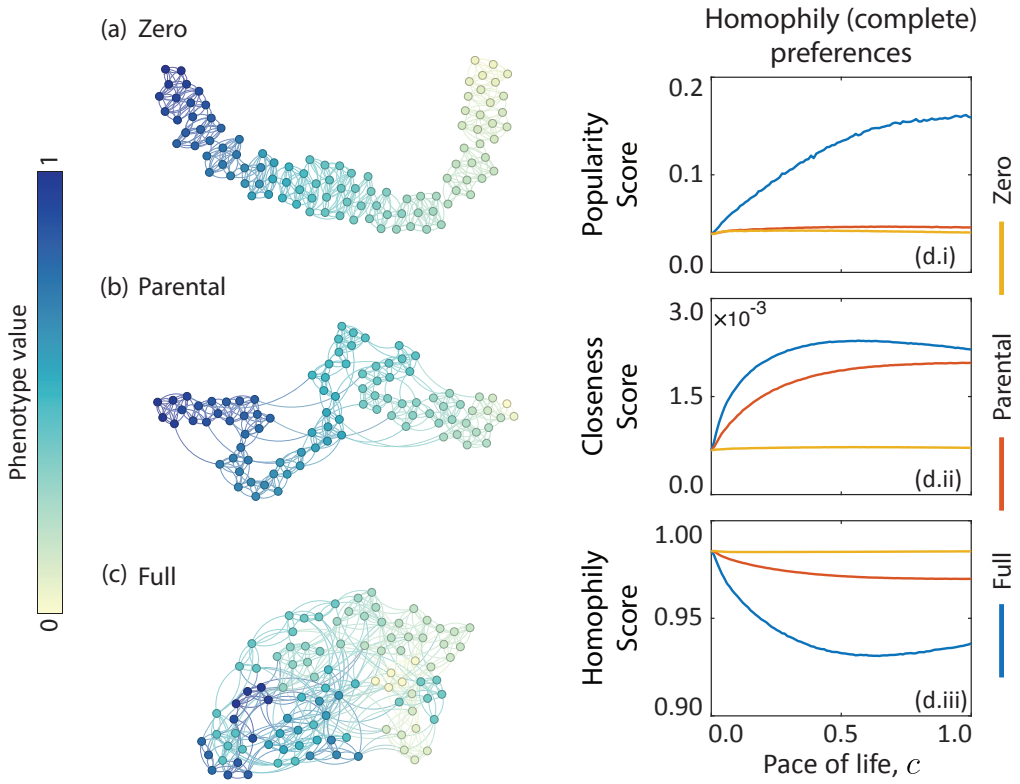

Figure 4: Model results with trait-based (complete knowledge) social preferences. (Left) Example social networks obtained from the model with pace of life $c = 0.5$ and social inheritance strategies: (a) zero, (b) parental, and (c) full. Darker colours correspond to higher trait values. (Right) The variation of the network-level measures with pace of life, c. Network-level scores are: (i) popularity, (ii) closeness, and (iii) homophily. Social inheritance strategies considered are full (blue), parental (red) and zero (yellow).

tion and cohesiveness. On the other hand, with full-inheritance, as pace of life increases, more connections in the network are obtained through social inheritance (and are less strongly assortative). As such, network assortativity decreases while popularity and closeness scores increase (Figure 4c). Parental inheritance balances network assortativity and cohesiveness. Parent-offspring bonds formed bridges across the network between individuals with potentially different trait values, increasing the closeness score without completely sacrificing the assortative structure. Homophily is maintained due to the greater sparsity of 'sub-optimal' social relationships in the network (Figure 4b). Note that this effect will depend on the heritability of the trait; reducing m (increasing trait heritability) would cause results for parental and full-inheritance to be similar to those for zero-inheritance.

Discussion

Our model showed that differences in pace of life history, which we represent through differences in demographic turnover, can constrain the structure of animal social networks, with the strength of the constraint depending upon additional factors such as individual social preferences and patterns of social inheritance. Our key finding is that stronger emergent social structure could be a more common feature of animals with slow pace of life. Furthermore, we show that emergent social network structure is primarily determined by social preferences for slow pace of life, while at a fast pace of life network structure is primarily influenced by social inheritance strategies. For faster paces of life, there are fewer opportunities for individuals to update their relationships based on social preference, and so inherited connections have more prominence. Our results also highlight the importance of social knowledge in shaping how phenotypic assortment shapes social organisation. Consequently, our findings allow us to explicitly link pace of life with the social structure of natural systems purely through ecological processes, providing an important baseline to quantify the role of life history in social evolutionary ecology.

Impact of Social Inheritance Across the Fast-Slow Continuum

We found that social inheritance influences the properties of the emergent social structure, with some patterns consistent across different social preferences. For example, a higher level of social inheritance (e.g., our full-inheritance scheme) produced networks with higher popularity scores and lower closeness scores for most considered social preference types. This relationship implies that greater social inheritance can result in more centralised and less cohesive social structures, which may have consequences for other ecological processes. For example, centralised networks will have individuals who engage in significantly more social interactions than average, resulting in possible 'superspreader' events, where outbreaks of a simple contagion (such as an infectious disease) may be less likely but more explosive when they occur (Lloyd-Smith *et al.* 2005). However, we also we note that *dynamic* social organisation may restrict the role of these individuals and lower disease risk (Hock & Fefferman 2012). Contrastingly, more cohesive social networks have shorter average path lengths between individuals and may therefore spread a complex contagion (like foraging or predator locations) more effectively (Evans *et al.* 2021). The fact that reduced social inheritance can promote group cohesion could mean that selection on it would depend upon the amount of benefit from greater environmental knowledge relative to the potential additional impact of, for example, natural enemies arising due to the loss of centralised structure. In general, we predict that selection pressures on social inheritance behaviours would be more prevalent in fast species, since the network properties varied the most across social inheritance schemes in these species.

Our results also indicate that social inheritance can influence the relationship between pace of life and the properties of the social network. For example, when the social dynamics are driven by closeness preferences, the social inheritance strategy determined if some network-level scores were increasing or decreasing with pace of life. Without investigating multiple social inheritance strategies, this more sophisticated impact of rates of demographic turnover may not have been observed. Therefore, inheritance (of out-connections) plays a key role in social network dynamics, suggesting that network modelling studies should explicitly account for various forms of social inheritance whenever demographic processes are included (Ilany & Akçay 2016).

Role of Knowledge in Social Network Dynamics

Greater social knowledge (i.e. of the group as a whole - 'complete' - rather than only an individual's own social network - 'incomplete') was found to reduce the impact of demographic turnover on social network organisation. With incomplete knowledge we find that demographic processes restrict the network assortativity, such that highly structured networks only emerge at slow paces of life. Therefore, we may expect homophily by less visible traits (like personality) to be present predominantly in slow species. With complete knowledge the emergent network structure is highly assortative across the entire fast-slow continuum. Therefore, we may expect to observe homophilic behaviours according to more easily observed phenotypes (like colour) in a wider variety of systems. While both of these kinds of homophily have been observed in nature (physical homophily: Mourier *et al.* 2012; Kelley & Evans 2018, personality homophily: Bhattacharjee *et al.* 2024; Massen & Koski 2014; Ebenau *et al.* 2019; Silk *et al.* 2003; Seyfarth *et al.* 2012; McPherson *et al.* 2001), their relative contributions to social structure for species given life histories and ecological contexts remains an open question in behavioural ecology, and our results provide some basic theoretical predictions to guide empirical work on this question.

We also found that when individuals have complete knowledge, greater levels of social inheritance lead to more cohesive network structures, but reduced assortativity. Parental inheritance yielded a high cohesiveness with a smaller reduction in assortativity. Therefore, the formation of parental bonds at birth may be favoured (in homophily-driven groups) when there is an evolutionary benefit to maintaining group cohesiveness, especially for fast species where social inheritance constrains network structure more. Collectively, our results for trait-based preferences highlight the potentially key role of information in animal social network organisation (Gokcekus *et al.* 2021) and draw attention to how this might vary across the fast-slow continuum. Future work may consider the impact of social knowledge across different social preferences and different inheritance schemes. While complete knowledge was considered comprehensively in Fefferman & Ng 2007, our contribution of demographic processes and social inheritance provides new opportunities to develop further theoretical exploration

of the mechanisms underlying animal social structure and dynamics.

Co-evolution of Social Behaviour and Pace of Life

Individual social network position has been related to fitness both directly (Brask *et al.* 2021; Snyder-Mackler *et al.* 2020; Farine & Whitehead 2015) and indirectly through correlation with fitness-related traits (Pasquaretta *et al.* 2014; McDonald 2007; Silk *et al.* 2010; Ellis *et al.* 2017). The global structure of the social network has also been shown to influence fitness (Evans *et al.* 2021; Ballard & Robel 1974; Robson & Traniello 2002; Clarke & Faulkes 1997; Ebensperger *et al.* 2016). Therefore, if groups themselves compete and act of units of selection (Philson *et al.* 2024; Wilson 1975; Kniffin 2021; Hock *et al.* 2010), there may be opportunities for multi-level selection upon features of life history strategies which influence both individual social position and group-level organisation. Since we found that pace of life history and social behaviour jointly influence the social network structure, we speculate that these features might co-evolve to shape the social network structure.

In this study, social behaviour is described by social preferences, which describe how individuals evaluate their own social network, and social inheritance strategies, which capture how offspring inherit the social relationships made by their parent. Therefore, since social preferences influenced the network properties most prominently at slower paces of life, we may expect that selection pressures on slow species to be on their social preferences, or other behavioural processes driving the self-organisation of the network. In contrast, for fast species, selection may be more likely to operate on social behaviours which are directly related to demography (in this case, social inheritance), because the demographic processes govern the social dynamics more predominantly for fast species. We may also expect selection on pace of life history based upon social behaviour. There are many examples where social species benefit from having highly centralised structures (Ballard & Robel 1974; Knörnschild *et al.* 2009; Clarke & Faulkes 1997; Robson & Traniello 2002; Brent *et al.* 2015), where few (keystone) individuals take more active social positions than others. In our model, self-organisation could only lead to a high level of centralisation for slow species (with popularity preferences), implying that species which organise according to popularity may face selection for increased longevity (at the expense of investment in reproduction) whenever centralisation presents a fitness benefit. Furthermore, since there is greater variability in individual network position with centralised structures (particularly in-degree centrality), there may be greater opportunity for natural selection on individual network position in such slow systems (Silk & Hodgson 2021). For example, keystone individuals are much more susceptible to infectious disease (Lloyd-Smith *et al.* 2005) than the average individual, but have significantly better access to social information (Evans *et al.* 2021, and selection will act more strongly on such well-connected individuals. Collectively this suggests the potential for multilevel selection (Philson *et al.* 2024; Wilson 1975; Kniffin 2021; Hock

et al. 2010) on pace of life depending upon the fitness advantages to centralisation at the group and individual level (Hock *et al.* 2010). By adding an explicit relationship between fitness and social network structure to our model, it would be possible to develop valuable new theory and more directly examine the co-evolutionary relationships between pace of life history and social behaviour, which could have a profound effect on our understanding of the evolution of animal sociality.

Model Limitations and Future Work

While our model incorporates many key features of the dynamics of natural social systems, it relies upon a set of simplifying assumptions. First, we assume that species update their social relationships at the same rate, independent of their pace of life. This assumption of a fixed rate of social relationship dynamics allows the parameter c to directly represent pace of life, facilitating straightforward analysis of model outcomes. However, we know little about how social updating covaries with pace of life (Silk & Hodgson 2021), and it may be that traits of fast species or co-evolutionary history break this assumption. In S2.2, we show that if this assumption is relaxed so the rate of socialisation increases or decreases slightly with pace of life, our results are qualitatively robust. We also explore the impact of more extreme relationships between the rate of sociality and pace of life.

Additionally, we assume that the population is homogeneous in its social behaviour. All individuals have identical social preferences and aim to keep the same number of connections. While this neglects well-documented intraspecies variation in social behaviour (Hock & Fefferman 2011; Schradin 2013; Kluiver *et al.* 2022), we are initially interested in the implications of varying social preferences and social inheritance in general, with cognitive theory broadly supportive of a fixed number of stable social relationships (Dunbar & Spoors 1995). Our choice of the optimal number of connections being 5 is also arbitrary, chosen to align with (Fefferman & Ng 2007). Variation in this quantity could also lead to social dynamics which are more or less robust to demographic processes. However, differences or heterogeneities in either the number of social relationships held by individuals or in their social preferences could easily be implemented in future work (Ng 2008). Additionally, individuals could have multiple preferences, possibly following the methodology of (Brask *et al.* 2024), which uses mixed social preferences in generative network approaches. Incorporating individual variation in social behaviour may be an interesting direction for future work given the potential importance for ecological processes (Allan *et al.* 2025; Lloyd-Smith *et al.* 2005; Stein 2011) and their interaction with social dynamics (Young *et al.* 2022, 2023; Hock & Fefferman 2011).

Conclusion

Our theoretical model provides key insights into how demographic turnover can constrain social network organisation, and how this might vary with pace of life. By considering this relationship, our work provides important insights into social evolutionary ecology. Our model is modular and highly general, so can easily be adapted to consider additional forms of social preferences or dynamics, as well as new demographic processes. Our work provides new predictions which can be tested empirically related to the eco-evolutionary dynamics of social networks, especially as our capability to conduct cross-species comparison of animal social networks grows (Albery *et al.* 2024; Moor *et al.* 2024). More generally, the improved understanding of the link between pace of life history and social network structure that this work provides can help us better understand the drivers of the diverse social life histories observed in nature.

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