# Social ageing and the ultimate drivers of social change in wild populations

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# Abstract

Social behaviour can change across an individual's life, which is referred to as social ageing. Many species become less social with age, but there are also species that do not exhibit age-based changes in sociality or become more social as they get older. Social ageing consists of two main components; sociality and ageing. Sociality, in the most fundamental sense, refers to group-living. The social environment consists of multiple dimensions and can be measured at different levels. Ageing is often measured as chronological age, but there is also biological ageing and considering this type of ageing could improve research. The different hallmarks of ageing have recently gotten much attention. Epigenetic markers might give new insights and be helpful for better understanding of social ageing. Network analyses are useful tools to measure social ageing.

There are multiple mechanisms that can cause social change and they can be divided by proximate and ultimate explanations. The ultimate mechanisms align with evolutionary hypotheses, such as the buffering hypothesis and main effects hypothesis. Additionally, environmental factors, as suggested by the silver-spoon hypothesis, might also impact social behaviour.

Despite the growing number of studies, social ageing is not explicitly defined yet. This can result in misleading research outcomes, for example when non-directed edges are used for directed behaviours in network analyses. Consensus on the definition would improve the quality of research and contribute to the understanding of social ageing. Further, the relative contributions of the different mechanisms that cause social change are not determined yet. Determining them would contribute to the understanding of social ageing as well.

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# Introduction

Social interactions help group-living organisms cope with socio-environmental challenges such as finding food, caring for offspring and evading predators (Brent et al., 2014). As a result, social interactions can be important for determining the resources that an individual has available for reproduction and maintenance (Siracusa et al., 2022). Studies across multiple species have shown that the most socially integrated individuals have better health outcomes, increased survival and improved reproductive performance (Snyder-Mackler et al., 2020) (Campos et al., 2020). These findings demonstrate that social relationships are an important component of the fitness of individuals in many group living species (Siracusa et al., 2022).

It is important to mention that these social relationships are not static. Instead, they are likely to change in form and function as individuals age. Diverse and complex patterns of age-based changes in social behaviour (social ageing), are seen in both humans and non-human animals (Wrzus et al., 2013) (Machanda & Rosati, 2020). For example, humans often exhibit higher levels of social selectivity in older age, by prioritizing emotionally meaningful relationships and smaller social networks (Charles & Carstensen, 2010) (Lang & Carstensen, 1994). Similar patterns have been observed in primates (Veenema et al., 1997) (Thompson & Cords, 2018), whales (Weiss et al., 2021), rodents (Kroeger et al., 2021) (Wey & Blumstein, 2010), deer (Alberty et al., 2022) and birds (Schroeder et al., 2024), where older individuals interact with fewer social partners and engage less in affiliate behaviour. Although reduced social behaviour and social network size are most common in old age, it is also clear that ageing individuals often remain interested in their social world and motivated to engage in social interactions (Almeling et al., 2016) (Rosati & Santos, 2017). Further, other studies found that individuals did not appear to exhibit age-based differences in sociality (Silk, 1994) (Silk et al., 2006) or that older individuals became more social with age (Suomi et al.,1996) (Corr, 2003). Thus, it is apparent that sociality, as with many traits, can vary significantly in how it is expressed across the lifespan (Hayward et al., 2015) (Machanda & Rosati, 2020) (Siracusa et al., 2022).

The relationship between age and sociality has been studied across a range of biological disciplines (Woodman et al., 2024). Social scientists have studied the social determinants of health to contribute to policy that reduces health differences and improves human health span, life span or life expectancy (Snyder-Mackler et al., 2020). This research started already around 120 year ago (Rowntree, 1901). Evolutionary biologists focused on the evolution of social behaviour and ageing, and how evolution affects social structure of generations (Korb & Heinze, 2021) (Lemaître et al., 2015) and behavioural ecologists were interested in the causes and consequences of social processes and how this is shaped by age (Machanda & Rosati, 2020) (Siracusa et al., 2023). Only over the past years, these distinct research fields started to converge (Snyder-Mackler et al., 2020) (Woodman et al., 2024). The latest research aims at increasing the understanding of age and society by integrating the study of ecology, evolutionary biology, behaviour and demography (Firth et al., 2024). In this way, social ageing is a relatively new area of research (Siracusa, 2022).

Most of the research on social ageing has focused on humans (Charles & Carstensen, 2010) (Iannuzzi et al., 2024) and other social mammals (Blumstein et al., 2018) (Drake et al., 2024), because of their close evolutionary relationship to humans, but other species, such as birds (Schroeder et al., 2024) (Moiron & Bouwhuis, 2024) and social insects (Cook et al., 2024) (Johnson & Carey, 2014) have been studied as well. In human studies, social engagement is often measured in large, social, cultural and economic structures that can integrate individuals into a shared socio-economic framework, even if they never interact (Redhead & Power, 2022), while in animals, social behaviour is assessed through observations of direct social interactions (Snyder-Mackler et al., 2020). Human studies can capture more dimensions of the social environment, but they are also more complicated, because social gradients in human health can be caused by more environmental factors, such as access to health care, diet and smoking. Additionally, studies in human populations often rely on retrospective reports, and obtaining longitudinal, population-representative is challenging. Experimental tests for causality in humans are difficult due to ethical and practical constrains (Bartolomucci et al., 2024) (Snyder-Mackler et al., 2020). Animal studies, though more limited in their ability to capture all dimensions of the social environment, are often simpler (Snyder-Mackler et al., 2020) and can overcome some of the challenges of humans studies (Bartolomucci et al., 2024). Animal studies can offer opportunities for long-term studies, experiments and cross-system insights and comparisons (Firth et al., 2024).

Understanding the relationship between age and sociality is also timely. In the past decades, socioeconomic differences in mortality have become steeper in human populations (Snyder-Mackler et al., 2020). A study in the United Kingdom found that the life expectancy gains were greater among less deprived individuals compared to more deprived individuals (Marmot, 2020). The life expectancy increased by up to 0.25 years for the top 60% in 2012-14 to 2015-17 and decreased with 0.25 years for the bottom 40% in the same period. Similarly, a study in the United States revealed large differences in mortality linked to socioeconomic status (as measured by income) (Chetty et al., 2016). There was a difference in life expectancy of 14.6 years between the richest and poorest men and a difference of 10.1 years for women in the period 2001-2014. Knowledge of the biological processes that link the social environment, disease and mortality risk is necessary for improving disease prediction, prevention and targeting interventions, as well as for addressing the causes and consequences of social inequalities and investigating the evolution of social group living and its relevance to health (Snyder-Mackler et al., 2020).

In wild animal populations, there is concern about the increasing impact of human activities that modify the demographics of wild populations. These impacts are diverse, varying from structural modifications to the physical environment, such as landscape fragmentation and pollution to changes in the social environment by influencing population size, composition and social interactions. Importantly, human-induced changes in population age structure, for example by supplemental feeding or selective harvesting, can change animal sociality (Woodman et al., 2024) (Williams & Lusseau, 2006). Understanding the relationship between age and sociality will be important for mitigating the potential negative effects of these environmental challenges on species. Additionally, this knowledge could improve conservation strategies by incorporating knowledge about how ageing impacts social structure, fitness and resilience in endangered populations (Firth et al., 2024).

In the last few years, multiple research articles have been published about social ageing, which have not yet been included in previous review papers. Therefore, I aim to collect and assimilate the most recent studies in this research area. My focus will be on social ageing by discussing its two main components; sociality and ageing. Additionally, I will explore the ultimate drivers that cause social change in wild populations. This review paper aims to provide an overview of current knowledge, highlight gaps in literature and thus propose direction for future research.

# What is social ageing

Social behaviour and social relationships can change across the lifespan (Machanda & Rosati, 2020) (Wrzus et al., 2013). This is referred to as social ageing. More precisely, social ageing can be defined as changes in individual sociality throughout the adult life stage (Siracusa et al., 2022). This includes changes in an individual's behaviour with age, changes in how others behave towards an individual as that individual gets older and changes in the emergent or latent phenotypes (e.g. social position or status) that arise as a result of these processes or other non-social behavioural changes such as altered space use (Siracusa et al., 2022).

To get a better understanding of social ageing, I will discuss its two main components; sociality and ageing. Additionally, I will discuss how social ageing can be measured using network analysis.

## Sociality

The terms 'sociality' and 'social' are commonly used, but they are often not explicitly defined in different disciplines (Kappeler et al., 2015) (Mason & Shan, 2017). To make it even more complicated, additional qualifiers such as 'highly social' or 'social complexity' are being used by researchers studying vertebrate, often without explicit definition. In contrast, researchers studying invertebrates have been using other categories to distinguish certain taxa, which makes comparisons across taxa difficult (Kappeler et al., 2015).

To characterize sociality, it is useful to first consider its opposite; species that live solitary. Individuals in solitary species typically receive little or no paternal care or help from conspecifics (Clutton-Brock, 1991) (Wcislo & Danforth, 1997). Crucially, in solitary species, adults do not associate with other adults on a regular basis. Aggregations of adult conspecifics are only temporary and either accidental or because they are attracted to a shared, temporary resource. Mating is the only exception in which solitary animals seek others to reproduce (Dröscher & Kappeler, 2013) (Sandell, 1989). However, even in these species, there may be limited contact through exchange of visual, acoustic or olfactory signals. Therefore, despite differences in quantity and quality, solitary species also exhibit social behaviour, which makes the term 'social species' misleading for referring to 'non-solitary species' (Kappeler et al., 2015).

In contrast, group-living species are permanently associated with each other and actively maintain group cohesion. Additionally, some species are flexible in their social behaviour and form groups temporarily or facultatively (Schradin, 2013) (Eickwort et al., 1996) (Stacey & Bock, 1978). However, the distinction between group-living and solitary has proven to be practical for studying sociality (Kappeler et al., 2015). Thus, in the most fundamental sense, sociality refers to living in groups (Eaton, 2015) (Alexander, 1974).

However, providing a definition of a social group that can be applied across all species has proven difficult (Ward & Webster, 2016). Wilson (1975) defined a group as 'any set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics'. Although this makes sense, it is not universally applicable. Aggregations in nature, such as animals using a water hole during a dry season or moths around a lamp, cannot be described as social groups. The key quality that distinguishes a social group is that it forms and is maintained by social attraction between group members. Thus, a social group can be defined as one where two or more individuals maintain proximity in space and time through the mechanism of social interaction (Ward & Webster, 2016). However, social groups could also be defined based on social relationships and these groups may be different from those based only on spatial proximity (Whey et al., 2008).

Yet, sociality involves more than just group-living. The social environment of animals consists of multiple dimensions that can change throughout their life (Firth et al., 2024). These dimensions include alterations in social behaviour (Newman et al., 2023), social roles (Ilany et al., 2021), types of interactions (Silk et al., 2006) and opportunities to interact (Alberty et al., 2021) (Alberty et al., 2022), as well as the overall structure of social networks individuals are embedded within (Woodman et al., 2024) (Firth et al., 2024). Sociality can be considered at different levels, including the individual level (Siracusa et al., 2022) and the group or population level (Gordon, 2024) (Siracusa et al., 2023) (Wey & Blumstein, 2010) (Williams, R. & Lusseau, 2y006) (Firth et al., 2024), sometimes also referred to as within-individual level and between-individuals level (Firth et al., 2024). A fundamental understanding of social ageing requires consideration of processes across all these levels, because the between-individual level can reveal insights that may have been missed if only the within-individual level was assessed. Including the between-individual level allows for the identification of cohort effects or selective disappearance, where individuals with certain phenotypes are more likely to be lost from the population over time (Forslund & Pärt, 1995) (Vaupel & Yashin, 1985) (Firth et al., 2024) (Woodman et al., 2024).

Social behaviours and social structures can often be measured and classified in various ways (Whitehead, 2008). For example, interactions can be classified into types like agonistic or cooperative, which can be used as an indicator of the competitive or cooperative nature of a group. Relationships between individuals can be classified based on their quality and patterns and may correlate with attributes such as age, sex or kinship. On the highest level, social structures are often measured based on group size (Whitehead, 2008). Some measures, such as group size, are relatively straightforward to measure (Whey et al., 2008). However, social complexity is considered an important measure that remains difficult to determine (Whitehead, 2008) (Kappeler, 2019). Researchers working on different taxa have been using different criteria and terms to define levels of social complexity (Rubenstein & Abbot, 2017) (Kappeler, 2019).

In insects (invertebrates), social systems have been classified from simple to complex based on the presence/absence of three key features; overlapping generations, cooperative brood care, and reproductive division of labor. Species that meet all these criteria are defined as ‘eusocial’ (Batra, 1966) and represent the highest level of sociality or social complexity. Species that meet only one or two of these traits are classified as solitary, sub-social, communal, quasi-, or semi-social, respectively (Michener, 1969) and therefore considered less socially complex (Kappeler, 2019). Among vertebrates, some obligate cooperative breeders, which share the three defining traits with eusocial invertebrates (Sherman et al., 1995), have also been classified as ‘highly social’ (Bateman et al., 2012) or as representing the ‘highest level of social complexity’ (Fischer et al., 2017). However, it remains unclear whether the presence or absence of cooperative breeding is the only or only important criterion for this assessment (Kappeler, 2019).

Very generally speaking, complexity is the opposite of simplicity. A system is considered complex if its parts are neither arranged completely randomly nor completely ordered (Kappeler et al., 2019). More specifically, complex social systems are those in which individuals interact in many different context with many different individuals, and often repeatedly interact with many of the same individuals over time (Freeberg et al., 2012). Thus, the number of individuals and their interactions are two key components of social complexity. Comparing levels of social complexity across species requires a scale that integrates measures of both group size and relationship diversity (Kappeler, 2019). Several studies have focused on either one of these measures, but at the moment, there is no single comprehensive measure or index of animal social complexity that can be used for meaningful interspecific comparisons or rankings (Kappeler, 2019) (Salguero-Gómez, 2024).

## Ageing

The concept of ageing might appear simpler than that of sociality, but it has nuances that need to be considered (Firth et al., 2024). Ageing in late life is related to senescence, which refers to a decline in physiological functioning that leads to a loss of organismal function, decreased fecundity and increased probability of death (Woodman et al., 2024). However, ageing itself broadly reflects a temporal parameter that measures the amount of time since birth (Woodman et al., 2024), and therefore, can be associated with various other changes in an individual’s biology, in addition to physiological senescence in late life, such as sexual maturation, the accumulation of resources and social experience or changing social environment as a result from natural selection (Woodman et al., 2024). In research, ageing is often measured as ‘chronological ageing’, which is the amount of time that has passed in an organism’s life (Firth et al., 2024). That being said, there is also ‘biological ageing’, which refers to the decline in Darwinian fitness with chronological age, resulting in an irreversible physical deterioration of biological functions (Tangili et al., 2023).

Individuals of the same chronological age can vary in their biological age and life expectancy (Tangili et al., 2023). Some may have a lower or higher biological age than predicted from their chronological age (Tangili et al., 2023). Those with a high biological age relative for their chronological age tend to have a shorter life expectancy, while those with a lower biological age generally have a longer life expectancy. As a result, biological age is a better predictor of variation in mortality and morbidity than chronological age (Tangili et al., 2023)

The different hallmarks of biological ageing have recently gotten much attention (Firth et al, 2024). Numerous biomarkers have been assessed to develop indicators of biological age (Tangili et al., 2023). DNA methylation (DNAm) involves the addition of a methyl group to a cytosine followed by a guanine on a CpG site in the DNA strand. Genome-wide DNAm levels change with chronological age, which suggests that DNAm may contribute to overall senescence (Tangili et al., 2023).

These observations have led to the development of so-called ‘epigenetic clocks’ as DNAm-based predictors of chronological age. In fact, epigenetic clocks have shown to be the most accurate bio-marker based predictors of chronological age. Estimates of epigenetic age can serve as a predictor of an individual’s health, i.e. biological age, based on the observation that epigenetic age increases relative to chronological age in individuals affected by diseases (Horvath & Ritz, 2015) (Levine et al., 2018). The models that predict chronological age are referred to as ‘chronological clocks’, while the models that predict biological age are commonly known as ‘biological clocks’ (Li et al., 2022). Age estimation using methylation was developed in mammals (Arneson et al., 2022), but similar patterns have been observed in more species, among birds (Haller et al., 2024), insects (Glastad et al., 2014) and fish (Mayne et al., 2020). These new insights into the patterns of DNA methylation and epigenetic ageing will be helpful to get a better understanding of social ageing (Firth et al, 2024).

## Measuring social ageing with network analysis

A commonly used method to measure social ageing is a social network analysis (SNA). Network analysis provides a tool for describing the social system of species and populations in a quantitative and comparable way. It delivers a description of the social structure of a species or population and also serves as a basis for a range of analyses such as affiliation or avoidance between conspecifics, interspecific interaction, mating behaviour, genetic networks and community-level linkages (Farine & Whitehead, 2015), thus capturing multiple dimensions of the social environment. Additionally, social network analysis provides an understanding of processes on both group- and individual-levels (Farine & Whitehead, 2015).

Networks are generally referred to as observed patterns of associations or interactions (Farine & Whitehead, 2015). They consist of nodes connected by edges (see figure 1). Nodes represent individuals, groups, populations or other entities and can hold attributes, such as identity or phenotypic traits of the individual it represents (Farine & Whitehead, 2015). Edges represent how two nodes relate to one another and can be used to describe how often they associate or interact, or to describe other relationships (Farine & Whitehead, 2015). Edges often have numeric values (*weighted edges*), describing the strength of the relationship (e.g. rates or numbers of interactions), but they may also be *binary* (either 0 or 1), indicating only the presence or absence of a relationship (e.g. whether a male and female have mated or not) (Farine & Whitehead, 2015).

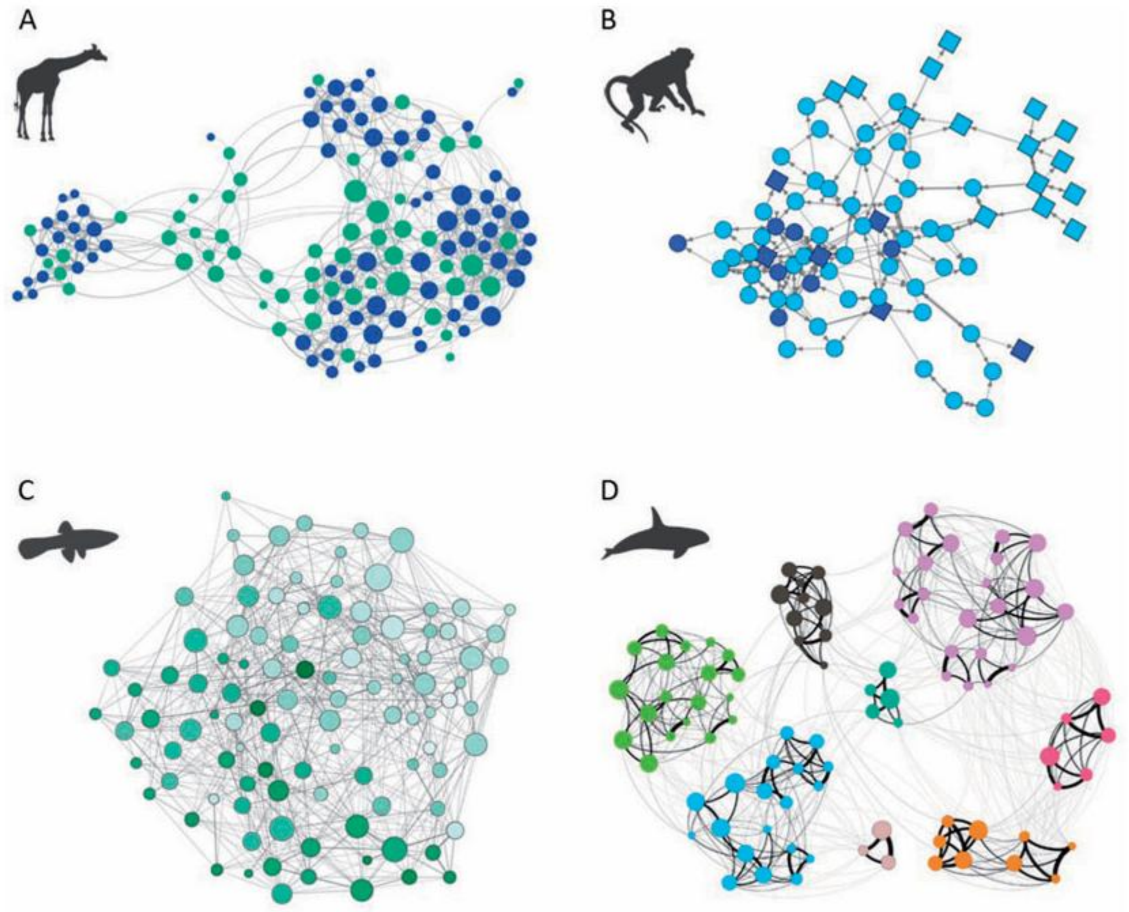

*Figure 1: Examples of animal social network graphs. In each graph, each circle represents an individual. Each line between two circles represent a connection between two individuals. Thicker lines signify a stronger social relationship (a higher rate of social interaction or association). (A) A social network of a population of giraffe, based on social associations (individuals observed in the same group). Females are shown in blue and males in green. Larger circles have higher degree and very weak connections are not shown for clarity. (B) A social network of a group of rhesus macaques, based on grooming interactions. Females are shown as circles and males as squares. Darker circles color indicates high-ranking individuals, and arrows point from the groomer to the individual being groomed. (C) A social network of a population of Trinidadian guppies, based on social interactions (individuals observed shoaling together). Larger circles have higher degree and darker circles signify individuals with a larger body size. (D) A social network of a killer whale population, based on social associations (individuals observed in the same group). Circle color indicates network communities and larger circles have higher within-community closeness (Brask & Croft, 2021).*

Network metrics are statistical measures used to determine characteristics of individuals or the whole network (Farine & Whitehead, 2015). Most of the metrics are individual based; they calculate a separate value for each individual. A few metrics, such as density, measure global network values. Almost all network metrics can be expressed either as a binary measure (B), a weighted measure (W) or a combination of both (BW) (Farine & Whitehead, 2015).

The most commonly used network metrics on node-level are:

Degree (B): the binary degree is the count of the number of edges connected to a node (Farine & Whitehead, 2015). If a network is directed, degree can be divided into in-degree and out-degree, which represent the number of incoming and outgoing edges, respectively. This measure reflects the gregariousness of individuals, by quantifying their number of associates or interaction partners. This information is important for understanding social dynamics within a group, because it influences the social status of an animal, including its dominance rank. Individuals with a higher in-degree than out-degree may have a higher status and a greater dominance within the group hierarchy. Thus, together with strength, these are the most common individual-level measures used in network analysis (Farine & Whitehead, 2015).

Strength (W): the weighted equivalent of binary degree is the sum of all edge weights connected to a node (Farine & Whitehead, 2015). If all connections are equal, then the strength will be the same as binary degree. Strength can also be divided into in-strength and out-strength for directed networks. This measure generally represents the expected total interaction or association rate per sample. For instance, a node with a strength of 2 would be expected to interact with approximately two other individuals on average (if using mostly association indices) (Farine & Whitehead, 2015).

Betweenness centrality (BW): the count of the number of shortest paths that flow through a node (Farine & Whitehead, 2015). This measures how important a node is for connecting distinct parts of a social network. A high betweenness centrality indicates that an individual is important for connection of communities. This highlights individuals that have a greater potential to switch between groups than others (Farine & Whitehead, 2015).

Eigenvector centrality (BW): the sum of the centralities of an individual's neighbors (Farine & Whitehead, 2015). High centrality indicates either a large degree being connected to associates with a high degree (or both). This shows the potential 'importance' of individuals in a network, as social hubs or for the spread of information or diseases through populations (Farine & Whitehead, 2015).

Page rank (BW): a measure of centrality for directed networks that divides the centrality (eigenvector) obtained through associates by the associates out-degree (Farine & Whitehead, 2015). This means that very central nodes pass only a small amount of centrality to each node that is connected to them, thus controlling the eigenvector centrality measure for many other nodes. Individuals with a large page rank are relatively important for connecting different parts of the network, which makes this measure useful for investigating flows of information or resources through networks (Farine & Whitehead, 2015).

Reach (BW): a measure of what proportion of all other nodes can be reached in one step, two steps, and so on (Farine & Whitehead, 2015). Thus, it also reveals the degree of separation in a network. This measure has not been explored much in animal social networks, but could be useful to investigate changes in social structure, such as the impact of removing key individuals in experiments. Additionally, it may provide insights into how quickly information or diseases spread through a population (Farine & Whitehead, 2015).

The most commonly used network metrics on network-level are:

Density (BW): the number of edges in a network divided by the total possible edges (B), or the sum of edge weights divided by the number of possible edges (W) (Farine & Whitehead, 2015). This measure might be valuable for normalizing observed degree distributions, as larger networks often have very low densities (Farine & Whitehead, 2015).

Homophily/assortativity (BW): the correlation in the phenotype of connected individuals (Farine & Whitehead, 2015). Positive assortment indicates that nodes are more connected than expected, while negative assortment indicates that alike nodes avoid each other. It's a powerful metric for identifying phenotypic structure in social networks. For instance, positive assortment by degree (gregariousness) has been linked with faster spread of information or disease through social networks (Farine & Whitehead, 2015).

Transitivity (BW): the proportion of triads (trios of nodes) that have three edges divided by the number of triads that have two edges (Farine & Whitehead, 2015). By comparing to null models, this reveals whether trios have the tendency to be more or less connected than expected. This might be particularly important when measuring interactions, because it captures the level of clustering in a network. For instance, grooming networks may have low transitivity if grooming follows the hierarchical structure (Farine & Whitehead, 2015).

# The ultimate drivers of social change

Changes in social behaviour or relationships with age can be caused by multiple mechanisms. These mechanisms of change in social behaviour can be divided by proximate and ultimate drivers. Proximate drivers give a mechanistic explanation for the change in social behaviour, such as molecular and physiological changes (Snyder-Mackler et al., 2020). Ultimate drivers give an evolutionary explanation, focusing on the costs and benefits of transitions to group-living (Snyder-Mackler et al., 2020). An overview of the mechanisms can be found in the article from Siracusa et al. (2022). This review paper will only focus on the ultimate drivers.

There are several benefits than come with sociality. Social animals often experience reduced predation risk trough group vigilance (Groenewoud et al., 2016) and cooperative defense mechanisms (Hellmann & Hamilton, 2014), which can increase their chance of survival (Salguero-Gómez, 2024). Many species, including meerkats (*Suricata suricatta*) (Groenewoud & Clutton-Brock, 2021) and fairy-wrens (*Malurus cyaneus*) (Arnold & Owens, 1998), exhibit cooperative breeding, where individuals assist in the care and rearing of offspring. This behaviour can enhance reproductive success by optimizing resource allocation (Koykka & Wild, 2016) and providing protection against predators (Poiani & Pagel, 1997). Cooperative foraging has been shown to improve foraging efficiency and foraging success (Snijders et al., 2021). Social connections also provide social support, which can reduce stress hormone levels (Wittig et al., 2016).

However, there are also costs that come with sociality. Social hierarchies can increase competition for mates, food or territory (Schoepf, & Schradin, 2012) (Stockley & Bro-Jørgensen, 2011) (Clutton-Brock & Huchard, 2013) and therefore lower the chance of survival (Salguero-Gómez, 2024). Additionally, competition for mates can result in skewed reproductive success (add 2 sources). (Allainé, 2000) (Poethke, & Liebig, 2008). Social interactions may also lead to stress, especially in animals that belong to strictly enforced hierarchies and lack access to social support, which has a negative effect on health and lifespan (Snyder-Mackler et al., 2020). Living in a group can also increase risk of pathogen and parasite transmission (Siracusa et al., 2024) and lastly, a higher level of sociality leads to reduced dispersal abilities and gene exchange (Corcobado et al., 2012).

## Increased selectivity and allocation of limited resources with age

Social ageing might result from increased selectivity and allocation of limited resources. As individuals age, they adjust their time and energy or cognitive capacity for social interactions. Such limitations may promote narrowing of social networks and selection for and increased focus on important or preferred social partners (Veenema et al., 1997) (Almeling et al., 2016). Along with physical and cognitive declines that promote increased selectivity in the choice of social partners, age-related reductions in immune function (i.e. immunosenescence) (Peters et al., 2019) (Phillips et al., 2020) might similarly influence how individuals adjust their sociality with age. Since social interactions play a role in disease transmission, individuals might narrow their social networks and reduce social engagement with age to avoid infection. This type of social avoidance is a common defense mechanism against pathogen transmission across species (Romano et al., 2020). Immunosenescence may also select for less risk-taking behaviour and competition avoidance. Old individuals might exhibit milder forms of aggression (Almeling et al., 2017) (Bernstein & Ehardt, 1985) or withdraw from social interactions to minimize negative social encounters (Almeling et al., 2017) (Ratnayeke, 1994) which might also explain increased attentiveness towards negative or threatening social stimuli with age (Rosati et al., 2018). Lastly, declines in food acquisition or nutrient processing with age may lead to greater self-preservation and less social cooperation (DeWall et al., 2008) (Siracusa et al., 2022).

## Changing reproductive value and effort across the lifespan

Social ageing might also result from a changing reproductive value and effort across the lifespan. In many mammals, reproductive value (the relative contribution of an individual of a given age to the future of the population (Fisher,1930)) declines with age after reproduction begins, affecting how individuals allocate social effort, often influenced by kinship dynamics (Rodrigues, 2018) (Hasegawa & Kutsukake, 2019). Helping behaviour is most likely to occur between individuals of low reproductive value and individuals of high reproductive value, given their levels of relatedness are similar (Rodrigues, 2018) (Hasegawa & Kutsukake, 2019) (Charlesworth & Charnov, 1981). This enables individuals to maximize their indirect fitness benefits by helping relatives with a high reproductive value or maximize their direct fitness benefits by avoiding cooperative or altruistic behaviour if their own reproductive value is high. This fitness trade-off will shape not only when individuals should allocate time and energy to social behaviour but also who they should direct that social effort toward (Rodrigues, 2018) (Hasegawa & Kutsukake, 2019) (Charlesworth & Charnov, 1981). For example, given that reproductive value declines with age, older individuals are expected to give more affiliate behaviour to younger relatives with higher reproductive value and receive less affiliation (Kurland, 1977). This might also lead to changes in social status as older individuals lose status to younger relatives (Combes & Altmann, 2001) (Chapais & Schulman, 1980) (Hrdy & Hrdy, 1976) (Siracusa et al., 2022).

## Demographic effects and shifting kinship dynamics across the lifespan

Social ageing might result from demographic effects and shifting kinship dynamics across the lifespan. Changes in birth, death, and dispersal rates, along with developmental traits, alter natural selection with age (Rodrigues, 2018), affecting social behaviour by altering opportunities for interaction, including similarity, familiarity and relatedness of group members. Similarity in age (Weiss et al., 2021) (Chiyo et al., 2011) (Widdig et al., 2001) and shared experience (Busia & Griggio, 2020) are important for the strength of social relationships. As individuals age, they often lose individuals they grew up with, leading to loss of social connections. In this way, within-individual declines in sociality with age can arise from population-level demographic changes. Local demography can also affect how relatedness to social partners changes with age, which stimulates advantageous within-individual shifts in social behaviour, because individuals may gain indirect fitness by supporting relatives (Croft et al., 2021) (Siracusa et al., 2022).

Kinships dynamics affect age-related social behaviour by mating and dispersal patterns. When mating occurs in social groups, mean relatedness to the group remains fairly stable for individuals that do not disperse, because they are replaced by new relatives or immigrants (Croft et al., 2021) (Johnstone & Cant, 2010). As a result, it is expected that levels of social affiliation and social differentiation remain relatively constant with age for philopatric individuals (the tendency of an animal to stay in, or return to, its home area (Coulson, 2016)). For dispersing individuals, mean relatedness to group members is expected to be low when they first join a group and to increase with age as they contribute offspring (Croft et al., 2021) (Johnstone & Cant, 2010). Dispersing individuals might therefore experience less aggression as they age and have larger, less differentiated social networks (Siracusa et al., 2022).

### *Support of evolutionary hypotheses*

Theory is used to predict these expected changes in social behaviour, because empirical evidence linking these explanations to social behaviour is still limited (Siracusa et al., 2022). Nevertheless, these explanations align with the two main evolutionary hypotheses that explain how strong affiliate relationships might enhance longevity (Blumstein et al., 2018).

The first one, the buffering hypothesis, proposes that social relationships may provide informational, emotional or tangible resources that enhance adaptive behavioural or neuroendocrine responses to acute or chronic stressors, such as illness, life events or life transitions. These social relationships help reduce or ‘buffers’ against the harmful effects of stressors on health. In this context, the term ‘social support’ refers to the real or perceived availability of social resources (Cobb, 1976) (Cohen & Wills, 1985) (Holt et al., 2010).

The second one, the main effects hypothesis, posits that social relationships may have protective health effects through more direct pathways, such as cognitive, emotional, behavioural, and biological effects, without necessarily providing explicit help or support. For example, social relationships may directly encourage or indirectly model healthy behaviours; therefore, being part of a social network is often associated with adherence to social norms that are related to health and self-care. Additionally, belonging to a social network provides individuals meaningful roles that contribute to self-esteem and purpose of life (Holt et al., 2010) (Cassel, 1976).

Evidence supporting both the buffering hypothesis (Ricci-bonot et al., 2021) (Gilmour & Bard, 2022) and the main effects hypothesis (Wittig et al., 2016) has been found. Some studies mentioned that only familiar individuals are effective at reducing cortisol responses (Hennessy et al., 2008) (Kikusui et al., 2006). However, a study on yellow-bellied marmots (*Marmota flaviventer*), a facultative social animal, found a significant negative impact of affiliative social relationship strength on longevity (Blumstein et al., 2018). More social marmots died at younger ages. This finding is in contrast with the buffering and main effects hypothesis. They suggested that the effect of sociality might depend on whether a species is obligately or facultatively social, and that in some species, strong social relationships are not beneficial and may even be costly (Blumstein et al., 2018).

An alternative for both hypotheses is the idea that intermediate levels of sociality may reduce senescence. Highly social individuals might face greater competition, social stress and disease transmission (Kappeler et al., 2015), while individuals with very low levels of sociality suffer from less social support and information transmission (Aplin et al., 2012) (Snyder-Mackler et al., 2020). This suggests that moderate sociality may be optimal. However, very few studies have looked at this so far.

### *Impact of environmental conditions*

Environmental conditions in early life can have an impact on the health and fitness outcome of an individual, which in turn can cause social ageing (Snyder-Mackler et al., 2020) (Dettmer & Chusyd, 2023). The silver spoon hypothesis posits that individuals born under good conditions, such as high availability of food, low risk of predation and few parasites, perform better during adulthood (Mainwaring et al., 2023). Evidence for this hypothesis was found in zebra finches (*Taeniopygia guttata castanotis*), where individuals with a high-protein diet in early life had higher survival rates and reproductive success as adults (Wilson & Burley, 2024).

In contrast, individuals born in environments with limited resources or exposed to significant early life adversity, such as maternal loss or the birth of a close-in-age younger sibling, often face constrains in their adult performance (Snyder-Mackler et al., 2020) (Wilson & Burley, 2024). For example, wild spotted hyenas (*Crocuta crocuta*) that lost their mother as juvenile had a lower chance of survival in adulthood (Strauss et al., 2020). Moreover, in yellow baboons (*Papio cynocephalus*), females exposed to higher levels of early adversity not only had a substantially shorted lifespan, but were also more socially isolated from other females in adulthood (Tung et al., 2016). Similarly, in African savannah elephants (*Loxodonta africana*), orphans displayed reduced social interactions with high-quality social partners, such as mature adults, compared to non-orphans (Goldenberg & Wittemyer, 2017).

# Discussion

The study of social ageing in wild populations is an emerging research field with a growing number of studies. However, within these studies, social ageing is often not explicitly defined. In general, social ageing refers to changes in sociality with age (Rudd et al., 2024) (Woodman et al., 2024). Most studies only considered changes in sociality in adulthood (Alberty et al., 2022) (Walmsley et al., 2024) (Campos et al., 2020). The definition of social ageing provided by Siracusa et al. (2022) mentions this and defines social ageing as changes that occur in adulthood. Although the primary interest lies in the changes that occur from younger to older adults (Siracusa et al., 2023), it is recommended to include information on juveniles, because sociality in later life can sometimes be explained by early life effects (Tung et al., 2016). This is included in the definition provided by Firth et al. (2024), who describes social ageing as changes that occur across all life stages from early development to later-life.

Moreover, studies across species have used different metrics to define sociality, which could give different research outcomes of social ageing. Consensus on the definition would improve the quality of research and contribute to the understanding of social ageing. This review paper focused on network analysis and the metrics that are used in those. Some studies have used directed networks (Croft et al., 2004) (Blaszczyk, 2017), while others have used non-directed networks (Siracusa et al., 2023) (Kusch, & Lane, 2021). Non-directed networks, by which non-directed edges are measured, could give misleading results if the behaviours are directed. For example, in rhesus monkeys (*Macaca mulatta)* (Datta, 1988) and chimpanzees (*Pan troglodytes*) (Thompson González, et al., 2021) older individuals receive less grooming than they give. Similarly, other studies found differences in received and given aggressive or affiliate behaviours based on directed-edge measures (Shimoji et al., 2014) (Turner et al., 2021) (Jones et al., 2010) (Buettner et al., 2015).

Considering ageing, studies often only measure chronological age, but including biological age as well could improve the precision of predictions related to age. Additionally, different hallmarks of ageing, such as epigenetic markers, are promising for an even better understanding of social ageing (Firth et al., 2024). These markers have already gotten a lot of attention in human health research (Iannuzzi et al., 2024) and are now gaining interest to improve ageing research wild animals (Campos et al., 2024).

In the second part of this review paper, I discussed three ultimate drivers that could cause social change. It is important highlight that these drivers are non-mutually exclusive (Siracusa et al., 2022). Proximate and ultimate drivers may operate simultaneously and potentially synergistically. Multiple mechanisms at the same level of explanation (i.e. proximate) can result in the same phenotypic outcome. This makes determining the relative contribution of these different explanations challenging. However, this could be a next step and would contribute to the understanding of the causes of social ageing (Siracusa et al., 2022).

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