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Social capital: an independent dimension of healthy ageing

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Abstract

Resources that are embedded in social relationships, such as shared knowledge, access to food, services, social support or cooperation, are all examples of social capital. Social capital is recognized as an important age-related mediator of health in humans and fitness-related traits in animals. A rich social capital in humans can slow down senescence and reverse age-related deficits. Some animals are able to adjust their social capital at different life stages (i.e., early, reproductive and post-reproductive life), which may promote individual fitness. However, the underlying biological mechanisms remain unknown. We suggest future research avenues to focus on social capital as a modifiable dimension to gain a better understanding of variations in senescence, and thereby provide new approaches to promote healthy ageing.

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The key role of social relationships in ageing

Humans are a social species. Any lack of social contact affects both mental and physical **health** (see Glossary for definition of health) (Rattan 2013; Rook 2015). Poor social interactions are even known to be a risk factor for all-cause mortality (Kawachi *et al.* 2008; Rook 2015; Snyder-Mackler *et al.* 2020). Although numerous studies report associations between social interactions and health outcomes, the underlying mechanisms are largely unknown. The number of animal studies on the physiological (e.g. stress) or ecological (e.g. food access) determinants of ageing has risen sharply over the past ten years (Lucas, Keller 2020; Snyder-Mackler *et al.* 2020). They suggest that complex and intertwined behavioural, psychological and biological pathways are likely involved (Box 1) (Rook 2015; Nattrass *et al.* 2019). However, these animal studies provided with contrasted results according to species traits (e.g. group size) (Lucas, Keller 2020) or individual traits (e.g. social status) (Snyder-Mackler *et al.* 2020). A large part of the ageing variations at both inter- and intra-specific levels is therefore still unexplained.

Resilience to stress and body energy homoeostasis is affected by **social resources** (i.e. the knowledge, services, social support or cooperation (Lakon *et al.* 2008; Brent *et al.* 2011; Thoits 2011; Wittig *et al.* 2016; Moscovice *et al.* 2020)) an individual has access to or has used (Lin *et al.* 2001), which is called **social capital**. Individual social capital is a widely used concept in human **healthy ageing** literature, and recent research on non-human animals seems to show that social capital represents a key set of components (see Box 2 and table 1) in adjusting **senescence** and influencing **fitness**. By adjusting, we mean that changes in social capital are not random but made in a way to increase fitness (survival and/or reproduction) and/or healthy ageing. This adjustment is the result of behavioural strategies (e.g., favouring, selecting or avoiding social interactions). Although these strategies may or may not be ruled by intermediary mechanisms (e.g., stress, genetics, mating system), the latter being most likely evolutionary selected (Sueur *et al.* 2019). Based on the fact that **social capital** varies with individual age and social group characteristics, we propose that it is the main factor that mediates the associations between sociality and healthy ageing. In this perspective, we propose that the mechanisms linking social capital to healthy ageing can be better understood by adopting an evolutionary and comparative approach within individuals and between humans and animals (Chiou *et al.* 2020; Emery Thompson *et al.* 2020; Machanda, Rosati 2020), thus providing greater insight into the observed variation in senescence rates and facilitating the identification of anti-ageing interventions.

Box 1: Biology of ageing, senescence and longevity in social animals

While an individual can have a long-life expectancy, it may not attain the same **fitness** as a conspecific due to an accelerated **senescence** of the reproductive function (figure 1). The rate of senescence at the individual level is expected to reflect the lifelong deleterious impact of costly traits such as growth, immunity or reproduction (Hamilton 1966). Inter-individual variability in the age of senescence onset is also a unique opportunity to investigate the genetic and socio-environmental factors that shape **ageing** trade-offs within a given population. Social stress has been known to modulate ageing pathways for the last decade (Blackburn, Epel 2012). However, interplay between social capital and age may highlight putative loops of intertwined pathways that modulate reproductive success and survival rate in both negative and positive ways ❶. In a resource-based explanation, an initial underlying mechanism relies on the impact of social capital on energy resource acquisition (for instance via the acquisition of knowledge or friendly relationships) ❷. However, variation in social capital may act indirectly through cellular and physiological changes that strengthen resilience to stress ❸ or body energy homoeostasis ❹. These effects are currently inferred from previous observations. Social isolation and interactions have been described as having opposite effects on stress hormones (Wittig *et al.* 2016), with potentially negative consequences but also adaptive responses observed at the physiological and cellular level (*e.g.* oxidative stress) (Katyare *et al.* 2003). Another study suggests that social isolation has negative effects on stress and energy balance (Koto *et al.* 2015). Inflammation is also an important biological mechanism that links social capital to unhealthy states (Uchino *et al.* 2018). Indeed, various forms of social adversity are associated with elevated expression of proinflammatory genes and decreased expression of genes related to innate

immune responses in humans (Cole 2014) and rhesus macaques (Simons, Tung 2019). These altered individual performances in the acquisition of energy from the environment will be reflected in the life-history trade-offs for the allocation of energy to individual fitness traits. Social isolation triggers an increased rate of telomere loss (a biological index of ageing) (Aydinonat *et al.* 2014) and disrupts energy homoeostasis. Increased telomerase activity in socially stressed individuals has also been described in the literature (Beery *et al.* 2012). This suggests that social variables do indeed impact cell-ageing proxies, as previously suggested for social rank and telomere length (Lewin *et al.* 2015; Bateson, Nettle 2018). However, as social capital likely varies over time and depends on individual physiological status, a feedback of physiology is expected on sociality (❺, ❻). For instance, some authors suggest possible causal effects of short telomeres on unhealthy behaviours as smoking in humans (Bateson, Nettle 2018). It means that some physiological traits (short telomeres) can conduct to some bad aspects of sociality (here being conformist with risky behaviours for health) enhancing the physiological traits (decreasing telomeres). Another example is the accelerated death of ill flies (*Drosophila melanogaster*) who are isolated from their conspecifics, likely because of reluctant physiological traits as cancer (Dawson *et al.* 2018). Because individuals have cancer, they are isolated from others but this in turn accelerates cancer progression. These studies confirm that the social capital – fitness relationships have auto-regulating properties, a finding that calls for dedicated studies to identify these causal links.

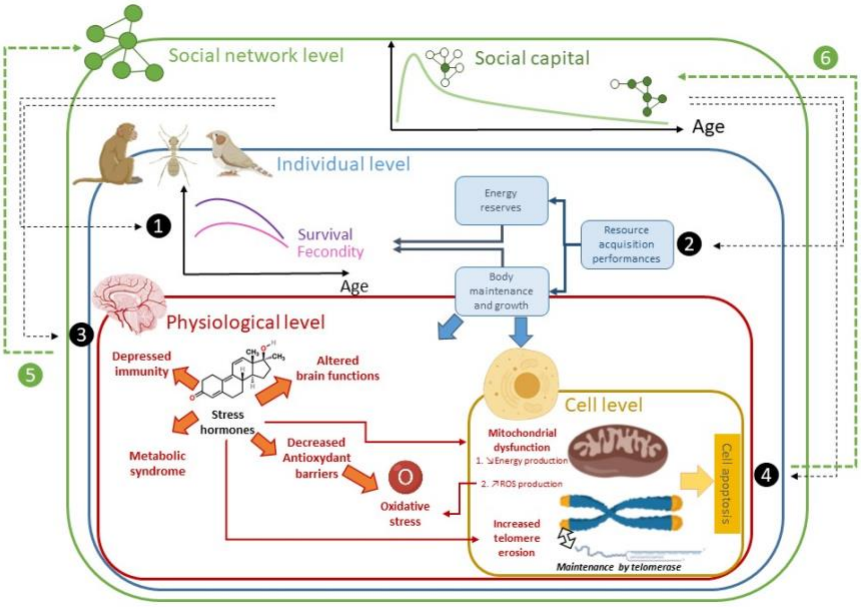

Figure 1: Schema of the proposed mutual influence of social capital, chronological age and biological age, from the cell level to the network.

Table 1: Components of social capital according to the studied species and the level of study.

	Variations inside a same group/colony	Variations between groups/colonies	Interspecific variations
Eusocial species (e.g. ants, bees, naked mole rats)	**Properties of social interactions** including number and duration of interactions, type of interactions (e.g., trophallaxes (Bles *et al.* 2018), antenna-to-antenna, grooming), intra-caste or inter-caste interactions. **Spatial distribution** of social interactions (Planckaert *et al.* 2019) according to individual mobility patterns **Individual positions within the social system** including, not exclusively, individual caste (e.g., male, queen, nest worker) or centrality index (Stroeymeyt *et al.* 2018)	**Properties of the colony** (Dornhaus *et al.* 2009) including, not exclusively, its size, the population distribution by caste (e.g., mono/polygyny, the ratio of individuals between caste), and the colony age. **Properties of the whole system of social interactions** (Quque *et al.* 2021) using network indicators such as community separation and its resilience.	**Properties of the colony,** including, among others, its size, the caste system specific characteristic (e.g., number of reproductive individuals, marked division of labour, short or long-lived males, worker dimorphism) (Jarvis 1981; Robinson 1992; Burda *et al.* 2000; Beshers, Fewell 2001) **Relation with other colonies** including the tolerance level and belonging to supercolony (Sunamura *et al.* 2011).
Cooperative breeding species	**Properties of social interactions** including number and duration of interactions, type of interactions (e.g., grooming, aggression, reproductive behaviour). (Drewe 2010; Dey *et al.* 2013) **Properties of social relationships** which may include kinship, sex, reproductive status and dominance hierarchy. (Reber *et al.* 2013) **Individual positions within social structures** including, not exclusively, individual status (e.g., reproductive or helpers) and its position between reproductive subgroups (Drewe *et al.* 2009; Madden *et al.* 2009, 2011)	**Properties of the colony**, may include its size, the number of helpers and offspring and the system of interactions between reproductive subgroups. (Covas *et al.* 2008)	**Properties of cooperative breeding**, including if its facultative or systematic and the level of competition for reproduction between helpers and male breeder. (Kimball *et al.* 2003; Hatchwell 2009; Riehl 2013; Griesser, Suzuki 2016; Bebbington *et al.* 2018) **Comparing evolutionary advantages of cooperative and not-cooperative breeding**, regarding *e.g.* longevity, reproductive success, life history. (Beauchamp 2014; Downing *et al.* 2015, 2021)

Primate societies and similar mammal societies	**Properties of social interactions** including number and duration of interactions, type of interactions (e.g., grooming, aggression, reproductive behaviour, exchange of resources) (Bret *et al.* 2013; Levé *et al.* 2016; Puga-Gonzalez *et al.* 2018; Sosa *et al.* 2019; Ramos *et al.* 2019) and their spatial distribution (Naud *et al.* 2016) **Properties of social relationships**, including, not exclusively, kinship (Best *et al.* 2014), dominance (Wroblewski *et al.* 2009), direction and reciprocity in conflicts and resources exchange (Puga-Gonzalez *et al.* 2018). **Individual position within social structures**, including, among others, centrality (Sosa *et al.* 2020), belonging to certain subgroups and dominance (Balasubramaniam *et al.* 2012) relative to the whole hierarchy	**Properties of the group**, including their size, and their age/sex distribution (Wrangham 1987; Kappeler, Schaik 2002) **Cultural variation** (Cronin *et al.* 2014; Borgeaud *et al.* 2016) including, among others, tolerance in aggression and exchange with non-kin, tool use **Properties of the interaction network**, including, among others, the level of community division resulting from non-kin interactions (Sueur *et al.* 2011). **Exchange with and tolerance of** other groups (between-group competition)	**Properties of the group,** including, their size, the mating system, the hierarchical structures, and affiliation between non-kin (Sueur *et al.* 2011). **Structure of the interaction network**s including their size, community structure and efficacy in exchange of information and ressources (Pasquaretta *et al.* 2014; Romano *et al.* 2018)
Humans	**Properties of social relationships which may include**, relation type (e.g., relatives, colleagues, friends) (Pinquart, Sörensen 2000), relationship diversity (Ali *et al.* 2018), marital status and quality (Robles *et al.* 2014; Kiecolt-Glaser, Wilson 2017; Kiecolt-Glaser *et al.* 2019), closeness and intimacy (Kelley *et al.* 1983; Debra J. Mashek 2004), homophily (Fowler *et al.* 2011; Montgomery *et al.* 2020) and their perceived valence (i.e., positive, negative, ambivalent) (Uchino *et al.* 2012a). **Properties of social interactions, which may include** perceived and received support (Lyyra, Heikkinen 2006; Nausheen *et al.* 2009; Gariepy *et al.* 2016), companionship (Rook 1987; Buunk, Verhoeven 1991), negative interactions (Rook 2001;	**International and intra-national comparison of individual-level social capital according, not exclusively,** to ethnic groups (Baron-Epel *et al.* 2008), welfare regime (Kääriäinen, Lehtonen 2006), regional economic growth (Beugelsdijk, Van Schaik 2005), or socio-economic status (Kim *et al.* 2006) **Community-level social properties such as** centrality (Strauss, Pollack 2003; Christakis, Fowler 2007), clustering (González *et al.* 2007; Christakis, Fowler 2008; Frank *et al.* 2013) dyadic	NA

	Akiyama *et al.* 2003) and their geospatial distribution (van den Berg *et al.* 2015; Kestens *et al.* 2017). **Individual position within social structures such as** centrality and periphery (Shakya *et al.* 2015), brokerage (Dekker 2006), and belonging to specific subgroups (Hynie *et al.* 2011) **Indicators of complex processes** such as social isolation (Holt-Lunstad *et al.* 2015; Smith *et al.* 2020) bonding and bridging capital (Kim *et al.* 2006; Murayama *et al.* 2015), social participation (Levasseur *et al.* 2010), social inclusion and exclusion (Wright, Stickley 2013).	distances (Christakis, Fowler 2007, 2008), social connectedness (Entwisle *et al.* 2007; Shakya *et al.* 2014) or components and cyclical structures (Helleringer, Kohler 2007)	

Social capital changes with chronological age

The social capital of an individual varies according to its life stage (i.e., early, reproductive or post-reproductive life) (McDonald, Mair 2010). In humans, non-human mammals and other species with long-lasting mother-offspring bonds, infants focus on a small number of strong relationships with their mother and individuals who share common traits (e.g., gender, kin). As adolescents, the individuals then expand the quantity and diversity of their social relationships, and become more selective upon reaching adulthood (Field, Minkler 1988) in order to adjust social capital in favour of resource acquisition (box 1).

Elephants (*Loxondota africana* (McComb *et al.* 2001)), chimpanzees (*Pan troglodytes* (Rosati *et al.* 2020)) and macaques (*Macaca sp.* (Brent *et al.* 2011; Almeling *et al.* 2016)) show comparable patterns of social changes with chronological age, even if they generally display higher interspecific than intraspecific longevity variation. In elephants, social relationships such as dominance are age-based (Wittemyer, Getz 2007). Matriarchs are the repositories of knowledge and manage relationships (McComb *et al.* 2001). In chimpanzees, ageing males display more mutual, positive and selective relationships than younger counterparts (Rosati *et al.* 2020; Silk 2020). Some authors proposed that the maintenance of social relationships with elders may improve their health status and longevity. Almeiling et al. (2016) reported that old Barbary macaques (*Macaca sylvanus*) appear to remain valuable alliances for young macaques, who continue grooming them to obtain social resources. These alliances result in a richer social capital with fewer injuries and better transmission of knowledge, all of which give access to resources for animals of all ages (McComb *et al.* 2001; Almeling *et al.* 2016). In mammal societies and many native human societies such as the Māori (Durie 1999), knowledge is a key resource provided by older group members. The fitness of both older and younger members increases because of the expertise and leadership of the elders (McComb *et al.* 2001; Nattrass *et al.* 2019; Migliano *et al.* 2020). Social capital also varies in **eusocial** insects. Throughout ontogenesis, worker ants or bees change from one caste to another (Münch *et al.* 2008). This is associated with age-related cognitive decline (Baker *et al.* 2012) and changes in their social capital; they no longer interact with the same individuals (Mersch *et al.* 2013; Richardson *et al.* 2020; Wild *et al.* 2021).

Different theories offer contrasting arguments to explain this change in social capital throughout life, based on ultimate (e.g. reproduction-life trade-off (Lahdenperä *et al.* 2004; Lemaître *et al.* 2020) and kin selection (Abbot *et al.* 2011)) or proximate (e.g. cognitive (Aartsen *et al.* 2004; Carstensen 2006) or cellular processes (Bateson, Nettle 2018)) approaches. Thus, comparing the age-specific changes in social capital between different animal species may help to identify the associations between the timing of these changes and the individual physiological markers of ageing.

Biological age changes with social capital

Social capital fluctuates according to the different stages of life (early-life, reproductive life, post-reproductive life) and may therefore influence individual health and biological age through stress and body energy homoeostasis. For example, early maternal loss leads to short, but not long-term stress increases in wild chimpanzees (Girard-Buttoz *et al.* 2021). Social isolation itself, i.e. independent of the usually associated increased risk of predation and lower feeding efficiency, causes death in carpenter ants (*Camponotus fellah* (Koto *et al.* 2015)) by disrupting energy homoeostasis. In reproductive fruit flies (*Drosophila melanogaster*), social isolation induces stress, significantly accelerates the progression of tumour growth, and triggers rapid death (Dawson *et al.* 2018). Of course, usually social isolation increases predation risks or decreases feeding efficiency, but the latter results were done in absence of predation and with ad libitum food. In primates, males often disperse and this social isolation period is the most dangerous for them (Campos *et al.* 2020). Conversely, helping (early-life stage **in cooperative breeders**) and being helped by others (reproductive stage) increase social capital and positively influence individual health, and ultimately fitness, in all age categories (Lemaître *et al.* 2015; Berger *et al.* 2018; Hammers *et al.* 2019). Of course, social capital can have a negative impact on fitness (Snyder-Mackler *et al.* 2020; Campos *et al.* 2020; Anderson *et al.* 2021), but this is relative to other group members, and this negative impact of social capital on fitness is still lower than the cost associated to solitary living (Krause, Ruxton 2002). Yet, perception of ambivalent relationships in humans is related to shorter telomere length (Uchino *et al.* 2012b)

which suggests that social capital could also negatively impact biological ageing. In a nutshell, social capital, as early as infancy, could be one of the main determinants of individual long-term fitness prospects.

In old macaques, maintaining an active social life has been suggested to stimulate and maintain brain activity through a good quality of life at both mental and physical levels (Almeling *et al.* 2016). Cognitive decline is observed in many non-human primate species (Emery Thompson *et al.* 2020; Lacreuse *et al.* 2020), but the interplay with the components of social capital is underappreciated. For instance, young lab animals who grow up alone may have difficulties developing good relationships when they become adults, which in turn may trigger faster senescence. Remarkably, the longevity of eusocial insect workers ranges from a few weeks to more than two years. This plasticity is largely controlled by social factors (Lucas, Keller 2020). Although these individuals are closely related genetically, distinct life trajectories can emerge as a result of variations in their social capital. Recent studies conducted in honeybees (*Apis mellifera* (Wild *et al.* 2021)) and carpenter ants (Richardson *et al.* 2020) confirm that social capital predicts survival better than chronological age. A high social demand exposes workers to an overload of social stimulations, speeding up senescence and decreasing longevity. Richardson et al. (Richardson *et al.* 2020) went further and concluded that the transition between castes is not hard wired or age dependent, but rather stochastic and dependent on changes in social capital. Bees and ants are also able to return to their previous caste and modify their interactions if a new demand appears in the colony (*e.g.,* following a nest predation event). This sole change in social capital results in molecular (Quque *et al.* 2019) and neuronal modifications (Münch *et al.* 2008) associated with reversible age-related phenotypes (Baker *et al.* 2012) (Box 1) and improved health, cognitive abilities and longevity. Social reprogramming in *Harpegnathos saltator* ants (from workers to gamergates) conducts to longevity-associated brain remodelling (Sheng *et al.* 2020). To sum up, social capital can reverse biological age.

Box 2: What are the components of social capital?

Although work on social capital abounds across disciplines, there is no consensus on its conceptualisation and operationalization (Bourdieu 1980; Putnam 1993; Kawachi *et al.* 2008; Fine 2010). Social capital can first be studied in terms of resources or services that are embedded in spatial associations (e.g., proximities, being close to an individual can provide access to food) or social interactions (e.g., grooming). Although social resources that are embedded in social relationships cannot be directly controlled using behavioural strategies, individuals can choose the individuals with whom they maintain relationships (Snyder-Mackler *et al.* 2020; Moscovice *et al.* 2020). Food is primarily an ecological resource, but access to it depends on the social capital of the individual (social support, cooperation, alliances, tolerance).

Because social relationships are the basis on which social capital is managed, the notion of social capital is often simplified to these social relationships, in which social resources are exchanged. These relationships can be described from their compositional (e.g., hierarchical position of the individuals) or structural (e.g., distributions of social relationships) properties. In many studies, social network indices such as degree (number of social relationships, see table 2 for metrics from social network analysis to measure the components of social capital) are used as a proxy of social capital. Most of the past studies have focused on the direct social relationships between individuals in a network (e.g., degree or strength (Sosa *et al.* 2020)), yet indirect relationships (*e.g.*, friend of our friend, betweenness or clustering coefficient (Sosa *et al.* 2020)) also influence social capital (Brent *et al.* 2011; Quque *et al.* 2021). These indirect connections affecting information but also disease (Romano *et al.* 2020) transmission networks may strengthen the cognition and longevity of species, in which cultural behaviour is important (Romano *et al.* 2020). Furthermore, cultural differences influence social capital in humans (Mulder *et al.* 2009); few studies have been conducted to date on this topic in non-human animals, and further studies should be carried out.

Lastly, social activities and geospatial locations can be studied in relation with social capital (Naud *et al.* 2020), but can also be integrated as components of the latter. Indeed, human social activities are linked to specific locations and both elements can be combined to better understand covariation between social capital and health (Naud *et al.* 2020). This covariation between social capital, location and task is obvious in eusocial insects (Richardson *et al.* 2020; Wild *et al.* 2021), but evidence is lacking in other species. Both Wild et al. (Wild *et al.* 2021) and Richardson et al. (Richardson *et al.* 2020) used information about social interactions, proximities, social activities and location to calculate a social capital index.

To summarise, the social capital components we need to identify are: resources embedded in social relationships (Lin *et al.* 2001) such as information and services (Moscovice *et al.* 2020), the composition and structure of social networks (individual but also group metrics), cultural differences, social activities and geospatial locations. Table 1 summarises the currently considered components of social capital according to the studied species and the level of studies. Table 2 summarises metrics from social network analysis to measure the components of social capital.

Future perspectives: the interplay between social capital and biological age matters

Organic (e.g., food) and inorganic (e.g., social) resources influence survival, growth and reproduction. Social resources alone define social capital. Individuals can act on social interactions or social activities to modify social capital and thus decrease stress, balance homoeostasis, and ultimately improve health. Because social capital is flexible and seems to be partly independent of chronological age, we suggest that social capital should be considered as a modifiable dimension (as defined in mathematics, Figure 2) within the health space (Sanromà, Adserà 2010), with its own regulatory processes and bidirectional effects on individual senescence. As proposed by Richardson et al. (Richardson *et al.* 2020), social capital is not directly linked to chronological age but can change with biological age. This modifiable characteristic involves large intra- and inter-specific variations in social capital, which in turn influence individual ageing rate and fitness.

These statements (i.e., the presence of variations in social capital leading to variations in ageing rate and fitness) give rise to future research directions that can be addressed in the three following questions:

1) What is the extent of our knowledge on social capital? Social capital is most certainly a complex concept. This is illustrated by the large number of existing definitions in human sciences (Putnam 1993; Lin *et al.* 2001; Rattan 2013) but also by the diversity of its potential components. Portes (Portes 2000) noted that 'the point is approaching at which social capital comes to be applied to so many events and in so many different contexts as to lose any distinct meaning.' Because social capital seems to be important for individual fitness and the evolution of sociality, it is crucial to acknowledge and apprehend its complexity. First, although most of the attention has been focused on the health benefits of social capital so far, the possible health risks associated with social capital also need to be considered, especially in terms of social overloading (Richardson *et al.* 2020; Wild *et al.* 2021) or exposure to pathogens (Romano *et al.* 2020). Page and collaborators (Page *et al.* 2017), for example, observed that mothers with higher betweenness and closeness centrality show more frequent instances of sickness, which somewhat counteracts other positive fitness effects. Other researchers have begun to acknowledge that social capital ranges across a large spectrum spanning from positive to negative consequences (Wacquant 1998; Portes 2014), the latter being associated with adverse health outcomes. Costs of sociality are important. For instance, high social status males experience accelerated epigenetic aging in wild baboons (Anderson *et al.* 2021) and higher oxidative damage but only during the mating season in mandrills (Beaulieu *et al.* 2014). We also need to consider other positive resources that can be considered components of social capital. For example, it has been shown that in addition to providing food (Quque *et al.* 2021), trophallaxes convey compounds that are essential to individual health and growth in a conserved way across several taxa (LeBoeuf *et al.* 2016), which seems to indicate a selection. Like eusocial insects, mammals share organic compounds through the social transmission of gut microbiome, which is known to influence health outcomes (Sarkar *et al.* 2020). This field of study extends to birds, in which the feeding of chicks may allow intergenerational transmission of such compounds (Lecomte *et al.* 2006), and thus ensure rapid adaptations to environmental changes (Badyaev, Uller 2009). Whether or not a richer social capital can improve adaptation in social species remains to be evaluated. Finding new components of social capital is a research horizon that needs to be explored. Box 2 shows that social capital may simply be directly related to the number of relationships or could be evaluated in a complex way with the inclusion of social activities and the locations in which these social activities are performed. How social capital should be operationalised also depends on the studied species, the conditions and the scales of the study (temporal scale and subject/social organisation scale, i.e., interspecific comparisons of individuals that are studied throughout their lifetime). Future research should further explore the potential components of social capital and their independent or additive/synergistic effects on ageing outcomes, in the laboratory but more importantly in natural settings to demonstrate similar effects under natural variation of social relationships.

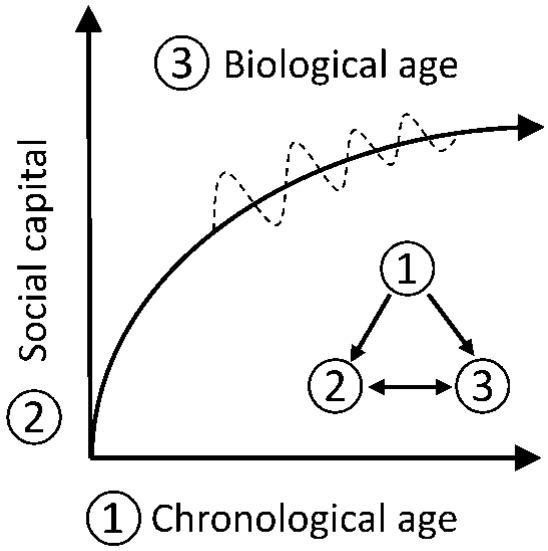

Figure 2: Changes in biological age (③, curved line) according to chronological age (①, x-axis) and social capital (②, y-axis). The dotted line represents variations observed in returning to a previous caste and solicitations in eusocial insects, but may result from intervention on social parameters in humans and other animals. The most recent research in animal species showed that biological age ③ is not only dependent on chronological age ① but also on social capital ② with an interplay between ② and ③. Interplay with ① cannot exist as chronological age cannot be altered.

Table 2: Metrics from social network analysis to measure the components of social capital. We define usual metrics used in social network analysis and give non-exhaustive example of their possible use in diverse systems to assess the components of social capital cited above in Table 1. We call network, the scales greater than the individual. It can be groups, colonies, species. A path is the successive connections that are necessary to link an individual A to an individual B within a given group. The shortest path is the one that minimises the number of necessary connections. We use the term 'resources' in a broad sense that can include, depending on the model studied: information, food, sexual partners...

Social metrics	Scale	Definition	Practical examples of the social network metrics to study social capital
degree	individual	* The number of connections (neighbours) of an individual * This metric can be undirected or directed, in this latter case we distinguish the case where individuals *emit* interaction towards their neighbours (*out-degree*) from the ones where individuals *receive* interactions (*in-degree*).	* Studying the individual degree highlights social immunity in eusocial insects. (Cremer *et al.* 2007) * Chicks' degree in cooperative breeders is a proxy for the intensity of parental care they can get. (Boheemen *et al.* 2019) * Humans live a longer and healthier life when maintaining numerous positive social relationships. (Umberson, Karas Montez 2010; Yang *et al.* 2016)
strength	individual	* The interaction number in which an individual is involved. * This metric can be undirected or directed, in this case we distinguish the interactions *given* (*out-strength*) from the ones *received* (*in-strength*).	* The number of given and emitted aggression between conspecifics affect the individual physiology, especially triggers oxidative stress. (Schrock *et al.* 2019) * Duration and number of trophallaxes vary according to the social role in black garden ants. (Quque *et al.* 2021) * Lower-rank individuals may benefit from higher-rank ones' protection through an intensive grooming behaviour. (Tiddi *et al.* 2012)
betweenness	individual	The number of shortest paths passing through an individual. Individuals with a high betweenness are crucial nodes through which a large amount of resource passes.	* Having a high betweenness may be an advantage regarding the access to resources but a drawback regarding the exposition to pathogens. (VanderWaal *et al.* 2014)
eigenvector	individual	This metric adds the neighbour amount of an individual to the neighbour amount of those neighbours. It reflects the possibility to access resources through direct and indirect connections.	* Chimpanzees with higher values of eigenvector centrality in early adulthood have been found more likely to be high-ranked in the hierarchy later in life. (Watts 2018)
closeness	individual	Gives the average distance (number of connections) necessary to reach all other members of the groups. So, counter-intuitively, a high closeness coefficient reflects social isolation.	* Closeness coefficients reliably predict hierarchy and dominance patterns, *e.g.* in pigs. (Büttner *et al.* 2019) * Social isolation is proved to be a major health issue in humans and non-human animals. (House *et al.* 1988)

modularity and clustering coefficient	network	These two metrics are based on different formula, but both assess whether individuals tend to cluster into modules characterised by a strong intra-module interaction but a weak inter-modules interaction.	* Such metrics highlight groups cooperating for access to resources and thus increasing their social capital. (Assenza *et al.* 2008; Kuperman, Risau-Gusman 2012)
diameter	network	Gives the longest path of the network and thus a clue about the speed all group members can access a resource.	* Diameter and other network metrics have been used in ants to measure the network plasticity in different ant colonies, and have been linked to pathogen resistance. (Stroeymeyt *et al.* 2018)
density	network	The number of connections observed within the group divided by all the possible connections.	* A density index may be used, for instance, to compare the degree of selectivity (high selectivity implies low density) of different groups of ravens to know if they share resources with specific individuals or not. (Kulahci *et al.* 2016)

2) How can we explain individual and species variations in health and longevity? This section is about ultimate mechanisms linking social capital to ageing. Among species, environmental factors have differently shaped age-specific trade-offs between growth, reproduction and survival. Some components of the social capital can be influenced by environmental factors but can also attenuate the impact of the latter, increasing or decreasing individual and species variations in health and longevity. Future studies should therefore address the co-evolution of interspecific variances in social capital and senescence rate. Animal species characterised by particular age-specific social capital can emerge as novel behavioural models to address questions in current human ageing research (Lemaître *et al.* 2015; Lucas, Keller 2020; Lacreuse *et al.* 2020). For instance, such studies may delineate how social capital modulates life period trade-offs (*i.e,.* early-life growth and subsequent young and adult survival, and reproductive success) and how adult social capital may have co-evolved with post-reproductive lifespan (Vágási *et al.* 2020). For example, female killer whales (*Orcinus orca*) live twice longer than males, and post-reproductive females have greater knowledge and lead the group, thus enhancing the survival of their grand-offspring (Nattrass *et al.* 2019). These old females, like elephant matriarch (McComb *et al.* 2001), have a rich social capital, live longer and also provide their offspring with a huge social capital. This grandmother hypothesis was primarily proposed in humans (Lahdenperä *et al.* 2004). In line with these observations, one can hypothesise that variations in social capital in different life stages influence variability in post-reproductive longevity (Figure 3b) and indirectly modulate sex differences in senescence (Lemaître *et al.* 2020). This means that sex-related differences in social capital could lead to sex-related differences in longevity because of health or because of fitness benefits of social capital. However, such sex-related differences in longevity can be buffered when males associate with females. For instance, male baboons who are more strongly bonded to females have longer lifespans (Campos *et al.* 2020). The subject of age-related cognitive processes requires longitudinal neurobiological studies focusing on the ageing brain within the context of social capital (Lacreuse *et al.* 2020). Finally, the interaction between social capital and life history traits has certainly been constrained by environmental factors such as predation risks, parasite prevalence or local population density. It is also important to note that non-social species like ctenophores or cnidarians have almost reached immortality (Petralia *et al.* 2014), or may live for centuries like the Galapagos turtle or the Greenland shark. This casts doubt on the incompressible limits of social benefits for longevity (Figure 3a and d). Multi-specific and multigenerational studies will help to discover the mechanisms that underlie the relationships of social capital with species life history and ecology.

3) How is social capital encoded to enhance fitness? This section is more about proximate mechanisms linking social capital to ageing and fitness. Although we know that social capital is related to individual fitness, little is known about the extent to which this relationship depends on species ecology and gender, or whether it is restricted to certain life-history traits. The role of social capital in variations of senescence onset or in senescence rate can be assessed in the context of **evolutionary theories of ageing** (Reznick *et al.* 2005). For instance, this can be done by determining how social capital modulates the energy trade-offs that can occur during the life trajectory of individuals (e.g. growth/reproduction and ageing trade-offs (Williams 1957; Hamilton 1966; Lemaître *et al.* 2015)). Potential biological mechanisms such as telomere rate of loss (Lewin *et al.* 2015), oxidative stress or mitochondrial dysfunction (Hood *et al.* 2018) (Box 1) that are already suspected to play a major role in ageing would have to be tested in the light of the social capital context. For example, extended sex-specific post-reproductive life in killer whales may have been co-selected with specific social traits and anti-ageing mechanisms that have positive effects on female fitness and their offspring (Kirkwood 1977; Lahdenperä *et al.* 2004). Age-related variations in social capital in cooperative breeders have already been linked with the fitness traits of individuals (see Berger *et al.* 2018; Hammers *et al.* 2019). However, we have yet to elucidate the question of how eusocial reproducers have acquired a specific social capital that probably enables them to successfully face higher reproduction rates and attain a longer lifespan than non-reproducers. How is the impact of social capital on senescence genetically or epigenetically encoded? For instance, personality, which is heritable, has an impact on longevity and pace of life (Réale *et al.* 2010), and one of its bases is sociality. Social capital could be encoded in this personality variable, a hypothesis that needs to be tested *via* the demonstration of a covariation at the individual level among social capital, personality and longevity. Understanding the genetics and epigenetics of sociality would be of help in unraveling mechanisms that link sociality to ageing outcomes

and fitness. In this respect, we propose that the recent development of genomics and proteomics to study ageing (Münch *et al.* 2008; Quque *et al.* 2019) should be extended to include the study of social capital. These investigations will likely extend our knowledge on how evolution has co-selected sociality and longevity (Lucas, Keller 2020; Vágási *et al.* 2020). Furthermore, these new findings could subsequently be leveraged to promote healthy ageing.

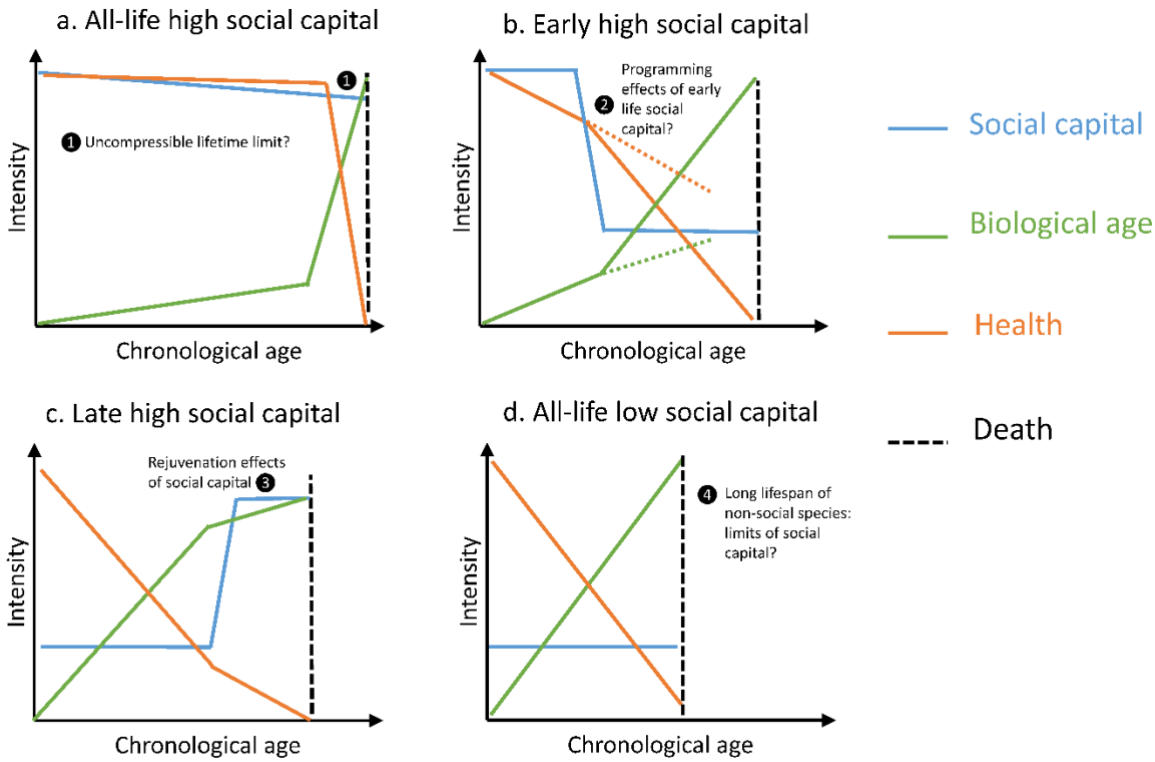

Figure 3: Variation (y-axis) of social capital (blue), biological age (green) and health (orange) over chronological age (x-axis) for an individual having access to (a.) life-long high social capital, (b.) only early-life high social capital, (c.) late-life high social capital, and (d.) life-long low social capital. Curves are theoretical and based on past research conducted in different species that are cited in the main text. They represent the global trajectory of the dimensions over the lifetime of an individual. Health is a state of physical, mental and social well-being that depends on internal (senescence) and external (pathogens, pollutants, etc.) factors. Individuals die when health level reaches zero (dashed black line). Biological age is a sum of intrinsic proxies and predicts health and survival prospects. These schematic representations also raise questions pertaining to the limits of social capital influence (both positive and negative) on longevity and health (❶ and ❹), or indeed on the programming of physiological and social processes in early life that may counteract ageing even if social capital evaporates over age (❷, dashed orange and green lines representing how biological age and health would change without these programming effects). Finally, Figure 3 also highlights the reversible interaction with senescence (❸).

Concluding remarks

The three points we developed indicate that working with social capital and markers of senescence along life will prove to be more powerful than standing with chronological age. Making these comparisons in animals is of paramount importance as animal studies allow (i) to reduce the number of confounding factors by controlling experimental conditions; (ii) to carry out studies over several generations in a relatively short timeframe, and study evolution through genetic and epigenetic effects; and (iii) to conduct invasive and integrative experimental studies going from the cell to the group level, which is impossible in humans. Experimental designs or observations of wild individuals throughout their lifespan and across several generations will help to better understand the long-term consequences of social capital. This is mainly possible through longitudinal studies (Clutton-Brock, Sheldon 2010) or multigenerational laboratory studies with a controlled environment and small changes in the study design (i.e., systematic heterogenization of study samples as group size, group composition, number of helpers) (Voelkl *et al.* 2018, 2020).

Taken together, currently available data suggest that focusing on social capital and markers of senescence throughout lifespan may explain individual health and fitness better than chronological age. The observation that mean lifespan is greater in eusocial than non-eusocial species leads us to question the co-evolution of sociality with senescence (Lucas, Keller 2020). Social capital adjustment further suggests that the basic assumptions that environmentally driven mortality shapes the selection of senescence may be more complex than we initially thought. Although mean lifespan is influenced by a large number of factors, the respective contribution of social capital versus other biological, ecological and environmental factors in the regulation of senescence and longevity remains an open question. Time is finite for most living animals, but social capital appears to be a promising tool to make senescence an adjustable parameter and to slow down the rate of ageing (Colchero *et al.* 2021).

Glossary

- **Ageing**: the only consensual definition is that it is a heterogeneous process of becoming older.
- **Biological age**: individual age as determined through different biological markers that change over time, but not necessarily related to chronological age. Biological age is composed of different stages (e.g., ontogeny, reproductive life, and senescence, including post-reproductive life). Contrary to chronological age, biological age considers the individual in relation to its date of death, while chronological age considers it in relation to its date of birth.
- **Cooperative breeding**: social system characterised by alloparental care: offspring receives care not only from their parents, but also from additional group members, often called helpers.
- **Chronological age** (or age): the age of an individual as measured from birth to a given date referring to time, usually based on the Gregorian calendar.
- **Eusociality**: highest level of sociality defined by cooperative brood care, overlapping generations, and division of labour into reproductive and non-reproductive groups.
- **Evolutionary theories of ageing**: proposals to explain the persistence of the deleterious process of ageing over several generations, despite the action of natural selection.
- **Fitness**: defined here as the individual's ability to transmit its genes directly (with offspring) or indirectly (by helping relatives, i.e., **inclusive fitness**) to future generations.
- **Health**: state of complete physical and mental independence in activities of daily living (Rattan 2013). Being healthy, in practical terms, means having adequate physical and mental independence in activities of daily living. The three main characteristics of the dynamic equilibrium between the occurrence of damage and the processes of maintenance and repair are damage control, stress response and constant remodelling and adaptation. These elements can be studied at different levels of the organism, as described in Box 1.
- **Healthy ageing**: process of maintaining functionality of a living system as age advances.
- **Longevity**: mean lifetime duration for a species.
- **Ontogeny**: development of an organism from fertilisation to the adult stage (reproductive stage).

- **Senescence**: progressive decline of biological functions, eventually leading to death. In evolutionary terms, senescence can be defined as the decrease in the age-specific contribution to fitness over lifetime.

- **Social capital:** resources embedded in a social structure which are accessed and/or mobilised in purposive action. The resources of an individual vary during its life, meaning that social capital fluctuates with age. In some studies, the number of partners or the connections an individual has within its network (Brent *et al.* 2011) are a proxy to measure social capital. Differences in social capital implies that group members have differentiated and contrasting relationships with each other (Moscovice *et al.* 2020), as observed in cooperative breeding or eusocial species. This means that it is difficult to seek to identify social capital components in communal breeding or gregarious species with few differentiated relationships (Moscovice *et al.* 2020). However, in these cases it would be possible to start with the use of simpler indices like group size or kinship size as social capital proxies.

- **Social resources:** Social resources are defined as any concrete or symbolic item that can be used as an object of exchange among people. Foa and Foa classified social resources into six categories for humans: love/affection, status, information, services, goods, and money (Foa, Foa 1980). Money can be replaced by access to food in non-human animals.

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Conflict of interest disclosure

The authors declare that they have no financial conflict of interest with the content of this article. CS is one of the PCI Network Sci recommenders.

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