

# 1 **Social capital: an independent dimension of healthy ageing**

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

## 23 **Keywords**

24 Social capital; ageing; senescence; health; trade-offs; evolution

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## 26 **The key role of social relationships in ageing**

27 Humans are a social species. Any lack of social contact affects both the mental and physical health of  
28 individuals [1,2]. Poor social interactions are even known to be a risk factor for all-cause mortality<sup>1,3,4</sup>.  
29 Although numerous studies report associations between social interactions and **health** outcomes (see  
30 Glossary for definition of health), the underlying mechanisms are largely unknown. The number of  
31 animal studies on the physiological (e.g. stress) or ecological (e.g. food access) determinants of ageing  
32 has risen sharply over the past ten years<sup>3,5</sup>. They suggest that complex and intertwined behavioural,  
33 psychological and biological pathways are likely involved (Box 1)<sup>1,6</sup>. However, these animal studies  
34 gave contrasted results according to species traits (e.g. group size)<sup>5</sup> or individual traits (e.g. social  
35 status)<sup>3</sup>. A large part of the ageing variations at both inter- and intra-specific levels is therefore still  
36 unexplained.

37 Resilience to stress and body energy homeostasis is affected by **social resources** (i.e. the knowledge,  
38 services, social support or cooperation<sup>7-11</sup>) an individual has access to or has used<sup>12</sup>, which is called  
39 **social capital**. Individual social capital is a widely used concept in human **healthy ageing** literature, and  
40 recent research on non-human animals seems to show that social capital represents a key set of  
41 components (see Box 2 and Table S1) in adjusting **senescence** and influencing **fitness**. Based on the  
42 fact that **social capital** varies with individual age and social group characteristics, we propose that it is  
43 the main factor that mediates the associations between sociality and healthy ageing. In this

44 perspective, we propose that the mechanisms linking social capital to healthy ageing can be better  
45 understood by adopting a comparative approach within individuals and between humans and animals,  
46 thus providing greater insight into the observed variation in senescence rates and facilitating the  
47 identification of anti-ageing interventions.

#### 48 **Social capital changes with chronological age**

49 The social capital of an individual varies according to its life stage (i.e., early, reproductive or post-  
50 reproductive life)<sup>13</sup>. In humans, non-human mammals and other species with long-lasting mother-  
51 offspring bonds, infants focus on a small number of strong relationships with their mother and with  
52 individuals who share common traits (e.g. gender, kin). As adolescents, the individuals then expand  
53 the quantity and diversity of their social relationships, and become more selective upon reaching  
54 adulthood<sup>14</sup> in order to adjust social capital in favour of resource acquisition (Figure 1).

55 Macaques (*Macaca sp.*<sup>8,15</sup>), chimpanzees (*Pan troglodytes*<sup>16</sup>) and elephants (*Loxodonta africana*<sup>17</sup>)  
56 show comparable patterns of social changes with chronological age, even if they generally display  
57 higher interspecific than intraspecific longevity variation. In chimpanzees, ageing males display more  
58 mutual, positive and selective relationships than younger counterparts<sup>16,18</sup>. Some authors proposed  
59 that the maintenance of social relationships with elders may improve their health status and longevity.  
60 Almeiling et al.<sup>15</sup> reported that old Barbary macaques (*Macaca sylvanus*) appear to remain valuable  
61 alliances for young macaques, who continue grooming them to obtain social resources. These alliances  
62 result in a richer social capital with fewer injuries and better transmission of knowledge, all of which  
63 give access to resources for animals of all ages<sup>15,17</sup>. In mammal societies and many native human  
64 societies such as the Māori<sup>19</sup>, knowledge is a key resource provided by older group members. The  
65 fitness of both older and younger members increases because of the expertise and leadership of the  
66 elders<sup>6,17,20</sup>. Social capital also varies in **eusocial** insects. Throughout ontogenesis, worker ants or bees  
67 change from one caste to another<sup>21</sup>. This is associated with age-related cognitive decline<sup>22</sup> and  
68 changes in their social capital; they no longer interact with the same individuals<sup>23–25</sup>.

69 Different theories offer contrasting arguments to explain this change in social capital throughout life,  
70 based on ultimate (e.g. reproduction-life trade-off<sup>26,27</sup> and kin selection<sup>28</sup>) or proximate (e.g. cognitive  
71<sup>29,30</sup> or cellular processes<sup>31</sup>) approaches. Thus, comparing the age-specific changes in social capital  
72 between different animal species may help to identify the associations between the timing of these  
73 changes and the individual physiological markers of ageing.

#### 74 **Biological age changes with social capital**

75 Social capital fluctuates according to the different stages of life (early-life, reproductive life, post-  
76 reproductive life) and may therefore influence individual health and biological age through stress and  
77 body energy homeostasis (Figure 2). Social isolation causes death in carpenter ants (*Camponotus fellah*  
78<sup>32</sup>) by disrupting energy homeostasis. In reproductive fruit flies (*Drosophila melanogaster*), social  
79 isolation induces stress, significantly accelerates the progression of tumour growth and triggers rapid  
80 death<sup>33</sup>. Conversely, helping (early-life stage in **cooperative breeders**) and being helped by others  
81 (reproductive stage) increases social capital and positively influences individual health, and ultimately  
82 fitness, in all age categories<sup>34–36</sup>. In a nutshell, social capital, as early as infancy, could be one of the  
83 main determinants of individual long-term fitness prospects.

84 In old macaques, maintaining an active social life has been suggested to stimulate and maintain brain  
85 activity through a good quality of life at both mental and physical levels<sup>15</sup>. Cognitive decline is observed  
86 in many non-human primate species<sup>37,38</sup>, but the interplay with the components of social capital is  
87 underappreciated. For instance, young lab animals who grow up alone may have difficulties developing  
88 good relationships when they become adults, which in turn may trigger faster senescence.  
89 Remarkably, the longevity of eusocial insect workers ranges from a few weeks to more than two years.  
90 This plasticity is largely controlled by social factors<sup>5</sup>. Although these individuals are closely related

91 genetically, distinct life trajectories can thus emerge as a result of variations in their social capital.  
92 Recent studies conducted in honeybees (*Apis mellifera*<sup>25</sup>) and carpenter ants<sup>24</sup> confirm that social  
93 capital predicts survival better than chronological age. A high social demand exposes workers to an  
94 overload of social stimulations, speeding up senescence and decreasing longevity. Richardson et al.<sup>24</sup>  
95 went further and concluded that the transition between castes is not hard wired or age dependent,  
96 but rather stochastic and dependent on changes in social capital. Bees and ants are also able to return  
97 to their previous caste and modify their interactions if a new demand appears in the colony (e.g.  
98 following a nest predation event). This sole change in social capital results in molecular<sup>39</sup> and neuronal  
99 modifications<sup>21</sup> associated with reversible age-related phenotypes<sup>22</sup> (Box 1) and improved health,  
100 cognitive abilities and longevity (Figure 1c). To sum up, a high social capital can reverse biological age.

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

103 Organic (e.g. food) and inorganic (e.g. social) resources influence survival, growth and reproduction.  
104 Social resources alone define social capital. Individuals can act on social interactions or social activities  
105 to modify social capital and thus decrease stress, balance homeostasis and ultimately improve health.  
106 Because social capital can reverse biological age (at least, in insects) and seems to be partly  
107 independent of chronological age, we suggest that social capital should be considered as a modifiable  
108 dimension (as defined in mathematics, Figure 2) within the health space<sup>40</sup>, with its own regulatory  
109 processes and bidirectional effects on individual senescence. As proposed by Richardson et al.<sup>24</sup>, social  
110 capital is not directly linked to chronological age but can change with age. This modifiable characteristic  
111 involves large intra- and inter-specific variations in social capital, which in turn influence individual  
112 ageing rate and fitness. These statements (i.e., the presence of variations in social capital leading to  
113 variations in ageing rate and fitness) give rise to future research directions that can be addressed in  
114 the three following questions:

115 1) How can we explain individual and species variations in health and longevity? Among species,  
116 environmental factors have shaped age-specific trade-offs between growth, reproduction and survival  
117 differently. Some components of the social capital can be influenced by environmental factors but can  
118 also attenuate the impact of the latter: future studies should therefore address the co-evolution of  
119 inter-specific variances in social capital and senescence rate. Animal species characterised by particular  
120 age-specific social capital can emerge as novel behavioural models to address questions in current  
121 human ageing research<sup>5,35,37</sup>. For instance, such studies may delineate how social capital modulates  
122 life period trade-offs (i.e. early-life growth and subsequent young and adult survival, reproductive  
123 success) and how adult social capital may have co-evolved with post-reproductive lifespan<sup>41</sup>. For  
124 example, female killer whales (*Orcinus orca*) live twice as long as males, and post-reproductive females  
125 have greater knowledge and lead the group, thus enhancing the survival of their grand-offspring<sup>6</sup>.  
126 These old females, like elephant matriarchs<sup>17</sup>, have a rich social capital, live longer and also provide  
127 their offspring with a huge social capital. This grandmother hypothesis was primarily proposed in  
128 humans<sup>27</sup>. In line with these observations, one can hypothesise that variations in social capital in  
129 different life stages influence variability in post-reproductive longevity (Figure 1b) and indirectly  
130 modulate sex-differences in senescence<sup>26</sup>. To understand the mechanistic underpinnings, the  
131 biological mechanisms of ageing such as telomere rate of loss<sup>42</sup>, oxidative stress or mitochondrial  
132 dysfunction<sup>43</sup> (Box 1) that are already suspected to be of particular importance would have to be  
133 tested in the light of the social capital context. The subject of age-related cognitive processes requires  
134 longitudinal neurobiological studies focusing on the ageing brain within the context of social capital<sup>37</sup>.  
135 Finally, the interaction between social capital and life history traits has certainly been constrained by  
136 environmental factors such as predation risks, parasite prevalence or local population density. It is also  
137 important to note that non-social species like ctenophores or cnidarians have almost reached  
138 immortality<sup>44</sup>, or may live for centuries like the Galapagos turtle or the Greenland shark. This casts  
139 doubt on the incompressible limits of social benefits for longevity (Figure 1a and d). Multi-specific and

140 multigenerational studies will help to discovering the nature of the molecular mechanisms that  
141 underlie the relationship of social capital with species life-history and ecology.

142 2) How is social capital encoded to enhance fitness? Although we know that social capital is related to  
143 individual fitness, little is known about how far this relationship depends on species ecology and  
144 gender, or whether it is restricted to certain life-history traits. The role of social capital in variations of  
145 senescence onset or in senescence rate can be assessed in the context of **evolutionary theories of**  
146 **ageing**<sup>45</sup>, for instance by determining how social capital modulates the energy trade-offs that can  
147 occur during the life trajectory of individuals (e.g. growth/reproduction and ageing trade-offs<sup>35,46,47</sup>).  
148 Specific life periods during which selection does not affect senescence (e.g. after adult reproduction)  
149 may be of particular interest because they may provide information about co-evolution of sociality and  
150 prolonged lifespan. For example, extended sex-specific post-reproductive life in killer whales may have  
151 been co-selected with specific social traits and anti-ageing mechanisms that have positive effects on  
152 female fitness and their offspring<sup>27,48</sup>. Age-related variations in social capital in cooperative breeders  
153 have already been linked with the fitness traits of individuals (see<sup>34,36</sup>). However, we have yet to  
154 elucidate the question of how eusocial reproducers have acquired a specific social capital that probably  
155 enables them to successfully face higher reproduction rates and attain a longer lifespan than non-  
156 reproducers. How is the impact of social capital on senescence genetically or epigenetically encoded?  
157 Understanding the genetics and epigenetics of sociality would be of help in unraveling mechanisms  
158 that link sociality to ageing outcomes. In this respect, we propose that the recent development of  
159 genomics and proteomics to study ageing<sup>21,39</sup>) should be extended to include the study of social  
160 capital. Exploring these mechanistic social and ageing interactions may also help us to gain a better  
161 understanding of why senescence has different effects on life-history traits, actuarial (i.e. mortality)  
162 and reproductive senescence, as shown by the huge variations we observed between individuals<sup>49</sup>.  
163 These investigations will likely extend our knowledge of how evolution has co-selected sociality and  
164 longevity<sup>5,41</sup>. Furthermore, these new findings could subsequently be leveraged to promote healthy  
165 ageing.

166 3) What is the extent of our knowledge on social capital? Social capital is most certainly a complex  
167 concept. This is illustrated by the large number of existing definitions in human sciences<sup>2,12,50</sup> but also  
168 by the diversity of its potential components. Portes<sup>51</sup> noted that " the point is approaching at which  
169 social capital comes to be applied to so many events and in so many different contexts as to lose any  
170 distinct meaning." Because social capital seems to be important for individual fitness and the evolution  
171 of sociality, it is crucial to acknowledge and apprehend the complexity of social capital. First, although  
172 most of the attention has been focused on the health benefits of social capital so far, the possible  
173 health risks associated with social capital also need to be considered, especially in terms of social  
174 overloading<sup>24,25</sup> or of exposure to pathogens<sup>52</sup>. Page and collaborators<sup>53</sup>, for example, observed that  
175 mothers with higher betweenness and closeness centrality show more frequent instances of sickness,  
176 which somewhat counteracts other positive fitness effects. Other researchers have begun to  
177 acknowledge that social capital ranges across a large spectrum spanning from positive to negative  
178 social capital<sup>54,55</sup>, the latter being associated with adverse health outcome. We also need to consider  
179 other positive resources that can be considered as components of social capital. For example, it has  
180 been shown that in addition to providing food<sup>56</sup>, trophallaxes convey compounds that are essential to  
181 individual health and growth in a conserved way across several taxa<sup>57</sup>, which seems to indicate a  
182 selection. Like eusocial insects, mammals share organic compounds through the social transmission of  
183 gut microbiome, which is known to influence health outcomes<sup>58</sup>. This field of study extends to birds,  
184 in which the feeding of chicks may allow intergenerational transmission of such compounds<sup>59</sup>, and  
185 thus ensure rapid adaptations to environmental changes<sup>60</sup>. Whether or not a richer social capital can  
186 improve adaptation in social species remains to be evaluated. Finding new components of social capital  
187 is a research horizon that needs to be explored. Box 2 shows that social capital may simply be directly  
188 related to the number of relationships or could be evaluated in a complex way with the inclusion of  
189 social activities and the locations in which these social activities are performed. How social capital

190 should be operationalised also depends on the studied species, the conditions and the scales of the  
191 study (temporal scale and subject/social organisation scale, i.e., make interspecific comparisons of  
192 individuals that are studied throughout their lifetime). Future research should further explore the  
193 potential components of social capital and their independent or additive/synergistic effects on ageing  
194 outcomes.

### 195 **Concluding remarks**

196 Taken together, currently available data suggest that focusing on social capital and markers of  
197 senescence throughout life may explain individual health and fitness better than chronological age.  
198 The observation that mean lifespan is greater in eusocial than non-eusocial species leads us to question  
199 the co-evolution of sociality with senescence<sup>5</sup>. Social capital adjustment further suggests that the basic  
200 assumptions that environmentally driven mortality shapes the selection of senescence may be more  
201 complex than we initially thought. Although mean lifespan is influenced by a large number of factors,  
202 the respective contribution of social capital versus other biological, ecological and environmental  
203 factors in the regulation of senescence and longevity remains an open question. Time is finite for most  
204 living animals, but social capital appears to be a promising tool to make senescence an adjustable  
205 parameter.

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

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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. 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<sup>47</sup>. 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<sup>61</sup>. 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 **①**. 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) **②**. However, variation in social capital may act indirectly through cellular and physiological changes that strengthen resilience to stress **③** or body energy homeostasis **④**. These effects are currently inferred from previous observations. Social isolation and interactions have been described as having opposite effects on stress hormones<sup>10</sup>, with potentially negative consequences but also adaptive responses observed at the physiological and cellular level (e.g. oxidative stress)<sup>62</sup>. Another study suggests that social isolation has pervasive effects on stress and energy balance<sup>32</sup>. Inflammation is also an important biological mechanism that links social capital to unhealthy states<sup>63</sup>. 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)<sup>64</sup> and disrupts energy homeostasis. Increased telomerase activity in socially stressed individuals has also been described in the literature<sup>65</sup>. This suggests that social variables do indeed impact cell-ageing proxies, as previously suggested for social rank and telomere length<sup>31,42</sup>. However, as social capital likely varies over time and depends on individual physiological status, a retroaction of physiology is expected on sociality (**⑤**, **⑥**). For instance, some authors suggest possible causal effects of short telomeres on unhealthy behaviours as smoking in humans<sup>31</sup>. Another example cited is the accelerated death of ill flies (*Drosophila melanogaster*) when isolated from conspecifics<sup>33</sup>. 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.

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### **Box 2: What are the components of social capital?**

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Although work on social capital abounds across disciplines, there is no consensus on its conceptualization and operationalization<sup>4,50,66,67</sup>. Social capital can first be studied in terms of resources or services that are embedded in spatial associations (e.g. proximities, as 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<sup>37</sup>. Food is primarily an ecological resource, but access to it depends on the social capital of the individual (social support, cooperation, alliances, tolerance).

As social relationships are the basis on which social capital is managed, the notion of social capital is often simplified as 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) 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, yet indirect relationships (e.g. friend of our friend) also influence social capital<sup>8,56</sup>. These indirect

254 connections affecting information transmission networks may strengthen the cognition and longevity  
255 of species, in which cultural behaviour is important <sup>52</sup>. Furthermore, cultural differences influence  
256 social capital in humans <sup>68</sup>; few studies have been conducted to date on this topic in non-human  
257 animals, and further studies should be carried out.

258 Lastly, social activities and geospatial locations can be studied in relation with social capital, but can  
259 also be integrated as components of the latter. Indeed, human social activities are linked to specific  
260 locations and both elements can be combined to better understand covariation between social capital  
261 and health <sup>69</sup>. This covariation between social capital, location and task is obvious in eusocial insects  
262 <sup>24,25</sup>, but evidence is lacking in other species. Both Wild et al. <sup>25</sup> and Richardson et al. <sup>24</sup> used information  
263 about social interactions, proximities, social activities and location to calculate a social capital index.

264 To summarise, the social capital components we need to identify are: resources embedded in social  
265 relationships <sup>12</sup> such as information and services <sup>7</sup>, the composition and structure of social networks,  
266 cultural differences, social activities and geospatial locations. Table S1 summarises the currently  
267 considered components of social capital according to the studied species and the level of studies.

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## 269 **Glossary:**

270 - **Ageing:** the only consensual definition is that it is a heterogeneous process of becoming older.

271 - **Biological age:** individual age as determined through different biological markers that change over  
272 time, but not necessarily related to chronological age. Biological age is composed of different stages  
273 (e.g., ontogeny, reproductive life, and senescence, including post-reproductive life). Contrary to  
274 chronological age, biological age considers the individual in relation to its date of death, while  
275 chronological age considers it in relation to its date of birth.

276 - **Cooperative breeding:** social system characterized by alloparental care: offspring receives care not  
277 only from their parents, but also from additional group members, often called helpers.

278 - **Chronological age (or age):** the age of an individual as measured from birth to a given date referring  
279 to time, usually based on the Gregorian calendar.

280 - **Eusociality:** highest level of sociality defined by cooperative brood care, overlapping generations,  
281 and division of labour into reproductive and non-reproductive groups.

282 - **Evolutionary theories of ageing:** proposals to explain the persistence of the deleterious process of  
283 ageing over several generations, despite the action of natural selection.

284 - **Fitness:** defined here as the individual's ability to transmit its genes directly (with offspring) or  
285 indirectly (by helping relatives, i.e. **inclusive fitness**) to future generations.

286 - **Health:** state of complete physical and mental independence in activities of daily living <sup>2</sup>. Being  
287 healthy, in practical terms, means having adequate physical and mental independence in activities of  
288 daily living. The main three characteristics of the dynamic equilibrium between the occurrence of  
289 damage and the processes of maintenance and repair are damage control, stress response and  
290 constant remodeling and adaptation. These elements can be studied at different levels of the  
291 organism, as described in Box 1.

292 - **Healthy ageing:** process of maintaining functionality of a living system as age advances.

293 - **Longevity:** mean lifetime duration for a species.

294 - **Ontogeny:** development of an organism from fertilization to the adult stage (reproductive stage).

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

298 - **Social capital:** resources embedded in a social structure which are accessed and / or mobilized in  
299 purposive action. The resources of an individual vary during its life, meaning that social capital  
300 fluctuates with age. In some studies, the number of partners or the connections an individual has  
301 within its network <sup>8</sup> are a proxy to measure social capital. Differences in social capital implies that  
302 group members have differentiated and contrasting relationships with each other <sup>7</sup>, as observed in  
303 cooperative breeding or eusocial species. This means that it is difficult to seek to identify social capital  
304 components in communal breeding or gregarious species with few differentiated relationships <sup>7</sup>.  
305 However, in these cases it would be possible to start with the use of simpler indices like group size or  
306 kinship size as social capital proxies.

307 - **Social resources:** Social resources are defined as any concrete or symbolic item that can be used as  
308 an object of exchange among people. Foa and Foa classified social resources into six categories for  
309 humans: love/affection, status, information, services, goods, and money <sup>70</sup>. Money can be replaced by  
310 access to food in non-human animals.

311

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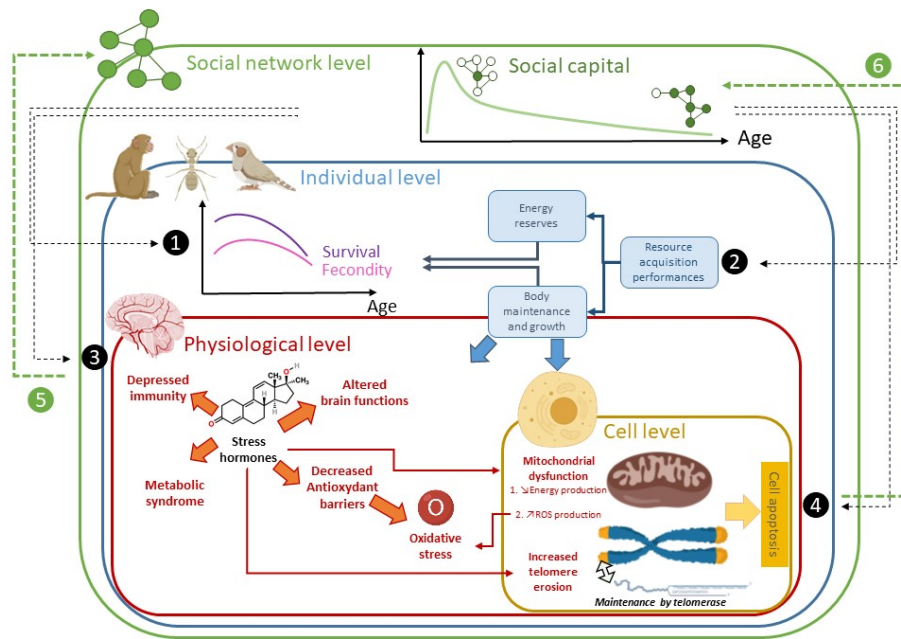
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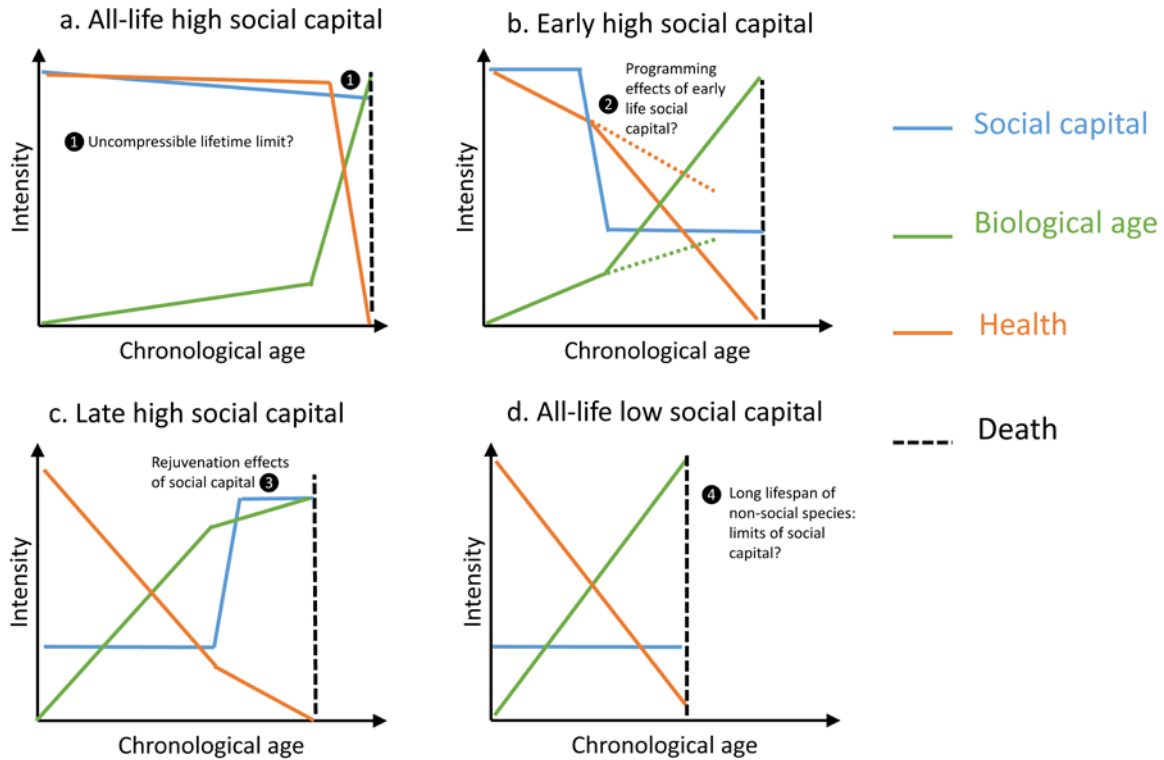
444 **Figure legends**



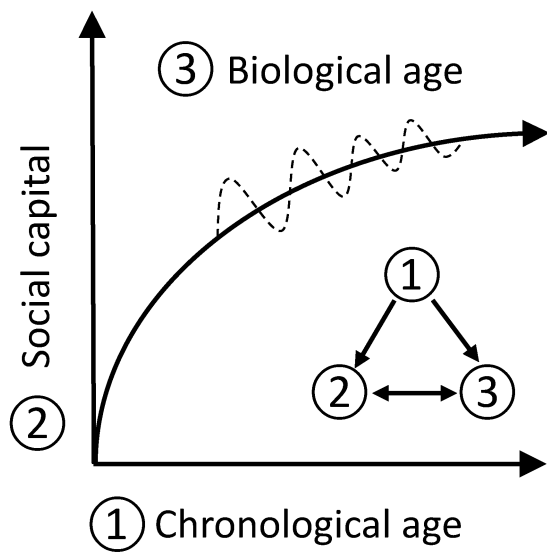
445

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

448



451 Figure 1: Variation (y-axis) of social capital (blue), biological age (green) and health (orange) over  
 452 chronological age (x-axis) for an individual having access to (a.) life-long high social capital, (b.) only  
 453 early-life high social capital, (c.) late-life high social capital, and (d.) life-long low social capital. Curves  
 454 are theoretical and based on past research conducted in different species that are cited in the main  
 455 text. They represent the global trajectory of the dimensions over the lifetime of an individual. Health  
 456 is a state of physical, mental and social well-being that depends on internal (senescence) and  
 457 external (pathogens, pollutants, etc.) factors. Individuals die when health level reaches zero (dashed  
 458 black line). Biological age is a sum of intrinsic proxies and predicts health and survival prospects.  
 459 These schematic representations also raise questions pertaining to the limits of social capital  
 460 influence (both positive and negative) on longevity and health (1 and 4), or indeed on the  
 461 programming of physiological and social processes in early life that may counteract ageing even if  
 462 social capital evaporates over age (2, dashed orange and green lines representing how biological  
 463 age and health would change without these programming effects). Finally, Figure 1 also highlights  
 464 the reversible interaction with senescence (3).



466

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

474

	Variations inside a same group/colony	Variations between groups/colonies	Interspecific variations
<b>Eusocial species (e.g. ants, bees)</b>	<p><b>Properties of social interactions</b> including number and duration of interactions, type of interactions (e.g., trophallaxes, antenna-to-antenna, grooming), intra-caste or inter-caste interactions.</p> <p><b>Spatial distribution</b> of social interactions according to individual mobility patterns</p> <p><b>Individual positions within the social system</b> including, not exclusively, individual caste (e.g., male, queen, nest worker) or centrality index</p>	<p><b>Properties of the colony</b> including, not exclusively, its size, the population distribution by caste (e.g., mono/polygyny, the ratio of individual between caste), and the colony age.</p> <p><b>Properties of the whole system of social interactions</b> using network indicators such as community separation and its resilience.</p>	<p><b>Properties of the colony</b>, including , among others, its size, the caste system specific characteristc (e.g., number of reproductive individuals, marked division of labour, short or long-lived males, worker dimorphism)</p> <p><b>Relation with other colonies</b> including the tolerance level and belonging to supercolony.</p>
<b>Cooperative breeding species</b>	<p><b>Properties of social interactions</b> including number and duration of interactions, type of interactions (e.g., grooming, agression, reproductive behavior)</p> <p><b>Properties of social relationship</b> which may include kinship, sex, reproductive status and dominance hierarchy</p> <p><b>Individual positions within the social system</b> including, not exclusively, individual status (e.g., reproductive or helpers) and its position between reproductive sub-groups</p>	<p><b>Properties of the colony</b>, may include its size, the number of helpers and offsprings and the system of interactions between reproductive sub-groups</p>	<p><b>Properties of cooperative breedings</b>, including if its facultative or systematic and the level of competition for reproduction between helpers and male breeder.</p> <p><b>Properties of the social interaction system</b>, including, the distribution of interaction within and between reproductive sub-groups.</p>

<p><b>Primate societies and similar mammal societies</b></p>	<p><b>Properties of social interactions</b> including number and duration of interactions, type of interactions (e.g., grooming, aggression, reproductive behavior, exchange of resources) and their spatial distribution</p>	<p><b>Properties of the group</b>, including their size, and their age/sex distribution</p>	<p><b>Properties of the group</b>, including, their size, the mating system, the hierarchical structures, and affiliation between non-kin.</p>
	<p><b>Properties of social relationships</b>, including, not exclusively, kinship, dominance, direction and reciprocity in conflicts and resources exchange.</p>	<p><b>Cultural variation</b> including, among others, tolerance in aggression and exchange with non-kin, tool use</p>	<p><b>Structure of the interaction networks</b> including their size, community structure and efficacy in exchange of information and resources</p>
	<p><b>Individual position within the social structure</b>, including, among others, centrality, belonging to certain subgroups and dominance relative to the whole hierarchy</p>	<p><b>Properties of the interaction network</b>, including, among other, the level of community division resulting from non-kin interactions.</p>	
		<p><b>Exchange with and tolerance of other groups</b> (between-group competition)</p>	
<p><b>Humans</b></p>	<p><b>Quantity and quality of social relationships, qualities can include</b>, but not exclusively, relation type (e.g., relatives, colleagues, friends), emotional closeness, relation satisfaction, trust, reciprocity or length of relationship.</p>	<p><b>Sociodemographic properties</b>, which can include, not exclusively, the distributions of age, gender, ethnicity, education and employment.</p>	<p>NA</p>
	<p><b>Frequency and quality of social interactions, qualities can include</b>, but not exclusively, what is exchanged (e.g., affection, information, money), its valence (i.e., pleasant or unpleasant), the geospatial locations and the more complex activities in which interactions take place (e.g., weekly meeting at work).</p>	<p><b>Properties of the whole system of social interactions</b> using network indicators such as community division and assortative mixing.</p>	
		<p><b>Cultural aspects</b> in terms, among others, of shared values and norms.</p>	
		<p><b>Organizational structure</b>, from political, institutional to smaller collective and associative organization.</p>	
	<p><b>Individual positions within the social structure which can include</b>, not exclusively, centrality index, belonging</p>	<p><b>Relations and exchange</b> in-between populations.</p>	

to certain subgroup, or  
social status (e.g.,  
employment, ethnicity,  
gender, age).

477