



HAL
open science

Social capital: an independent dimension of healthy ageing

Cédric Sueur, Martin Quque, Alexandre Naud, Audrey Bergouignan, François Criscuolo

► **To cite this version:**

Cédric Sueur, Martin Quque, Alexandre Naud, Audrey Bergouignan, François Criscuolo. Social capital: an independent dimension of healthy ageing. 2021. hal-03831440v1

HAL Id: hal-03831440

<https://hal.science/hal-03831440v1>

Preprint submitted on 26 Jul 2021 (v1), last revised 26 Oct 2022 (v4)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

2 Cédric Sueur^{1,2}, Martin Quque^{1,3}, Alexandre Naud^{1,4}, Audrey Bergouignan^{1,5}, François Criscuolo¹

3 ¹ Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

4 ² Institut Universitaire de France, Saint-Michel 103, 75005 Paris, France

5 ³ Center for Nonlinear Phenomena and Complex Systems (Cenoli) - CP 231, Université Libre de
6 Bruxelles (ULB), Campus Plaine, Boulevard du Triomphe, Building NO - level 5, B-1050, Bruxelles,
7 Belgium.

8 ⁴ Ecole de Sante Publique, Centre de Recherche du Centre Hospitalier, Université de Montréal,
9 Canada

10 ⁵ Division of Endocrinology, Metabolism, and Diabetes and Anschutz Health and Wellness Center,
11 University of Colorado, School of Medicine, Aurora, CO 80045, USA

12

13

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

25

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^{1,3,4}.
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^{3,5}. They suggest that complex and intertwined behavioural,
33 psychological and biological pathways are likely involved (Box 1)^{1,6}. However, these animal studies
34 gave contrasted results according to species traits (e.g. group size)⁵ or individual traits (e.g. social
35 status)³. 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 cooperation⁷⁻¹¹) an individual has access to or has used¹², 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)¹³. 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 adulthood¹⁴ in order to adjust social capital in favour of resource acquisition (Figure 1).

55 Macaques (*Macaca sp.*^{8,15}), chimpanzees (*Pan troglodytes*¹⁶) and elephants (*Loxodonta africana*¹⁷)
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^{16,18}. Some authors proposed
59 that the maintenance of social relationships with elders may improve their health status and longevity.
60 Almeiling et al.¹⁵ 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^{15,17}. In mammal societies and many native human
64 societies such as the Māori¹⁹, 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^{6,17,20}. Social capital also varies in **eusocial** insects. Throughout ontogenesis, worker ants or bees
67 change from one caste to another²¹. This is associated with age-related cognitive decline²² and
68 changes in their social capital; they no longer interact with the same individuals^{23–25}.

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^{26,27} and kin selection²⁸) or proximate (e.g. cognitive
71^{29,30} or cellular processes³¹) 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*
78³²) 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 death³³. 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^{34–36}. 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 levels¹⁵. Cognitive decline is observed
86 in many non-human primate species^{37,38}, 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 factors⁵. 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*²⁵) and carpenter ants²⁴ 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.²⁴
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 molecular³⁹ and neuronal
99 modifications²¹ associated with reversible age-related phenotypes²² (Box 1) and improved health,
100 cognitive abilities and longevity (Figure 1c). To sum up, a high social capital can reverse biological age.

101

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 space⁴⁰, with its own regulatory
109 processes and bidirectional effects on individual senescence. As proposed by Richardson et al.²⁴, 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^{5,35,37}. 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 lifespan⁴¹. 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-offspring⁶.
126 These old females, like elephant matriarchs¹⁷, 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 humans²⁷. 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 senescence²⁶. To understand the mechanistic underpinnings, the
131 biological mechanisms of ageing such as telomere rate of loss⁴², oxidative stress or mitochondrial
132 dysfunction⁴³ (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 capital³⁷.
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 immortality⁴⁴, 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**⁴⁵, 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^{35,46,47}).
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^{27,48}. Age-related variations in social capital in cooperative breeders
153 have already been linked with the fitness traits of individuals (see^{34,36}). 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^{21,39}) 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 individuals⁴⁹.
163 These investigations will likely extend our knowledge of how evolution has co-selected sociality and
164 longevity^{5,41}. 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^{2,12,50} but also
168 by the diversity of its potential components. Portes⁵¹ 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^{24,25} or of exposure to pathogens⁵². Page and collaborators⁵³, 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^{54,55}, 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 food⁵⁶, trophallaxes convey compounds that are essential to
181 individual health and growth in a conserved way across several taxa⁵⁷, 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 outcomes⁵⁸. This field of study extends to birds,
184 in which the feeding of chicks may allow intergenerational transmission of such compounds⁵⁹, and
185 thus ensure rapid adaptations to environmental changes⁶⁰. 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 senescence⁵. 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.

206
207
208
209
210
211
212
213
214
215
216
217
218
219
220
221
222
223
224
225
226
227
228
229
230
231
232
233
234
235
236

Box 1: Biology of ageing, senescence and longevity in social animals
Please insert Figure I Here

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 reproduction⁴⁷. 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 decade⁶¹. 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 hormones¹⁰, with potentially negative consequences but also adaptive responses observed at the physiological and cellular level (e.g. oxidative stress)⁶². Another study suggests that social isolation has pervasive effects on stress and energy balance³². Inflammation is also an important biological mechanism that links social capital to unhealthy states⁶³. 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)⁶⁴ and disrupts energy homeostasis. Increased telomerase activity in socially stressed individuals has also been described in the literature⁶⁵. This suggests that social variables do indeed impact cell-ageing proxies, as previously suggested for social rank and telomere length^{31,42}. 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 humans³¹. Another example cited is the accelerated death of ill flies (*Drosophila melanogaster*) when isolated from conspecifics³³. 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.

237

238

Box 2: What are the components of social capital?

239
240
241
242
243
244
245
246
247
248
249
250
251
252
253

Although work on social capital abounds across disciplines, there is no consensus on its conceptualization and operationalization^{4,50,66,67}. 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^{3,7}. 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^{8,56}. These indirect

254 connections affecting information transmission networks may strengthen the cognition and longevity
255 of species, in which cultural behaviour is important ⁵². Furthermore, cultural differences influence
256 social capital in humans ⁶⁸; 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 ⁶⁹. This covariation between social capital, location and task is obvious in eusocial insects
262 ^{24,25}, but evidence is lacking in other species. Both Wild et al. ²⁵ and Richardson et al. ²⁴ 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 ¹² such as information and services ⁷, 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.

268

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 ². 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 ⁸ are a proxy to measure social capital. Differences in social capital implies that
302 group members have differentiated and contrasting relationships with each other ⁷, 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 ⁷.
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 ⁷⁰. Money can be replaced by
310 access to food in non-human animals.

311

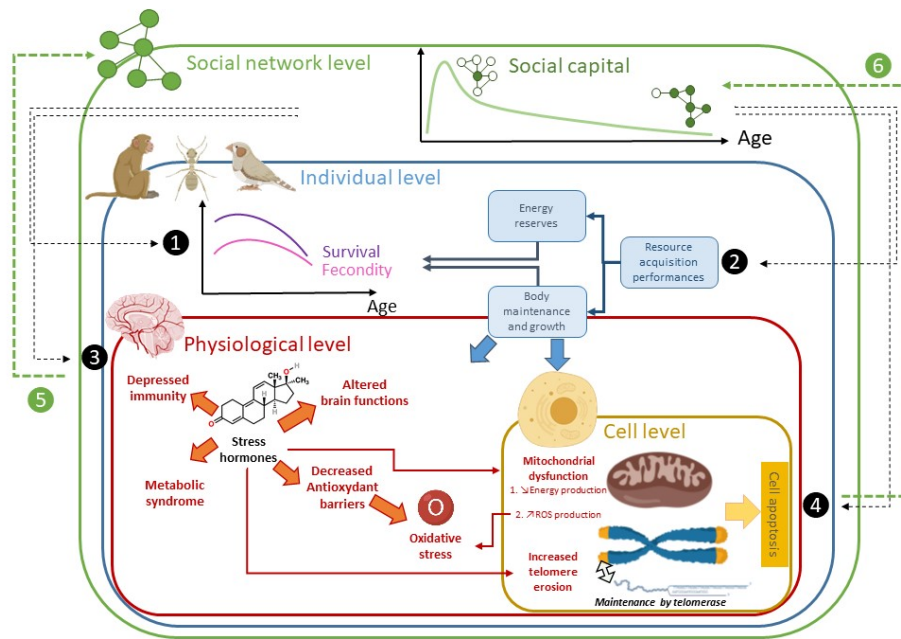
312 **References**

- 313 1. Rook, K. S. Social networks in later life: Weighing positive and negative effects on health and
314 well-being. *Curr. Dir. Psychol. Sci.* **24**, 45–51 (2015).
- 315 2. Rattan, S. I. Healthy ageing, but what is health? *Biogerontology* **14**, 673–677 (2013).
- 316 3. Snyder-Mackler, N. *et al.* Social determinants of health and survival in humans and other
317 animals. *Science* **368**, (2020).
- 318 4. Kawachi, I., Subramanian, S. V. & Kim, D. Social capital and health. in *Social capital and health* 1–
319 26 (Springer, 2008).
- 320 5. Lucas, E. R. & Keller, L. The co-evolution of longevity and social life. *Funct. Ecol.* **34**, 76–87 (2020).
- 321 6. Natrass, S. *et al.* Postreproductive killer whale grandmothers improve the survival of their
322 grandoffspring. *Proc. Natl. Acad. Sci.* **116**, 26669–26673 (2019).
- 323 7. Moscovice, L. R., Sueur, C. & Aureli, F. How socio-ecological factors influence the differentiation
324 of social relationships: an integrated conceptual framework. *Biol. Lett.* **16**, 20200384 (2020).
- 325 8. Brent, L., Semple, S., Dubuc, C., Heistermann, M. & MacLarnon, A. Social capital and physiological
326 stress levels in free-ranging adult female rhesus macaques. *Physiol. Behav.* **102**, 76–83 (2011).
- 327 9. Lakon, C. M., Godette, D. C. & Hipp, J. R. Network-based approaches for measuring social capital.
328 in *Social capital and health* 63–81 (Springer, 2008).
- 329 10. Wittig, R. M. *et al.* Social support reduces stress hormone levels in wild chimpanzees across
330 stressful events and everyday affiliations. *Nat. Commun.* **7**, (2016).
- 331 11. Thoits, P. A. Mechanisms Linking Social Ties and Support to Physical and Mental Health. *J. Health*
332 *Soc. Behav.* **52**, 145–161 (2011).
- 333 12. Lin, N., Fu, Y. & Hsung, R.-M. Measurement techniques for investigations of social capital. *Soc.*
334 *Cap. Theory Res.* 57–81 (2001).
- 335 13. McDonald, S. & Mair, C. A. Social Capital Across the Life Course: Age and Gendered Patterns of
336 Network Resources 1. in vol. 25 335–359 (Wiley Online Library, 2010).
- 337 14. Field, D. & Minkler, M. Continuity and Change in Social Support Between Young-old and Old-old
338 or Very-old Age. *J. Gerontol.* **43**, P100–P106 (1988).
- 339 15. Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A. M. & Fischer, J. Motivational
340 shifts in aging monkeys and the origins of social selectivity. *Curr. Biol.* **26**, 1744–1749 (2016).
- 341 16. Rosati, A. G. *et al.* Social selectivity in aging wild chimpanzees. *Science* **370**, 473–476 (2020).
- 342 17. McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. Matriarchs As Repositories of Social
343 Knowledge in African Elephants. *Science* **292**, 491–494 (2001).

- 344 18. Silk, J. The upside of aging. *Science* **370**, 403–404 (2020).
- 345 19. Durie, M. Kaumatautanga reciprocity: Maori elderly and whanau. *N. Z. J. Psychol.* **28**, 102 (1999).
- 346 20. Migliano, A. B. *et al.* Hunter-gatherer multilevel sociality accelerates cumulative cultural
347 evolution. *Sci. Adv.* **6**, eaax5913 (2020).
- 348 21. Münch, D., Amdam, G. V. & Wolschin, F. Ageing in a eusocial insect: molecular and physiological
349 characteristics of life span plasticity in the honey bee. *Funct. Ecol.* **22**, 407–421 (2008).
- 350 22. Baker, N., Wolschin, F. & Amdam, G. V. Age-related learning deficits can be reversible in
351 honeybees *Apis mellifera*. *Exp. Gerontol.* **47**, 764–772 (2012).
- 352 23. Mersch, D. P., Crespi, A. & Keller, L. Tracking individuals shows spatial fidelity is a key regulator of
353 ant social organization. *Science* **340**, 1090–1093 (2013).
- 354 24. Richardson, T. O. *et al.* Ant Behavioral Maturation Is Mediated by a Stochastic Transition
355 between Two Fundamental States. *Curr. Biol.* **30**, 1–8 (2020).
- 356 25. Wild, B. *et al.* Social networks predict the life and death of honey bees. *BioRxiv* (2020).
- 357 26. Lemaître, J.-F. *et al.* Sex differences in adult lifespan and aging rates of mortality across wild
358 mammals. *Proc. Natl. Acad. Sci.* **117**, 8546–8553 (2020).
- 359 27. Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. Fitness benefits of
360 prolonged post-reproductive lifespan in women. *Nature* **428**, 178–181 (2004).
- 361 28. Abbot, P. *et al.* Inclusive fitness theory and eusociality. *Nature* **471**, E1–E4 (2011).
- 362 29. Carstensen, L. L. The Influence of a Sense of Time on Human Development. *Science* **312**, 1913–
363 1915 (2006).
- 364 30. Aartsen, M. J., van Tilburg, T., Smits, C. H. M. & Knipscheer, K. C. P. M. A Longitudinal Study of
365 the Impact of Physical and Cognitive Decline on the Personal Network in Old Age. *J. Soc. Pers.*
366 *Relatsh.* **21**, 249–266 (2004).
- 367 31. Bateson, M. & Nettle, D. Why are there associations between telomere length and behaviour?
368 *Philos. Trans. R. Soc. B Biol. Sci.* **373**, 20160438 (2018).
- 369 32. Koto, A., Mersch, D., Hollis, B. & Keller, L. Social isolation causes mortality by disrupting energy
370 homeostasis in ants. *Behav. Ecol. Sociobiol.* **69**, 583–591 (2015).
- 371 33. Dawson, E. H. *et al.* Social environment mediates cancer progression in *Drosophila*. *Nat.*
372 *Commun.* **9**, (2018).
- 373 34. Berger, V., Lemaître, J.-F., Allainé, D., Gaillard, J.-M. & Cohas, A. Early and adult social
374 environments shape sex-specific actuarial senescence patterns in a cooperative breeder. *Am.*
375 *Nat.* **192**, 525–536 (2018).
- 376 35. Lemaître, J.-F. *et al.* Early-late life trade-offs and the evolution of ageing in the wild. *Proc. R. Soc.*
377 *B Biol. Sci.* **282**, 20150209 (2015).
- 378 36. Hammers, M. *et al.* Breeders that receive help age more slowly in a cooperatively breeding bird.
379 *Nat. Commun.* **10**, 1–10 (2019).
- 380 37. Lacreuse, A., Raz, N., Schmidtke, D., Hopkins, W. D. & Herndon, J. G. Age-related decline in
381 executive function as a hallmark of cognitive ageing in primates: an overview of cognitive and
382 neurobiological studies. *Philos. Trans. R. Soc. B* (2020) doi:10.1098/rstb.2019.0618.
- 383 38. Emery Thompson, M., Rosati, A. G. & Snyder-Mackler, N. Insights from evolutionarily relevant
384 models for human ageing. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190605 (2020).
- 385 39. Quque, M. *et al.* Division of labour in the black garden ant (*Lasius niger*) leads to three distinct
386 proteomes. *J. Insect Physiol.* 103907 (2019) doi:10.1016/j.jinsphys.2019.103907.
- 387 40. Sanromà, M. & Adserà, J. M. From electronic medical records to the personal health space: how
388 ICTs will transform healthcare in the next decade. in 473–482 (2010).
- 389 41. Vágási, C. I. *et al.* Is degree of sociality associated with reproductive senescence? A comparative
390 analysis across birds and mammals. *bioRxiv* 2020.10.29.360636 (2020)
391 doi:10.1101/2020.10.29.360636.
- 392 42. Lewin, N., Treidel, L. A., Holekamp, K. E., Place, N. J. & Hausmann, M. F. Socioecological
393 variables predict telomere length in wild spotted hyenas. *Biol. Lett.* **11**, 20140991 (2015).
- 394 43. Hood, W. R. *et al.* The mitochondrial contribution to animal performance, adaptation, and life-
395 history variation. *Integr. Comp. Biol.* **58**, 480–485 (2018).

- 396 44. Petralia, R. S., Mattson, M. P. & Yao, P. J. Aging and longevity in the simplest animals and the
397 quest for immortality. *Ageing Res. Rev.* **16**, 66–82 (2014).
- 398 45. Reznick, D., Bryant, M. & Holmes, D. The evolution of senescence and post-reproductive lifespan
399 in guppies (*Poecilia reticulata*). *PLoS Biol* **4**, e7 (2005).
- 400 46. Williams, G. C. Pleiotropy, Natural Selection, and the Evolution of Senescence. *Evolution* **11**, 398–
401 411 (1957).
- 402 47. Hamilton, W. D. The moulding of senescence by natural selection. *J. Theor. Biol.* **12**, 12–45
403 (1966).
- 404 48. Kirkwood, T. B. Evolution of ageing. *Nature* **270**, 301–304 (1977).
- 405 49. Gaillard, J. & Lemaître, J. The Williams’ legacy: A critical reappraisal of his nine predictions about
406 the evolution of senescence. *Evolution* **71**, 2768–2785 (2017).
- 407 50. Putnam, R. The prosperous community: Social capital and public life. *Am. Prospect* **13**, (1993).
- 408 51. Portes, A. The two meanings of social capital. in vol. 15 1–12 (Springer, 2000).
- 409 52. Romano, V., MacIntosh, A. J. J. & Sueur, C. Stemming the Flow: Information, Infection, and Social
410 Evolution. *Trends Ecol. Evol.* **35**, 849–853 (2020).
- 411 53. Page, A. E. *et al.* Hunter-Gatherer Social Networks and Reproductive Success. *Sci. Rep.* **7**, 1153
412 (2017).
- 413 54. Portes, A. & Landolt, P. The downside of social capital. (1996).
- 414 55. Wacquant, L. J. Negative social capital: State breakdown and social destitution in America’s
415 urban core. *Neth. J. Hous. Built Environ.* **13**, 25 (1998).
- 416 56. Quque, M. *et al.* Hierarchical networks of food exchange in the black garden ant *Lasius niger*.
417 *Insect Sci.* (2020).
- 418 57. LeBoeuf, A. C. *et al.* Oral transfer of chemical cues, growth proteins and hormones in social
419 insects. *Elife* **5**, e20375 (2016).
- 420 58. Sarkar, A. *et al.* Microbial transmission in animal social networks and the social microbiome. *Nat.*
421 *Ecol. Evol.* **4**, 1020–1035 (2020).
- 422 59. Lecomte, N. *et al.* Alloparental feeding in the king penguin. *Anim. Behav.* **71**, 457–462 (2006).
- 423 60. Badyaev, A. V. & Uller, T. Parental effects in ecology and evolution: mechanisms, processes and
424 implications. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 1169–1177 (2009).
- 425 61. Blackburn, E. H. & Epel, E. S. Too toxic to ignore. *Nature* **490**, 169–171 (2012).
- 426 62. Katyare, S. S., Balasubramanian, S. & Parmar, D. V. Effect of corticosterone treatment on
427 mitochondrial oxidative energy metabolism in developing rat brain. *Exp. Neurol.* **183**, 241–248
428 (2003).
- 429 63. Uchino, B. N. *et al.* Social support, social integration, and inflammatory cytokines: A meta-
430 analysis. *Health Psychol.* **37**, 462–471 (2018).
- 431 64. Aydinonat, D. *et al.* Social isolation shortens telomeres in African Grey parrots (*Psittacus*
432 *erithacus erithacus*). *PLoS One* **9**, e93839 (2014).
- 433 65. Beery, A. K. *et al.* Chronic stress elevates telomerase activity in rats. *Biol. Lett.* **8**, 1063–1066
434 (2012).
- 435 66. Fine, B. *Theories of social capital: Researchers behaving badly.* (Pluto press, 2010).
- 436 67. Bourdieu, P. Le capital social: notes provisoires. *Actes Rech. En Sci. Soc.* **31**, 2–3 (1980).
- 437 68. Mulder, M. B. *et al.* Intergenerational Wealth Transmission and the Dynamics of Inequality in
438 Small-Scale Societies. *Science* **326**, 682–688 (2009).
- 439 69. Naud, A., Sueur, C., Chaix, B. & Kestens, Y. Combining social network and activity space data for
440 health research: tools and methods. *Health Place* **66**, 102454 (2020).
- 441 70. Foa, E. B. & Foa, U. G. Resource theory. in *Social exchange* 77–94 (Springer, 1980).
- 442
- 443

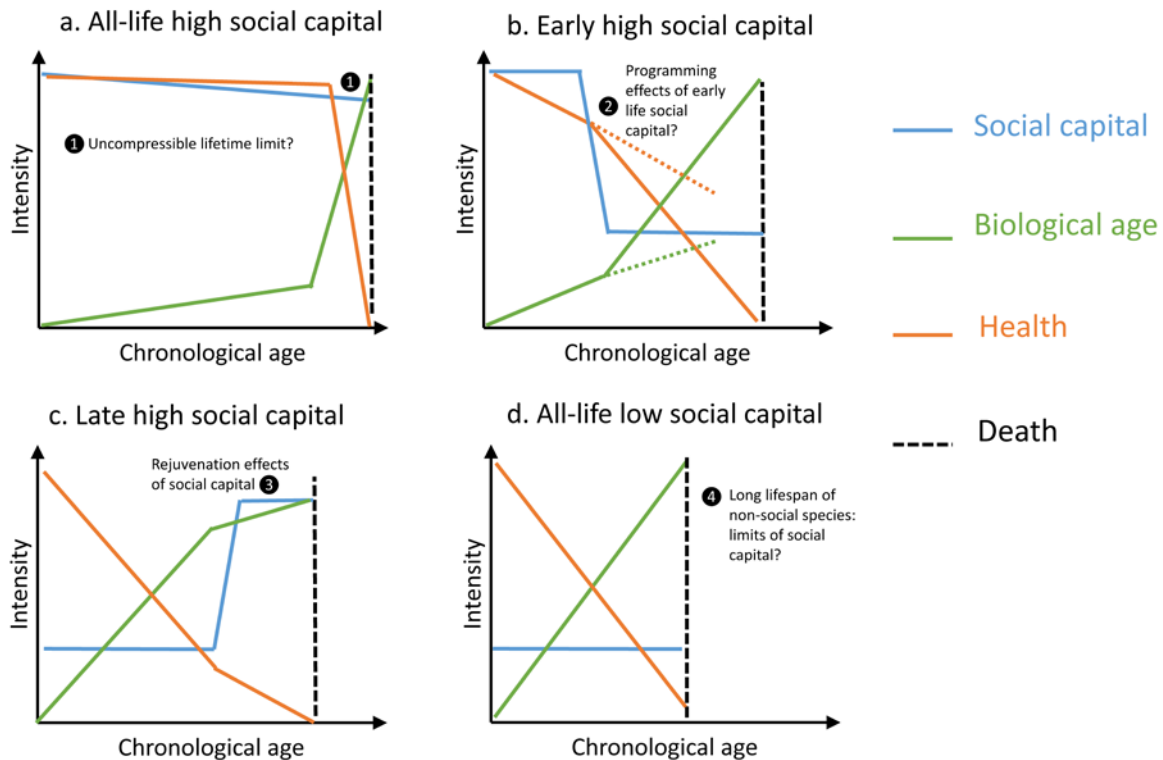
444 **Figure legends**



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.

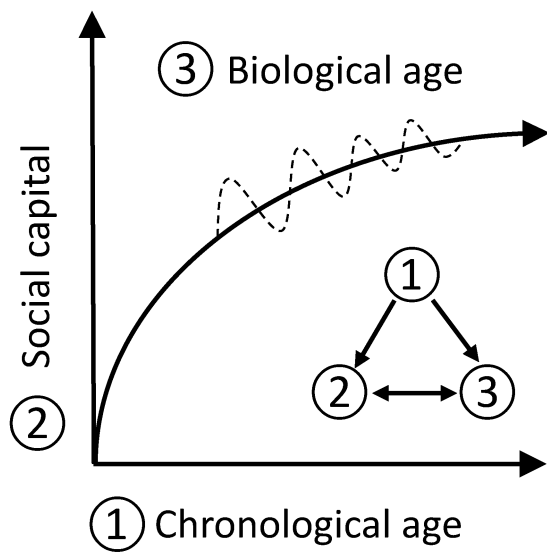
448



450

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).

465



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 |
|---|---|---|--|
| Eusocial species (e.g. ants, bees) | <p>Properties of social interactions including number and duration of interactions, type of interactions (e.g., trophallaxes, antenna-to-antenna, grooming), intra-caste or inter-caste interactions.</p> <p>Spatial distribution of social interactions according to individual mobility patterns</p> <p>Individual positions within the social system including, not exclusively, individual caste (e.g., male, queen, nest worker) or centrality index</p> | <p>Properties of the colony 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>Properties of the whole system of social interactions using network indicators such as community separation and its resilience.</p> | <p>Properties of the colony, 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>Relation with other colonies including the tolerance level and belonging to supercolony.</p> |
| Cooperative breeding species | <p>Properties of social interactions including number and duration of interactions, type of interactions (e.g., grooming, agression, reproductive behavior)</p> <p>Properties of social relationship which may include kinship, sex, reproductive status and dominance hierarchy</p> <p>Individual positions within the social system including, not exclusively, individual status (e.g., reproductive or helpers) and its position between reproductive sub-groups</p> | <p>Properties of the colony, may include its size, the number of helpers and offsprings and the system of interactions between reproductive sub-groups</p> | <p>Properties of cooperative breedings, including if its facultative or systematic and the level of competition for reproduction between helpers and male breeder.</p> <p>Properties of the social interaction system, including, the distribution of interaction within and between reproductive sub-groups.</p> |

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

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

477