



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-03831440v2

HAL Id: hal-03831440

<https://hal.science/hal-03831440v2>

Preprint submitted on 9 Sep 2021 (v2), 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**
16 **recognized as an important age-related mediator of health in humans and fitness-related traits in**
17 **animals. A rich social capital in humans can slow down senescence and reverse age-related deficits.**
18 **Some animals are able to adjust their social capital at different life stages (i.e., early, reproductive**
19 **and post-reproductive life), which may promote individual fitness. However, the underlying**
20 **biological mechanisms remain unknown. We suggest future research avenues to focus on social**
21 **capital as a modifiable dimension to gain a better understanding of variations in senescence, and**
22 **thereby 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 mental and physical **health** (see
28 Glossary for definition of health)^{1,2}. Poor social interactions are even known to be a risk factor for all-
29 cause mortality^{1,3,4}. Although numerous studies report associations between social interactions and
30 health outcomes, the underlying mechanisms are largely unknown. The number of animal studies on
31 the physiological (e.g. stress) or ecological (e.g. food access) determinants of ageing has risen sharply
32 over the past ten years^{3,9}. They suggest that complex and intertwined behavioural, psychological and
33 biological pathways are likely involved (Box 1)^{1,10}. However, these animal studies provided with
34 contrasted results according to species traits (e.g. group size)⁹ or individual traits (e.g. social status)
35 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 cooperation¹¹⁻¹⁵) an individual has access to or has used¹⁶, which is called
39 **social capital**. Individual social capital is a widely used concept in human **healthy ageing** literature,
40 and 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**. By adjusting,
42 we mean that changes in social capital are not random but made in a way to increase fitness (survival
43 and/or reproduction) and/or healthy ageing. This adjustment is the result of behavioural strategies

44 (e.g., favouring, selecting or avoiding social interactions). Although these strategies may or may not
45 be ruled by intermediary mechanisms (e.g., stress, genetics, mating system), the latter being most
46 likely evolutionary selected¹⁷. Based on the fact that **social capital** varies with individual age and
47 social group characteristics, we propose that it is the main factor that mediates the associations
48 between sociality and healthy ageing. In this perspective, we propose that the mechanisms linking
49 social capital to healthy ageing can be better understood by adopting an evolutionary and
50 comparative approach within individuals and between humans and animals¹⁸⁻²⁰, thus providing
51 greater insight into the observed variation in senescence rates and facilitating the identification of
52 anti-ageing interventions.

53 **Social capital changes with chronological age**

54 The social capital of an individual varies according to its life stage (i.e., early, reproductive or post-
55 reproductive life)²¹. In humans, non-human mammals and other species with long-lasting mother-
56 offspring bonds, infants focus on a small number of strong relationships with their mother and
57 individuals who share common traits (e.g., gender, kin). As adolescents, the individuals then expand
58 the quantity and diversity of their social relationships, and become more selective upon reaching
59 adulthood²² in order to adjust social capital in favour of resource acquisition (box 1).

60 Elephants (*Loxodonta africana*²³), chimpanzees (*Pan troglodytes*²⁴) and macaques (*Macaca sp.*^{12,25})
61 show comparable patterns of social changes with chronological age, even if they generally display
62 higher interspecific than intraspecific longevity variation. In elephants, social relationships such as
63 dominance are age-based²⁶. Matriarchs are the repositories of knowledge and manage
64 relationships²³. In chimpanzees, ageing males display more mutual, positive and selective
65 relationships than younger counterparts^{24,27}. Some authors proposed that the maintenance of social
66 relationships with elders may improve their health status and longevity. Almeiling et al.²⁵ reported
67 that old Barbary macaques (*Macaca sylvanus*) appear to remain valuable alliances for young
68 macaques, who continue grooming them to obtain social resources. These alliances result in a richer
69 social capital with fewer injuries and better transmission of knowledge, all of which give access to
70 resources for animals of all ages^{23,25}. In mammal societies and many native human societies such as
71 the Māori²⁸, knowledge is a key resource provided by older group members. The fitness of both
72 older and younger members increases because of the expertise and leadership of the elders^{10,23,29}.
73 Social capital also varies in **eusocial** insects. Throughout ontogenesis, worker ants or bees change
74 from one caste to another³⁰. This is associated with age-related cognitive decline³¹ and changes in
75 their social capital; they no longer interact with the same individuals³²⁻³⁴.

76 Different theories offer contrasting arguments to explain this change in social capital throughout life,
77 based on ultimate (e.g. reproduction-life trade-off^{35,36} and kin selection³⁷) or proximate (e.g.
78 cognitive^{38,39} or cellular processes⁴⁰) approaches. Thus, comparing the age-specific changes in social
79 capital between different animal species may help to identify the associations between the timing of
80 these changes and the individual physiological markers of ageing.

81 **Biological age changes with social capital**

82 Social capital fluctuates according to the different stages of life (early-life, reproductive life, post-
83 reproductive life) and may therefore influence individual health and biological age through stress and
84 body energy homeostasis. For example, early maternal loss leads to short, but not long-term stress
85 increases in wild chimpanzees⁴¹. Social isolation itself, i.e. independent of the usually associated
86 increased risk of predation and lower feeding efficiency, causes death in carpenter ants
87 (*Camponotus fellah*⁴²) by disrupting energy homeostasis. In reproductive fruit flies (*Drosophila*
88 *melanogaster*), social isolation induces stress, significantly accelerates the progression of tumour
89 growth, and triggers rapid death⁴³. Of course, usually social isolation increases predation risks or
90 decreases feeding efficiency, but the latter results were done in absence of predation and with ad
91 libitum food. In primates, males often disperse and this social isolation period is the most dangerous

92 for them⁵. Conversely, helping (early-life stage **in cooperative breeders**) and being helped by others
93 (reproductive stage) increase social capital and positively influence individual health, and ultimately
94 fitness, in all age categories⁴⁴⁻⁴⁶. Of course, social capital can have a negative impact on fitness^{3,5,6},
95 but this is relative to other group members, and this negative impact of social capital on fitness is still
96 lower than the cost associated to solitary living⁷. Yet, perception of ambivalent relationships in
97 humans is related to shorter telomere length⁸ which suggest that social capital could also negatively
98 impact biological ageing. In a nutshell, social capital, as early as infancy, could be one of the main
99 determinants of individual long-term fitness prospects.

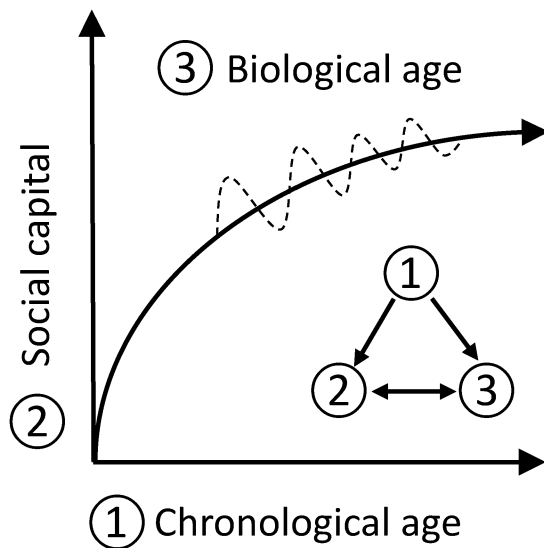
100 In old macaques, maintaining an active social life has been suggested to stimulate and maintain brain
101 activity through a good quality of life at both mental and physical levels²⁵. Cognitive decline is
102 observed in many non-human primate species^{20,47}, but the interplay with the components of social
103 capital is underappreciated. For instance, young lab animals who grow up alone may have difficulties
104 developing good relationships when they become adults, which in turn may trigger faster
105 senescence. Remarkably, the longevity of eusocial insect workers ranges from a few weeks to more
106 than two years. This plasticity is largely controlled by social factors⁹. Although these individuals are
107 closely related genetically, distinct life trajectories can emerge as a result of variations in their social
108 capital. Recent studies conducted in honeybees (*Apis mellifera*³⁴) and carpenter ants³³ confirm that
109 social capital predicts survival better than chronological age. A high social demand exposes workers
110 to an overload of social stimulations, speeding up senescence and decreasing longevity. Richardson
111 et al.³³ went further and concluded that the transition between castes is not hard wired or age
112 dependent, but rather stochastic and dependent on changes in social capital. Bees and ants are also
113 able to return to their previous caste and modify their interactions if a new demand appears in the
114 colony (e.g., following a nest predation event). This sole change in social capital results in molecular
115⁴⁸ and neuronal modifications³⁰ associated with reversible age-related phenotypes³¹ (Box 1) and
116 improved health, cognitive abilities and longevity. Social reprogramming in *Harpegnathos saltator*
117 ants (from workers to gamergates) conducts to longevity-associated brain remodelling⁴⁹. To sum up,
118 social capital can reverse biological age.

119

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

121 Organic (e.g., food) and inorganic (e.g., social) resources influence survival, growth and reproduction.
122 Social resources alone define social capital. Individuals can act on social interactions or social
123 activities to modify social capital and thus decrease stress, balance homeostasis, and ultimately
124 improve health. Because social capital is flexible and seems to be partly independent of chronological
125 age, we suggest that social capital should be considered as a modifiable dimension (as defined in
126 mathematics, Figure 1) within the health space⁵⁰, with its own regulatory processes and bidirectional
127 effects on individual senescence. As proposed by Richardson et al.³³, social capital is not directly
128 linked to chronological age but can change with biological age. This modifiable characteristic involves
129 large intra- and inter-specific variations in social capital, which in turn influence individual ageing rate
130 and fitness.

131



132

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

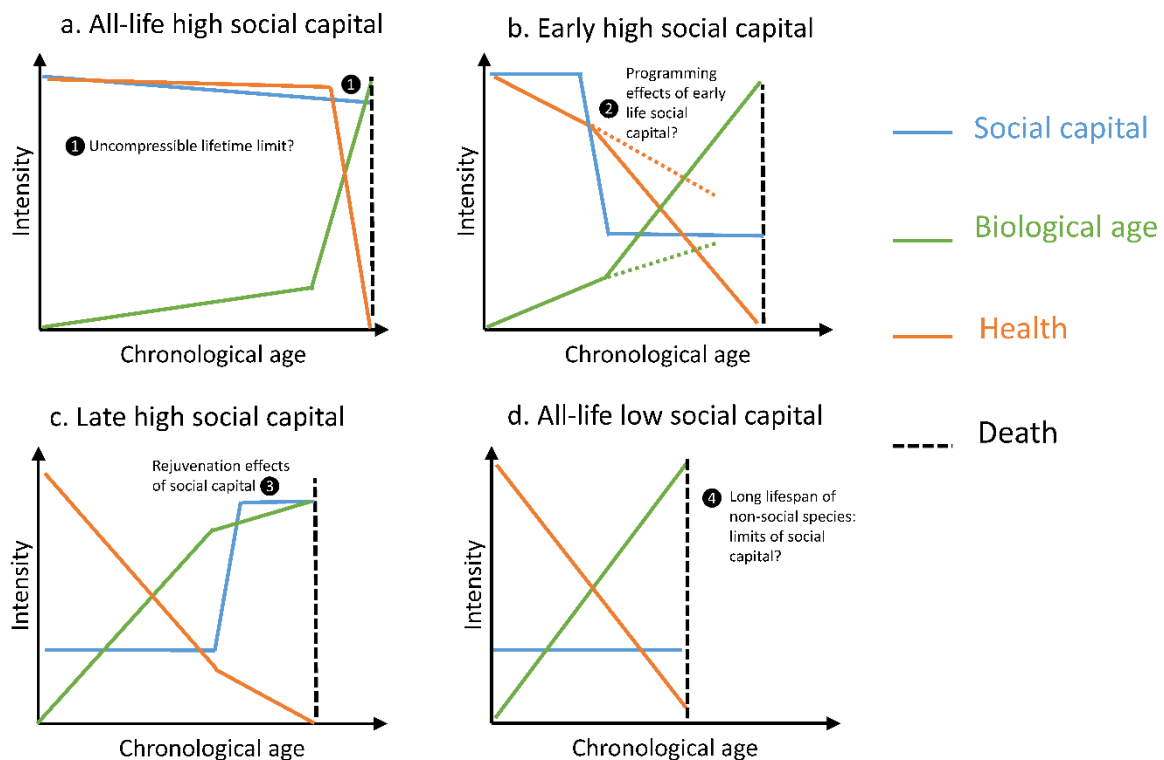
139

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

143 1) What is the extent of our knowledge on social capital? Social capital is most certainly a complex
 144 concept. This is illustrated by the large number of existing definitions in human sciences ^{2,16,51} but
 145 also by the diversity of its potential components. Portes ⁵² noted that " the point is approaching at
 146 which social capital comes to be applied to so many events and in so many different contexts as to
 147 lose any distinct meaning." Because social capital seems to be important for individual fitness and
 148 the evolution of sociality, it is crucial to acknowledge and apprehend its complexity. First, although
 149 most of the attention has been focused on the health benefits of social capital so far, the possible
 150 health risks associated with social capital also need to be considered, especially in terms of social
 151 overloading ^{33,34} or exposure to pathogens ⁵³. Page and collaborators ⁵⁴, for example, observed that
 152 mothers with higher betweenness and closeness centrality show more frequent instances of
 153 sickness, which somewhat counteracts other positive fitness effects. Other researchers have begun
 154 to acknowledge that social capital ranges across a large spectrum spanning from positive to negative
 155 consequences ^{55,56}, the latter being associated with adverse health outcomes. Costs of sociality are
 156 important. For instance, high social status males experience accelerated epigenetic aging in wild
 157 baboons ⁶ and higher oxidative damage but only during the mating season in mandrills ⁵⁷. We also
 158 need to consider other positive resources that can be considered components of social capital. For
 159 example, it has been shown that in addition to providing food ⁵⁸, trophallaxes convey compounds
 160 that are essential to individual health and growth in a conserved way across several taxa ⁵⁹, which
 161 seems to indicate a selection. Like eusocial insects, mammals share organic compounds through the
 162 social transmission of gut microbiome, which is known to influence health outcomes ⁶⁰. This field of
 163 study extends to birds, in which the feeding of chicks may allow intergenerational transmission of

164 such compounds⁶¹, and thus ensure rapid adaptations to environmental changes⁶². Whether or not
165 a richer social capital can improve adaptation in social species remains to be evaluated. Finding new
166 components of social capital is a research horizon that needs to be explored. Box 2 shows that social
167 capital may simply be directly related to the number of relationships or could be evaluated in a
168 complex way with the inclusion of social activities and the locations in which these social activities
169 are performed. How social capital should be operationalized also depends on the studied species, the
170 conditions and the scales of the study (temporal scale and subject/social organisation scale, i.e.,
171 interspecific comparisons of individuals that are studied throughout their lifetime). Future research
172 should further explore the potential components of social capital and their independent or
173 additive/synergistic effects on ageing outcomes, in laboratory but more importantly in natural
174 settings to demonstrate similar effects under natural variation of social relationships.

175 2) How can we explain individual and species variations in health and longevity? This section is about
176 ultimate mechanisms linking social capital to ageing. Among species, environmental factors have
177 differently shaped age-specific trade-offs between growth, reproduction and survival. Some
178 components of the social capital can be influenced by environmental factors but can also attenuate
179 the impact of the latter, increasing or decreasing individual and species variations in health and
180 longevity. Future studies should therefore address the co-evolution of inter-specific variances in
181 social capital and senescence rate. Animal species characterized by particular age-specific social
182 capital can emerge as novel behavioural models to address questions in current human ageing
183 research^{9,45,47}. For instance, such studies may delineate how social capital modulates life period
184 trade-offs (i.e., early-life growth and subsequent young and adult survival, and reproductive success)
185 and how adult social capital may have co-evolved with post-reproductive lifespan⁶³. For example,
186 female killer whales (*Orcinus orca*) live twice longer than males, and post-reproductive females have
187 greater knowledge and lead the group, thus enhancing the survival of their grand-offspring¹⁰. These
188 old females, like elephant matriarchs²³, have a rich social capital, live longer and also provide their
189 offspring with a huge social capital. This grandmother hypothesis was primarily proposed in humans
190³⁶. In line with these observations, one can hypothesize that variations in social capital in different life
191 stages influence variability in post-reproductive longevity (Figure 2b) and indirectly modulate sex-
192 differences in senescence³⁵. This means that sex-related differences in social capital could lead to
193 sex-related differences in longevity because of health or because of fitness benefits of social capital.
194 However, such sex-related differences in longevity can be buffered when males associate with
195 females. For instance, male baboons who are more strongly bonded to females have longer lifespans
196⁵. The subject of age-related cognitive processes requires longitudinal neurobiological studies
197 focusing on the ageing brain within the context of social capital⁴⁷. Finally, the interaction between
198 social capital and life history traits has certainly been constrained by environmental factors such as
199 predation risks, parasite prevalence or local population density. It is also important to note that non-
200 social species like ctenophores or cnidarians have almost reached immortality⁶⁴, or may live for
201 centuries like the Galapagos turtle or the Greenland shark. This casts doubt on the incompressible
202 limits of social benefits for longevity (Figure 2a and d). Multi-specific and multigenerational studies
203 will help to discover the mechanisms that underlie the relationships of social capital with species life-
204 history and ecology.



205

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

220

221 3) How is social capital encoded to enhance fitness? This section is more about proximate
 222 mechanisms linking social capital to ageing and fitness. Although we know that social capital is
 223 related to individual fitness, little is known about the extent to which this relationship depends on
 224 species ecology and gender, or whether it is restricted to certain life-history traits. The role of social
 225 capital in variations of senescence onset or in senescence rate can be assessed in the context of
 226 **evolutionary theories of ageing**⁶⁵. For instance, this can be done by determining how social capital
 227 modulates the energy trade-offs that can occur during the life trajectory of individuals (e.g.
 228 growth/reproduction and ageing trade-offs^{45,66,67}). Potential biological mechanisms such as telomere
 229 rate of loss⁶⁸, oxidative stress or mitochondrial dysfunction⁶⁹ (Box 1) that are already suspected to
 230 play a major role in ageing would have to be tested in the light of the social capital context. For
 231 example, extended sex-specific post-reproductive life in killer whales may have been co-selected
 232 with specific social traits and anti-ageing mechanisms that have positive effects on female fitness and

233 their offspring^{36,70}. Age-related variations in social capital in cooperative breeders have already been
234 linked with the fitness traits of individuals (see^{44,46}). However, we have yet to elucidate the question
235 of how eusocial reproducers have acquired a specific social capital that probably enables them to
236 successfully face higher reproduction rates and attain a longer lifespan than non-reproducers. How is
237 the impact of social capital on senescence genetically or epigenetically encoded? For instance,
238 personality, which is heritable, has an impact on longevity and pace of life⁷¹, and one of its basis is
239 sociality. Social capital could be encoded in this personality variable, a hypothesis that need to be
240 tested *via* the demonstration of a covariation at the individual level among social capital, personality
241 and longevity. Understanding the genetics and epigenetics of sociality would be of help in unraveling
242 mechanisms that link sociality to ageing outcomes and fitness. In this respect, we propose that the
243 recent development of genomics and proteomics to study ageing^{30,48} should be extended to include
244 the study of social capital. These investigations will likely extend our knowledge on how evolution
245 has co-selected sociality and longevity^{9,63}. Furthermore, these new findings could subsequently be
246 leveraged to promote healthy ageing.

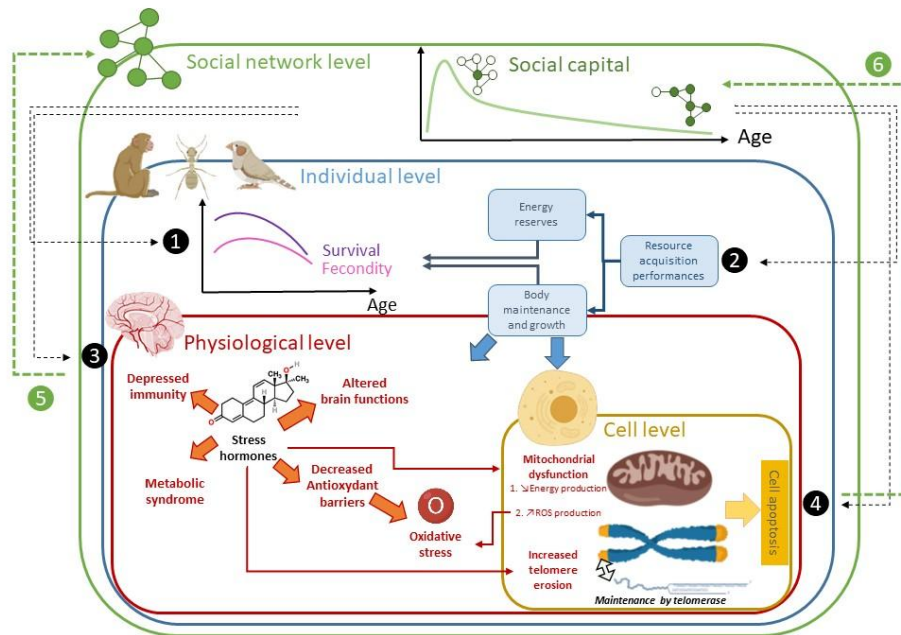
247 **Concluding remarks**

248 The three points we developed indicate that working with social capital and markers of senescence
249 along life will prove to be more powerful than standing with chronological age. Making these
250 comparisons in animals is of paramount importance as animal studies allow (i) to reduce the number
251 of confounding factors by controlling experimental conditions; (ii) to carry out studies over several
252 generations in a relatively short timeframe, and study evolution through genetic and epigenetic
253 effects; and (iii) to conduct invasive and integrative experimental studies going from the cell to the
254 group level, which is impossible in humans. Experimental designs or observations of wild individuals
255 throughout their lifespan and across several generations will help to better understand the long-term
256 consequences of social capital. This is mainly possible through longitudinal studies⁷² or
257 multigenerational laboratory studies with a controlled environment and small changes in the study
258 design (i.e., systematic heterogenization of study samples as group size, group composition, number
259 of helpers)^{73,74}.

260 Taken together, currently available data suggest that focusing on social capital and markers of
261 senescence throughout lifespan may explain individual health and fitness better than chronological
262 age. The observation that mean lifespan is greater in eusocial than non-eusocial species leads us to
263 question the co-evolution of sociality with senescence⁹. Social capital adjustment further suggests
264 that the basic assumptions that environmentally driven mortality shapes the selection of senescence
265 may be more complex than we initially thought. Although mean lifespan is influenced by a large
266 number of factors, the respective contribution of social capital versus other biological, ecological and
267 environmental factors in the regulation of senescence and longevity remains an open question. Time
268 is finite for most living animals, but social capital appears to be a promising tool to make senescence
269 an adjustable parameter and to slow down the rate of ageing⁷⁵.

270
271

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



272

273 Figure 3: Schema of the proposed mutual influence of social capital, chronological age and biological
274 age, from the cell level to the network.

275 While an individual can have a long-life expectancy, it may not attain the same **fitness** as a
276 conspecific due to an accelerated **senescence** of the reproductive function (figure 3). The rate of
277 senescence at the individual level is expected to reflect the lifelong deleterious impact of costly traits
278 such as growth, immunity or reproduction⁶⁷. Inter-individual variability in the age of senescence
279 onset is also a unique opportunity to investigate the genetic and socio-environmental factors that
280 shape **ageing** trade-offs within a given population. Social stress has been known to modulate ageing
281 pathways for the last decade⁷⁶. However, interplay between social capital and age may highlight
282 putative loops of intertwined pathways that modulate reproductive success and survival rate in both
283 negative and positive ways **1**. In a resource-based explanation, an initial underlying mechanism
284 relies on the impact of social capital on energy resource acquisition (for instance via the acquisition
285 of knowledge or friendly relationships) **2**. However, variation in social capital may act indirectly
286 through cellular and physiological changes that strengthen resilience to stress **3** or body energy
287 homeostasis **4**. These effects are currently inferred from previous observations. Social isolation and
288 interactions have been described as having opposite effects on stress hormones¹⁴, with potentially
289 negative consequences but also adaptive responses observed at the physiological and cellular level
290 (e.g. oxidative stress)⁷⁷. Another study suggests that social isolation has negative effects on stress
291 and energy balance⁴². Inflammation is also an important biological mechanism that links social
292 capital to unhealthy states⁷⁸. Indeed, various forms of social adversity are associated with elevated
293 expression of proinflammatory genes and decreased expression of genes related to innate immune
294 responses in humans⁷⁹ and rhesus macaques⁸⁰. These altered individual performances in the
295 acquisition of energy from the environment will be reflected in the life-history trade-offs for the
296 allocation of energy to individual fitness traits. Social isolation triggers an increased rate of telomere
297 loss (a biological index of ageing)⁸¹ and disrupts energy homeostasis. Increased telomerase activity in
298 socially stressed individuals has also been described in the literature⁸². This suggests that social
299 variables do indeed impact cell-ageing proxies, as previously suggested for social rank and telomere
300 length^{40,68}. However, as social capital likely varies over time and depends on individual physiological
301 status, a feedback of physiology is expected on sociality (**5**, **6**). For instance, some authors

302 suggest possible causal effects of short telomeres on unhealthy behaviours as smoking in humans⁴⁰.
303 It means that some physiological traits (short telomeres) can conduct to some bad aspects of
304 sociality (here being conformist with risky behaviours for health) enhancing the physiological traits
305 (decreasing telomeres). Another example is the accelerated death of ill flies (*Drosophila*
306 *melanogaster*) who are isolated from their conspecifics, likely because of reluctant physiological
307 traits as cancer⁴³. Because individuals have cancer, they are isolated from others but this in turn
308 accelerates cancer progression. These studies confirm that the social capital – fitness relationships
309 have auto-regulating properties, a finding that calls for dedicated studies to identify these causal
310 links.

311

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

313 Although work on social capital abounds across disciplines, there is no consensus on its
314 conceptualization and operationalization^{4,51,83,84}. Social capital can first be studied in terms of
315 resources or services that are embedded in spatial associations (e.g., proximities, being close to an
316 individual can provide access to food) or social interactions (e.g., grooming). Although social
317 resources that are embedded in social relationships cannot be directly controlled using behavioural
318 strategies, individuals can choose the individuals with whom they maintain relationships^{3,11}. Food is
319 primarily an ecological resource, but access to it depends on the social capital of the individual (social
320 support, cooperation, alliances, tolerance).

321 Because social relationships are the basis on which social capital is managed, the notion of social
322 capital is often simplified to these social relationships, in which social resources are exchanged.
323 These relationships can be described from their compositional (e.g., hierarchical position of the
324 individuals) or structural (e.g., distributions of social relationships) properties. In many studies, social
325 network indices such as degree (number of social relationships, see table S2 for metrics from social
326 network analysis to measure the components of social capital) are used as a proxy of social capital.
327 Most of the past studies have focused on the direct social relationships between individuals in a
328 network (e.g., degree or strength⁸⁵), yet indirect relationships (e.g., friend of our friend, betweenness
329 or clustering coefficient⁸⁵) also influence social capital^{12,58}. These indirect connections affecting
330 information but also disease⁵³ transmission networks may strengthen the cognition and longevity of
331 species, in which cultural behaviour is important⁵³. Furthermore, cultural differences influence social
332 capital in humans⁸⁶; few studies have been conducted to date on this topic in non-human animals,
333 and further studies should be carried out.

334 Lastly, social activities and geospatial locations can be studied in relation with social capital⁸⁷, but can
335 also be integrated as components of the latter. Indeed, human social activities are linked to specific
336 locations and both elements can be combined to better understand covariation between social
337 capital and health⁸⁷. This covariation between social capital, location and task is obvious in eusocial
338 insects^{33,34}, but evidence is lacking in other species. Both Wild et al.³⁴ and Richardson et al.³³ used
339 information about social interactions, proximities, social activities and location to calculate a social
340 capital index.

341 To summarize, the social capital components we need to identify are: resources embedded in social
342 relationships¹⁶ such as information and services¹¹, the composition and structure of social networks
343 (individual but also group metrics), cultural differences, social activities and geospatial locations.
344 Table S1 summarizes the currently considered components of social capital according to the studied
345 species and the level of studies. Table S2 summarizes metrics from social network analysis to
346 measure the components of social capital.

347

348

- 349 **Glossary:**
- 350 - **Ageing:** the only consensual definition is that it is a heterogeneous process of becoming older.
- 351 - **Biological age:** individual age as determined through different biological markers that change over
352 time, but not necessarily related to chronological age. Biological age is composed of different stages
353 (e.g., ontogeny, reproductive life, and senescence, including post-reproductive life). Contrary to
354 chronological age, biological age considers the individual in relation to its date of death, while
355 chronological age considers it in relation to its date of birth.
- 356 - **Cooperative breeding:** social system characterized by alloparental care: offspring receives care not
357 only from their parents, but also from additional group members, often called helpers.
- 358 - **Chronological age (or age):** the age of an individual as measured from birth to a given date referring
359 to time, usually based on the Gregorian calendar.
- 360 - **Eusociality:** highest level of sociality defined by cooperative brood care, overlapping generations,
361 and division of labour into reproductive and non-reproductive groups.
- 362 - **Evolutionary theories of ageing:** proposals to explain the persistence of the deleterious process of
363 ageing over several generations, despite the action of natural selection.
- 364 - **Fitness:** defined here as the individual's ability to transmit its genes directly (with offspring) or
365 indirectly (by helping relatives, i.e., **inclusive fitness**) to future generations.
- 366 - **Health:** state of complete physical and mental independence in activities of daily living². Being
367 healthy, in practical terms, means having adequate physical and mental independence in activities of
368 daily living. The main three characteristics of the dynamic equilibrium between the occurrence of
369 damage and the processes of maintenance and repair are damage control, stress response and
370 constant remodeling and adaptation. These elements can be studied at different levels of the
371 organism, as described in Box 1.
- 372 - **Healthy ageing:** process of maintaining functionality of a living system as age advances.
- 373 - **Longevity:** mean lifetime duration for a species.
- 374 - **Ontogeny:** development of an organism from fertilization to the adult stage (reproductive stage).
- 375 - **Senescence:** progressive decline of biological functions, eventually leading to death. In evolutionary
376 terms, senescence can be defined as the decrease in the age-specific contribution to fitness over
377 lifetime.
- 378 - **Social capital:** resources embedded in a social structure which are accessed and / or mobilized in
379 purposive action. The resources of an individual vary during its life, meaning that social capital
380 fluctuates with age. In some studies, the number of partners or the connections an individual has
381 within its network¹² are a proxy to measure social capital. Differences in social capital implies that
382 group members have differentiated and contrasting relationships with each other¹¹, as observed in
383 cooperative breeding or eusocial species. This means that it is difficult to seek to identify social
384 capital components in communal breeding or gregarious species with few differentiated
385 relationships¹¹. However, in these cases it would be possible to start with the use of simpler indices
386 like group size or kinship size as social capital proxies.
- 387 - **Social resources:** Social resources are defined as any concrete or symbolic item that can be used as
388 an object of exchange among people. Foa and Foa classified social resources into six categories for
389 humans: love/affection, status, information, services, goods, and money⁸⁸. Money can be replaced
390 by access to food in non-human animals.

391 **References**

- 392 1. Rook, K. S. Social networks in later life: Weighing positive and negative effects on health and
393 well-being. *Curr. Dir. Psychol. Sci.* **24**, 45–51 (2015).
- 394 2. Rattan, S. I. Healthy ageing, but what is health? *Biogerontology* **14**, 673–677 (2013).
- 395 3. Snyder-Mackler, N. *et al.* Social determinants of health and survival in humans and other
396 animals. *Science* **368**, (2020).
- 397 4. Kawachi, I., Subramanian, S. V. & Kim, D. Social capital and health. in *Social capital and health* 1–
398 26 (Springer, 2008).
- 399 5. Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F. & Alberts, S. C. Social bonds, social
400 status and survival in wild baboons: a tale of two sexes. *Philos. Trans. R. Soc. B* **375**, 20190621
401 (2020).
- 402 6. Anderson, J. A. *et al.* High social status males experience accelerated epigenetic aging in wild
403 baboons. *eLife* **10**, e66128 (2021).
- 404 7. Krause, J. & Ruxton, G. D. *Living in groups*. (Oxford University Press, 2002).
- 405 8. Uchino, B. N. *et al.* Social relationships and health: Is feeling positive, negative, or both
406 (ambivalent) about your social ties related to telomeres? *Health Psychol.* **31**, 789 (2012).
- 407 9. Lucas, E. R. & Keller, L. The co-evolution of longevity and social life. *Funct. Ecol.* **34**, 76–87 (2020).
- 408 10. Natrass, S. *et al.* Postreproductive killer whale grandmothers improve the survival of their
409 grandoffspring. *Proc. Natl. Acad. Sci.* **116**, 26669–26673 (2019).
- 410 11. Moscovice, L. R., Sueur, C. & Aureli, F. How socio-ecological factors influence the differentiation
411 of social relationships: an integrated conceptual framework. *Biol. Lett.* **16**, 20200384 (2020).
- 412 12. Brent, L., Semple, S., Dubuc, C., Heistermann, M. & MacLarnon, A. Social capital and physiological
413 stress levels in free-ranging adult female rhesus macaques. *Physiol. Behav.* **102**, 76–83 (2011).
- 414 13. Lakon, C. M., Godette, D. C. & Hipp, J. R. Network-based approaches for measuring social capital.
415 in *Social capital and health* 63–81 (Springer, 2008).
- 416 14. Wittig, R. M. *et al.* Social support reduces stress hormone levels in wild chimpanzees across
417 stressful events and everyday affiliations. *Nat. Commun.* **7**, (2016).

- 418 15. Thoits, P. A. Mechanisms Linking Social Ties and Support to Physical and Mental Health. *J. Health*
419 *Soc. Behav.* **52**, 145–161 (2011).
- 420 16. Lin, N., Fu, Y. & Hsung, R.-M. Measurement techniques for investigations of social capital. *Soc.*
421 *Cap. Theory Res.* 57–81 (2001).
- 422 17. Sueur, C., Romano, V., Sosa, S. & Puga-Gonzalez, I. Mechanisms of network evolution: a focus on
423 socioecological factors, intermediary mechanisms, and selection pressures. *Primates* 1–15
424 (2019).
- 425 18. Chiou, K. L. *et al.* Rhesus macaques as a tractable physiological model of human ageing. *Philos.*
426 *Trans. R. Soc. B Biol. Sci.* **375**, 20190612 (2020).
- 427 19. Machanda, Z. P. & Rosati, A. G. Shifting sociality during primate ageing. *Philos. Trans. R. Soc. B*
428 *Biol. Sci.* **375**, 20190620 (2020).
- 429 20. Emery Thompson, M., Rosati, A. G. & Snyder-Mackler, N. Insights from evolutionarily relevant
430 models for human ageing. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190605 (2020).
- 431 21. McDonald, S. & Mair, C. A. Social Capital Across the Life Course: Age and Gendered Patterns of
432 Network Resources 1. in vol. 25 335–359 (Wiley Online Library, 2010).
- 433 22. Field, D. & Minkler, M. Continuity and Change in Social Support Between Young-old and Old-old
434 or Very-old Age. *J. Gerontol.* **43**, P100–P106 (1988).
- 435 23. McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. Matriarchs As Repositories of Social
436 Knowledge in African Elephants. *Science* **292**, 491–494 (2001).
- 437 24. Rosati, A. G. *et al.* Social selectivity in aging wild chimpanzees. *Science* **370**, 473–476 (2020).
- 438 25. Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A. M. & Fischer, J. Motivational
439 shifts in aging monkeys and the origins of social selectivity. *Curr. Biol.* **26**, 1744–1749 (2016).
- 440 26. Wittemyer, G. & Getz, W. M. Hierarchical dominance structure and social organization in African
441 elephants, *Loxodonta africana*. *Anim. Behav.* **73**, 671–681 (2007).
- 442 27. Silk, J. The upside of aging. *Science* **370**, 403–404 (2020).
- 443 28. Durie, M. Kaumatautanga reciprocity: Maori elderly and whanau. *N. Z. J. Psychol.* **28**, 102 (1999).

- 444 29. Migliano, A. B. *et al.* Hunter-gatherer multilevel sociality accelerates cumulative cultural
445 evolution. *Sci. Adv.* **6**, eaax5913 (2020).
- 446 30. Münch, D., Amdam, G. V. & Wolschin, F. Ageing in a eusocial insect: molecular and physiological
447 characteristics of life span plasticity in the honey bee. *Funct. Ecol.* **22**, 407–421 (2008).
- 448 31. Baker, N., Wolschin, F. & Amdam, G. V. Age-related learning deficits can be reversible in
449 honeybees *Apis mellifera*. *Exp. Gerontol.* **47**, 764–772 (2012).
- 450 32. Mersch, D. P., Crespi, A. & Keller, L. Tracking individuals shows spatial fidelity is a key regulator of
451 ant social organization. *Science* **340**, 1090–1093 (2013).
- 452 33. Richardson, T. O. *et al.* Ant Behavioral Maturation Is Mediated by a Stochastic Transition
453 between Two Fundamental States. *Curr. Biol.* **30**, 1–8 (2020).
- 454 34. Wild, B. *et al.* Social networks predict the life and death of honey bees. *Nat. Commun.* **12**, 1–12
455 (2021).
- 456 35. Lemaître, J.-F. *et al.* Sex differences in adult lifespan and aging rates of mortality across wild
457 mammals. *Proc. Natl. Acad. Sci.* **117**, 8546–8553 (2020).
- 458 36. Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. Fitness benefits of
459 prolonged post-reproductive lifespan in women. *Nature* **428**, 178–181 (2004).
- 460 37. Abbot, P. *et al.* Inclusive fitness theory and eusociality. *Nature* **471**, E1–E4 (2011).
- 461 38. Carstensen, L. L. The Influence of a Sense of Time on Human Development. *Science* **312**, 1913–
462 1915 (2006).
- 463 39. Aartsen, M. J., van Tilburg, T., Smits, C. H. M. & Knipscheer, K. C. P. M. A Longitudinal Study of
464 the Impact of Physical and Cognitive Decline on the Personal Network in Old Age. *J. Soc. Pers.*
465 *Relatsh.* **21**, 249–266 (2004).
- 466 40. Bateson, M. & Nettle, D. Why are there associations between telomere length and behaviour?
467 *Philos. Trans. R. Soc. B Biol. Sci.* **373**, 20160438 (2018).
- 468 41. Girard-Buttoz, C. *et al.* Early maternal loss leads to short- but not long-term effects on diurnal
469 cortisol slopes in wild chimpanzees. *eLife* **10**, e64134 (2021).

- 470 42. Koto, A., Mersch, D., Hollis, B. & Keller, L. Social isolation causes mortality by disrupting energy
471 homeostasis in ants. *Behav. Ecol. Sociobiol.* **69**, 583–591 (2015).
- 472 43. Dawson, E. H. *et al.* Social environment mediates cancer progression in *Drosophila*. *Nat.*
473 *Commun.* **9**, (2018).
- 474 44. Berger, V., Lemaître, J.-F., Allainé, D., Gaillard, J.-M. & Cohas, A. Early and adult social
475 environments shape sex-specific actuarial senescence patterns in a cooperative breeder. *Am.*
476 *Nat.* **192**, 525–536 (2018).
- 477 45. Lemaître, J.-F. *et al.* Early-late life trade-offs and the evolution of ageing in the wild. *Proc. R. Soc.*
478 *B Biol. Sci.* **282**, 20150209 (2015).
- 479 46. Hammers, M. *et al.* Breeders that receive help age more slowly in a cooperatively breeding bird.
480 *Nat. Commun.* **10**, 1–10 (2019).
- 481 47. Lacreuse, A., Raz, N., Schmidtke, D., Hopkins, W. D. & Herndon, J. G. Age-related decline in
482 executive function as a hallmark of cognitive ageing in primates: an overview of cognitive and
483 neurobiological studies. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190618 (2020).
- 484 48. Quque, M. *et al.* Division of labour in the black garden ant (*Lasius niger*) leads to three distinct
485 proteomes. *J. Insect Physiol.* 103907 (2019) doi:10.1016/j.jinsphys.2019.103907.
- 486 49. Sheng, L. *et al.* Social reprogramming in ants induces longevity-associated glia remodeling. *Sci.*
487 *Adv.* **6**, eaba9869 (2020).
- 488 50. Sanromà, M. & Adserà, J. M. From electronic medical records to the personal health space: how
489 ICTs will transform healthcare in the next decade. in 473–482 (2010).
- 490 51. Putnam, R. The prosperous community: Social capital and public life. *Am. Prospect* **13**, (1993).
- 491 52. Portes, A. The two meanings of social capital. in vol. 15 1–12 (Springer, 2000).
- 492 53. Romano, V., MacIntosh, A. J. J. & Sueur, C. Stemming the Flow: Information, Infection, and Social
493 Evolution. *Trends Ecol. Evol.* **35**, 849–853 (2020).
- 494 54. Page, A. E. *et al.* Hunter-Gatherer Social Networks and Reproductive Success. *Sci. Rep.* **7**, 1153
495 (2017).

- 496 55. Portes, A. & Landolt, P. The downside of social capital. (1996).
- 497 56. Wacquant, L. J. Negative social capital: State breakdown and social destitution in America's
498 urban core. *Neth. J. Hous. Built Environ.* **13**, 25 (1998).
- 499 57. Beaulieu, M., Mboumba, S., Willaume, E., Kappeler, P. M. & Charpentier, M. J. E. The oxidative
500 cost of unstable social dominance. *J. Exp. Biol.* jeb. 104851 (2014) doi:10.1242/jeb.104851.
- 501 58. Quque, M. *et al.* Hierarchical networks of food exchange in the black garden ant *Lasius niger*.
502 *Insect Sci.* (2020).
- 503 59. LeBoeuf, A. C. *et al.* Oral transfer of chemical cues, growth proteins and hormones in social
504 insects. *Elife* **5**, e20375 (2016).
- 505 60. Sarkar, A. *et al.* Microbial transmission in animal social networks and the social microbiome. *Nat.*
506 *Ecol. Evol.* **4**, 1020–1035 (2020).
- 507 61. Lecomte, N. *et al.* Alloparental feeding in the king penguin. *Anim. Behav.* **71**, 457–462 (2006).
- 508 62. Badyaev, A. V. & Uller, T. Parental effects in ecology and evolution: mechanisms, processes and
509 implications. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 1169–1177 (2009).
- 510 63. Vágási, C. I. *et al.* Is degree of sociality associated with reproductive senescence? A comparative
511 analysis across birds and mammals. *bioRxiv* 2020.10.29.360636 (2020)
512 doi:10.1101/2020.10.29.360636.
- 513 64. Petralia, R. S., Mattson, M. P. & Yao, P. J. Aging and longevity in the simplest animals and the
514 quest for immortality. *Ageing Res. Rev.* **16**, 66–82 (2014).
- 515 65. Reznick, D., Bryant, M. & Holmes, D. The evolution of senescence and post-reproductive lifespan
516 in guppies (*Poecilia reticulata*). *PLoS Biol* **4**, e7 (2005).
- 517 66. Williams, G. C. Pleiotropy, Natural Selection, and the Evolution of Senescence. *Evolution* **11**, 398–
518 411 (1957).
- 519 67. Hamilton, W. D. The moulding of senescence by natural selection. *J. Theor. Biol.* **12**, 12–45
520 (1966).

- 521 68. Lewin, N., Treidel, L. A., Holekamp, K. E., Place, N. J. & Hausmann, M. F. Socioecological
522 variables predict telomere length in wild spotted hyenas. *Biol. Lett.* **11**, 20140991 (2015).
- 523 69. Hood, W. R. *et al.* The mitochondrial contribution to animal performance, adaptation, and life-
524 history variation. *Integr. Comp. Biol.* **58**, 480–485 (2018).
- 525 70. Kirkwood, T. B. Evolution of ageing. *Nature* **270**, 301–304 (1977).
- 526 71. Réale, D. *et al.* Personality and the emergence of the pace-of-life syndrome concept at the
527 population level. *Philos. Trans. Biol. Sci.* **365**, 4051–4063 (2010).
- 528 72. Clutton-Brock, T. & Sheldon, B. C. Individuals and populations: the role of long-term, individual-
529 based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol. Pers. Ed.* **25**,
530 562–573 (2010).
- 531 73. Voelkl, B., Vogt, L., Sena, E. S. & Würbel, H. Reproducibility of preclinical animal research
532 improves with heterogeneity of study samples. *PLOS Biol.* **16**, e2003693 (2018).
- 533 74. Voelkl, B. *et al.* Reproducibility of animal research in light of biological variation. *Nat. Rev.*
534 *Neurosci.* **21**, 384–393 (2020).
- 535 75. Colchero, F. *et al.* The long lives of primates and the ‘invariant rate of ageing’ hypothesis. *Nat.*
536 *Commun.* **12**, 3666 (2021).
- 537 76. Blackburn, E. H. & Epel, E. S. Too toxic to ignore. *Nature* **490**, 169–171 (2012).
- 538 77. Katyare, S. S., Balasubramanian, S. & Parmar, D. V. Effect of corticosterone treatment on
539 mitochondrial oxidative energy metabolism in developing rat brain. *Exp. Neurol.* **183**, 241–248
540 (2003).
- 541 78. Uchino, B. N. *et al.* Social support, social integration, and inflammatory cytokines: A meta-
542 analysis. *Health Psychol.* **37**, 462–471 (2018).
- 543 79. Cole, S. W. Human social genomics. *PLoS Genet.* **10**, e1004601 (2014).
- 544 80. Simons, N. D. & Tung, J. Social status and gene regulation: conservation and context dependence
545 in primates. *Trends Cogn. Sci.* **23**, 722–725 (2019).

- 546 81. Aydinonat, D. *et al.* Social isolation shortens telomeres in African Grey parrots (*Psittacus*
547 *erithacus erithacus*). *PLoS One* **9**, e93839 (2014).
- 548 82. Beery, A. K. *et al.* Chronic stress elevates telomerase activity in rats. *Biol. Lett.* **8**, 1063–1066
549 (2012).
- 550 83. Fine, B. *Theories of social capital: Researchers behaving badly*. (Pluto press, 2010).
- 551 84. Bourdieu, P. Le capital social: notes provisoires. *Actes Rech. En Sci. Soc.* **31**, 2–3 (1980).
- 552 85. Sosa, S., Sueur, C. & Puga-Gonzalez, I. Network measures in animal social network analysis: their
553 strengths, limits, interpretations and uses. *Methods Ecol. Evol.* **n/a**, (2020).
- 554 86. Mulder, M. B. *et al.* Intergenerational Wealth Transmission and the Dynamics of Inequality in
555 Small-Scale Societies. *Science* **326**, 682–688 (2009).
- 556 87. Naud, A., Sueur, C., Chaix, B. & Kestens, Y. Combining social network and activity space data for
557 health research: tools and methods. *Health Place* **66**, 102454 (2020).
- 558 88. Foa, E. B. & Foa, U. G. Resource theory. in *Social exchange* 77–94 (Springer, 1980).
- 559 89. Bles, O., Deneubourg, J.-L. & Nicolis, S. C. Food dissemination in ants: robustness of the
560 trophallactic network against resource quality. *J. Exp. Biol.* **221**, jeb192492 (2018).
- 561 90. Planckaert, J., Nicolis, S. C., Deneubourg, J.-L., Sueur, C. & Bles, O. A spatiotemporal analysis of
562 the food dissemination process and the trophallactic network in the ant *Lasius niger*. *Sci. Rep.* **9**,
563 1–11 (2019).
- 564 91. Stroeymeyt, N. *et al.* Social network plasticity decreases disease transmission in a eusocial insect.
565 *Science* **362**, 941–945 (2018).
- 566 92. Dornhaus, A., Holley, J.-A. & Franks, N. R. Larger colonies do not have more specialized workers
567 in the ant *Temnothorax albigripennis*. *Behav. Ecol.* **20**, 922–929 (2009).
- 568 93. Beshers, S. N. & Fewell, J. H. Models of division of labor in social insects. *Annu. Rev. Entomol.* **46**,
569 413–440 (2001).
- 570 94. Robinson, G. E. Regulation of division of labor in insect societies. *Annu. Rev. Entomol.* **37**, 637–
571 665 (1992).

- 572 95. Burda, H., Honeycutt, R. L., Begall, S., Locker-Grütjen, O. & Scharff, A. Are naked and common
573 mole-rats eusocial and if so, why? *Behav. Ecol. Sociobiol.* **47**, 293–303 (2000).
- 574 96. Jarvis, J. U. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science*
575 **212**, 571–573 (1981).
- 576 97. Sunamura, E. *et al.* Workers select mates for queens: a possible mechanism of gene flow
577 restriction between supercolonies of the invasive Argentine ant. *Naturwissenschaften* **98**, 361
578 (2011).
- 579 98. Drewe, J. A. Who infects whom? Social networks and tuberculosis transmission in wild meerkats.
580 *Proc. R. Soc. B Biol. Sci.* **277**, 633–642 (2010).
- 581 99. Dey, C. J., Reddon, A. R., O'Connor, C. M. & Balshine, S. Network structure is related to social
582 conflict in a cooperatively breeding fish. *Anim. Behav.* **85**, 395–402 (2013).
- 583 100. Reber, S. A., Townsend, S. W. & Manser, M. B. Social monitoring via close calls in meerkats.
584 *Proc. R. Soc. B Biol. Sci.* **280**, 20131013 (2013).
- 585 101. Drewe, J. A., Madden, J. R. & Pearce, G. P. The social network structure of a wild meerkat
586 population: 1. Inter-group interactions. *Behav. Ecol. Sociobiol.* **63**, 1295–1306 (2009).
- 587 102. Madden, J. R., Drewe, J. A., Pearce, G. P. & Clutton-Brock, T. H. The social network structure
588 of a wild meerkat population: 2. Intragroup interactions. *Behav. Ecol. Sociobiol.* **64**, 81 (2009).
- 589 103. Madden, J. R., Drewe, J. A., Pearce, G. P. & Clutton-Brock, T. H. The social network structure
590 of a wild meerkat population: 3. Position of individuals within networks. *Behav. Ecol. Sociobiol.*
591 **65**, 1857–1871 (2011).
- 592 104. Covas, R., Plessis, M. A. du & Doutrelant, C. Helpers in colonial cooperatively breeding
593 sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding
594 conditions. *Behav. Ecol. Sociobiol.* **63**, 103–112 (2008).
- 595 105. Hatchwell, B. J. The evolution of cooperative breeding in birds: kinship, dispersal and life
596 history. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 3217–3227 (2009).

- 597 106. Riehl, C. Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B Biol. Sci.*
598 **280**, 20132245 (2013).
- 599 107. Griesser, M. & Suzuki, T. N. Occasional cooperative breeding in birds and the robustness of
600 comparative analyses concerning the evolution of cooperative breeding. *Zool. Lett.* **2**, 7 (2016).
- 601 108. Kimball, R. T., Parker, P. G. & Bednarz, J. C. Occurrence and evolution of cooperative breeding
602 among the diurnal raptors (Accipitridae and Falconidae). *The Auk* **120**, 717–729 (2003).
- 603 109. Bebbington, K. *et al.* Joint care can outweigh costs of nonkin competition in communal
604 breeders. *Behav. Ecol.* **29**, 169–178 (2018).
- 605 110. Beauchamp, G. Do avian cooperative breeders live longer? *Proc. R. Soc. B Biol. Sci.* **281**,
606 20140844 (2014).
- 607 111. Downing, P. A., Cornwallis, C. K. & Griffin, A. S. Sex, long life and the evolutionary transition
608 to cooperative breeding in birds. *Proc. R. Soc. B Biol. Sci.* **282**, 20151663 (2015).
- 609 112. Downing, P. A., Griffin, A. S. & Cornwallis, C. K. Hard-working helpers contribute to long
610 breeder lifespans in cooperative birds. *Philos. Trans. R. Soc. B Biol. Sci.* **376**, 20190742 (2021).
- 611 113. Sosa, S. O. *et al.* Impact of Group Management and Transfer on Individual Sociality in
612 Highland Cattle (*Bos taurus*). *Front. Vet. Sci.* **6**, 183 (2019).
- 613 114. Ramos, A., Manizan, L., Rodriguez, E., Kemp, Y. J. M. & Sueur, C. The social network structure
614 of a semi-free roaming European bison herd (*Bison bonasus*). *Behav. Processes* **158**, 97–105
615 (2019).
- 616 115. Puga-Gonzales, I. *et al.* Proximate Mechanisms Underlying Primates' Complex Social
617 Networks: A Modelling and Comparative Approach. *Folia Primatol. (Basel)* **88**, 126–127 (2017).
- 618 116. Naud, A. *et al.* Relations between Spatial Distribution, Social Affiliations and Dominance
619 Hierarchy in a Semi-Free Mandrill Population. *Front. Psychol.* **7**, 612 (2016).
- 620 117. Best, E. C., Dwyer, R. G., Seddon, J. M. & Goldizen, A. W. Associations are more strongly
621 correlated with space use than kinship in female eastern grey kangaroos. *Anim. Behav.* **89**, 1–10
622 (2014).

- 623 118. Wroblewski, E. E. *et al.* Male dominance rank and reproductive success in chimpanzees, Pan
624 troglodytes schweinfurthii. *Anim. Behav.* **77**, 873–885 (2009).
- 625 119. Puga-Gonzalez, I. *et al.* Mechanisms of reciprocity and diversity in social networks: a
626 modeling and comparative approach. *Behav. Ecol.* **29**, 745–760 (2018).
- 627 120. Balasubramaniam, K. N. *et al.* Hierarchical steepness, counter-aggression, and macaque
628 social style scale. *Am. J. Primatol.* **74**, 915–925 (2012).
- 629 121. Wrangham, R. W. Evolution of social structure. in *Primate Societies* 227–239 (B.B. Smuts, D.L.
630 Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker, 1987).
- 631 122. Kappeler, P. M. & Schaik, C. P. van. Evolution of Primate Social Systems. *Int. J. Primatol.* **23**,
632 707–740 (2002).
- 633 123. Cronin, K. A., Van Leeuwen, E. J. C., Vreeman, V. & Haun, D. B. M. Population-level variability
634 in the social climates of four chimpanzee societies. *Evol. Hum. Behav.* (2014)
635 doi:10.1016/j.evolhumbehav.2014.05.004.
- 636 124. Borgeaud, C., Sosa, S., Bshary, R., Sueur, C. & van de Waal, E. Intergroup Variation of Social
637 Relationships in Wild Vervet Monkeys: A Dynamic Network Approach. *Front. Psychol.* **7**, 915
638 (2016).
- 639 125. Sueur, C. *et al.* A comparative network analysis of social style in macaques. *Anim. Behav.* **82**,
640 845–852 (2011).
- 641 126. Pasquaretta, C. *et al.* Social networks in primates: smart and tolerant species have more
642 efficient networks. *Sci. Rep.* **4**, (2014).
- 643 127. Romano, V., Shen, M., Pansanel, J., MacIntosh, A. J. & Sueur, C. Social transmission in
644 networks: global efficiency peaks with intermediate levels of modularity. *Behav. Ecol. Sociobiol.*
645 **72**, 154 (2018).
- 646 128. Pinqart, M. & Sörensen, S. Influences of socioeconomic status, social network, and
647 competence on subjective well-being in later life: a meta-analysis. *Psychol. Aging* **15**, 187–224
648 (2000).

- 649 129. Ali, T., Nilsson, C. J., Weuve, J., Rajan, K. B. & de Leon, C. F. M. Effects of social network
650 diversity on mortality, cognition and physical function in the elderly: a longitudinal analysis of the
651 Chicago Health and Aging Project (CHAP). *J Epidemiol Community Health* **72**, 990–996 (2018).
- 652 130. Kiecolt-Glaser, J. K. & Wilson, S. J. Lovesick: How couples' relationships influence health.
653 *Annu. Rev. Clin. Psychol.* **13**, 421–443 (2017).
- 654 131. Kiecolt-Glaser, J. K., Wilson, S. J. & Madison, A. Marriage and gut (microbiome) feelings:
655 tracing novel dyadic pathways to accelerated aging. *Psychosom. Med.* **81**, 704–710 (2019).
- 656 132. Robles, T. F., Slatcher, R. B., Trombello, J. M. & McGinn, M. M. Marital quality and health: a
657 meta-analytic review. *Psychol. Bull.* **140**, 140 (2014).
- 658 133. Kelley, H. H. *et al.* Analyzing close relationships. *Close Relatsh.* **20**, 67 (1983).
- 659 134. Debra J. Mashek, A. A. (editors). *Handbook of closeness and intimacy*. (Lawrence Erlbaum
660 Associates, 2004).
- 661 135. Montgomery, S. C. *et al.* Peer social network processes and adolescent health behaviors: A
662 systematic review. *Prev. Med.* **130**, 105900 (2020).
- 663 136. Fowler, J. H., Settle, J. E. & Christakis, N. A. Correlated genotypes in friendship networks.
664 *Proc. Natl. Acad. Sci.* **108**, 1993–1997 (2011).
- 665 137. Uchino, B. N. *et al.* Social relationships and health: Is feeling positive, negative, or both
666 (ambivalent) about your social ties related to telomeres? *Health Psychol.* **31**, 789 (2012).
- 667 138. Nausheen, B., Gidron, Y., Peveler, R. & Moss-Morris, R. Social support and cancer
668 progression: a systematic review. *J. Psychosom. Res.* **67**, 403–415 (2009).
- 669 139. Garipey, G., Honkaniemi, H. & Quesnel-Vallee, A. Social support and protection from
670 depression: systematic review of current findings in Western countries. *Br. J. Psychiatry* **209**,
671 284–293 (2016).
- 672 140. Lyrra, T.-M. & Heikkinen, R.-L. Perceived social support and mortality in older people. *J.*
673 *Gerontol. B. Psychol. Sci. Soc. Sci.* **61**, S147–S152 (2006).

- 674 141. Rook, K. S. Social support versus companionship: Effects on life stress, loneliness, and
675 evaluations by others. *J. Pers. Soc. Psychol.* **52**, 1132 (1987).
- 676 142. Buunk, B. P. & Verhoeven, K. Companionship and support at work: A microanalysis of the
677 stress-reducing features of social interaction. *Basic Appl. Soc. Psychol.* **12**, 243–258 (1991).
- 678 143. Akiyama, H., Antonucci, T., Takahashi, K. & Langfahl, E. S. Negative interactions in close
679 relationships across the life span. *J. Gerontol. B. Psychol. Sci. Soc. Sci.* **58**, P70–P79 (2003).
- 680 144. Rook, K. S. Emotional Health and Positive Versus Negative Social Exchanges: A Daily Diary
681 Analysis. *Appl. Dev. Sci.* **5**, 86–97 (2001).
- 682 145. van den Berg, P., Kemperman, A., De Kleijn, B. & Borgers, A. Locations that support social
683 activity participation of the aging population. *Int. J. Environ. Res. Public Health* **12**, 10432–10449
684 (2015).
- 685 146. Kestens, Y., Wasfi, R., Naud, A. & Chaix, B. “Contextualizing Context”: Reconciling
686 Environmental Exposures, Social Networks, and Location Preferences in Health Research. *Curr.*
687 *Environ. Health Rep.* **4**, 51–60 (2017).
- 688 147. Shakya, H. B., Christakis, N. A. & Fowler, J. H. Social network predictors of latrine ownership.
689 *Soc. Sci. Med.* **125**, 129–138 (2015).
- 690 148. Dekker, D. Measures of Simmelian tie strength, Simmelian brokerage, and, the Simmelianly
691 brokered. (2006).
- 692 149. Hynie, M., Crooks, V. A. & Barragan, J. Immigrant and refugee social networks: determinants
693 and consequences of social support among women newcomers to Canada. *Can. J. Nurs. Res.*
694 *Arch.* 26–47 (2011).
- 695 150. Holt-Lunstad, J., Smith, T. B., Baker, M., Harris, T. & Stephenson, D. Loneliness and Social
696 Isolation as Risk Factors for Mortality: A Meta-Analytic Review. *Perspect. Psychol. Sci.* **10**, 227–
697 237 (2015).

- 698 151. Smith, K. J., Gavey, S., Riddell, N. E., Kontari, P. & Victor, C. The association between
699 loneliness, social isolation and inflammation: A systematic review and meta-analysis. *Neurosci.*
700 *Biobehav. Rev.* **112**, 519–541 (2020).
- 701 152. Kim, D., Subramanian, S. V. & Kawachi, I. Bonding versus bridging social capital and their
702 associations with self rated health: a multilevel analysis of 40 US communities. *J. Epidemiol.*
703 *Community Health* **60**, 116–122 (2006).
- 704 153. Murayama, H. *et al.* Are neighborhood bonding and bridging social capital protective against
705 depressive mood in old age? A multilevel analysis in Japan. *Soc. Sci. Med.* **124**, 171–179 (2015).
- 706 154. Levasseur, M., Richard, L., Gauvin, L. & Raymond, É. Inventory and analysis of definitions of
707 social participation found in the aging literature: Proposed taxonomy of social activities. *Soc. Sci.*
708 *Med.* **71**, 2141–2149 (2010).
- 709 155. Wright, N. & Stickley, T. Concepts of social inclusion, exclusion and mental health: a review of
710 the international literature. *J. Psychiatr. Ment. Health Nurs.* **20**, 71–81 (2013).
- 711 156. Baron-Epel, O., Weinstein, R., Haviv-Mesika, A., Garty-Sandalon, N. & Green, M. S. Individual-
712 level analysis of social capital and health: a comparison of Arab and Jewish Israelis. *Soc. Sci. Med.*
713 **66**, 900–910 (2008).
- 714 157. Kääriäinen, J. & Lehtonen, H. The variety of social capital in welfare state regimes—a
715 comparative study of 21 countries. *Eur. Soc.* **8**, 27–57 (2006).
- 716 158. Beugelsdijk, S. & Van Schaik, T. Social capital and growth in European regions: an empirical
717 test. *Eur. J. Polit. Econ.* **21**, 301–324 (2005).
- 718 159. Christakis, N. A. & Fowler, J. H. The spread of obesity in a large social network over 32 years.
719 *N. Engl. J. Med.* **357**, 370–379 (2007).
- 720 160. Strauss, R. S. & Pollack, H. A. Social marginalization of overweight children. *Arch. Pediatr.*
721 *Adolesc. Med.* **157**, 746–752 (2003).
- 722 161. Christakis, N. A. & Fowler, J. H. The Collective Dynamics of Smoking in a Large Social Network.
723 *N. Engl. J. Med.* **358**, 2249–2258 (2008).

- 724 162. González, M. C., Herrmann, H. J., Kertész, J. & Vicsek, T. Community structure and ethnic
725 preferences in school friendship networks. *Phys. Stat. Mech. Its Appl.* **379**, 307–316 (2007).
- 726 163. Frank, K. A., Muller, C. & Mueller, A. S. The embeddedness of adolescent friendship
727 nominations: The formation of social capital in emergent network structures. *Am. J. Sociol.* **119**,
728 216–253 (2013).
- 729 164. Entwisle, B., Faust, K., Rindfuss, R. R. & Kaneda, T. Networks and contexts: Variation in the
730 structure of social ties. *Am. J. Sociol.* **112**, 1495–1533 (2007).
- 731 165. Shakya, H. B., Christakis, N. A. & Fowler, J. H. Association between social network
732 communities and health behavior: an observational sociocentric network study of latrine
733 ownership in rural India. *Am. J. Public Health* **104**, 930–937 (2014).
- 734 166. HELLERINGER, S. & KOHLER, H.-P. Sexual network structure and the spread of HIV in Africa:
735 evidence from Likoma Island, Malawi. *Aids* **21**, 2323–2332 (2007).
- 736 167. Cremer, S., Armitage, S. A. O. & Schmid-Hempel, P. Social immunity. *Curr. Biol.* **17**, R693–
737 R702 (2007).
- 738 168. Boheemen, L. A. van *et al.* Compensatory and additive helper effects in the cooperatively
739 breeding Seychelles warbler (*Acrocephalus sechellensis*). *Ecol. Evol.* **9**, 2986–2995 (2019).
- 740 169. Yang, Y. C. *et al.* Social relationships and physiological determinants of longevity across the
741 human life span. *Proc. Natl. Acad. Sci.* **113**, 578–583 (2016).
- 742 170. Umberson, D. & Karas Montez, J. Social relationships and health: A flashpoint for health
743 policy. *J. Health Soc. Behav.* **51**, S54–S66 (2010).
- 744 171. Schrock, A. E., Leard, C., Lutz, M. C., Meyer, J. S. & Gazes, R. P. Aggression and social support
745 predict long-term cortisol levels in captive tufted capuchin monkeys (*Cebus [Sapajus] apella*).
746 *Am. J. Primatol.* **81**, e23001 (2019).
- 747 172. Tiddi, B., Aureli, F. & Schino, G. Grooming up the hierarchy: The exchange of grooming and
748 rank-related benefits in a New World primate. *PLoS ONE* **7**, e36641 (2012).

- 749 173. VanderWaal, K. L., Atwill, E. R., Isbell, L. A. & McCowan, B. Linking social and pathogen
750 transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *J. Anim. Ecol.*
751 **83**, 406–414 (2014).
- 752 174. Watts, D. P. Male dominance relationships in an extremely large chimpanzee community at
753 Ngogo, Kibale National Park, Uganda. *Behaviour* **155**, 969–1009 (2018).
- 754 175. Büttner, K., Czycholl, I., Mees, K. & Krieter, J. Agonistic interactions in pigs—comparison of
755 dominance indices with parameters derived from social network analysis in three age groups.
756 *Animals* **9**, 929 (2019).
- 757 176. House, J. S., Landis, K. R. & Umberson, D. Social relationships and health. *Science* **241**, 540–
758 545 (1988).
- 759 177. Assenza, S., Gómez-Gardeñes, J. & Latora, V. Enhancement of cooperation in highly clustered
760 scale-free networks. *Phys. Rev. E* **78**, 017101 (2008).
- 761 178. Kuperman, M. N. & Risau-Gusman, S. Relationship between clustering coefficient and the
762 success of cooperation in networks. *Phys. Rev. E* **86**, 016104 (2012).
- 763 179. Kulahci, I. G. *et al.* Social networks predict selective observation and information spread in
764 ravens. *R. Soc. Open Sci.* **3**, 160256 (2016).
- 765
- 766

767 Table S1: Components of social capital according to the studied species and the level of study.

Eusocial species (e.g. ants, bees, naked mole-rats)	Variations inside a same group/colony	Variations between groups/colonies	Interspecific variations
	<p>Properties of social interactions including number and duration of interactions, type of interactions (e.g., trophallaxes⁸⁹, antenna-to-antenna, grooming), intra-caste or inter-caste interactions.</p>	<p>Properties of the colony⁹² 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 colony, including, among others, its size, the caste system specific characteristic (e.g., number of reproductive individuals, marked division of labor, short or long-lived males, worker dimorphism)⁹³⁻⁹⁶</p>
	<p>Spatial distribution of social interactions⁹⁰ according to individual mobility patterns</p>	<p>Properties of the whole system of social interactions⁵⁸ using network indicators such as community separation and its resilience.</p>	<p>Relation with other colonies including the tolerance level and belonging to supercolony⁹⁷.</p>
	<p>Individual positions within the social system including, not exclusively, individual caste (e.g., male, queen, nest worker) or centrality index⁹¹</p>		

Cooperative breeding species

Properties of social interactions including number and duration of interactions, type of interactions (e.g., grooming, aggression, reproductive behavior).^{98,99}

Properties of social relationships which may include kinship, sex, reproductive status and dominance hierarchy.¹⁰⁰

Individual positions within social structures including, not exclusively, individual status (e.g., reproductive or helpers) and its position between reproductive sub-groups.^{101–103}

Primate societies and similar mammal societies

Properties of social interactions including number and duration of interactions, type of interactions (e.g., grooming, aggression, reproductive behavior, exchange of resources)^{113–115} and their spatial distribution¹¹⁶

Properties of social relationships, including, not exclusively, kinship¹¹⁷, dominance¹¹⁸, direction and reciprocity in conflicts and resources exchange¹¹⁹.

Individual position within social structures, including, among others, centrality⁸⁵, belonging to certain subgroups and dominance¹²⁰ relative to the whole hierarchy

Properties of the colony, may include its size, the number of helpers and offspring and the system of interactions between reproductive sub-groups.¹⁰⁴

Properties of the group, including their size, and their age/sex distribution^{121,122}

Cultural variation^{123,124} including, among others, tolerance in aggression and exchange with non-kin, tool use

Properties of the interaction network, including, among other, the level of community division resulting from non-kin interactions¹²⁵.

Exchange with and tolerance of other groups (between-group competition)

Properties of cooperative breeding, including if its facultative or systematic and the level of competition for reproduction between helpers and male breeder.^{105–109}

Comparing evolutionary advantages of cooperative and not-cooperative breeding, regarding e.g. longevity, reproductive success, life history.^{110–112}

Properties of the group, including, their size, the mating system, the hierarchical structures, and affiliation between non-kin¹²⁵.

Structure of the interaction networks including their size, community structure and efficacy in exchange of information and resources^{126,127}

Humans

Properties of social relationships which may include, relation type (e.g., relatives, colleagues, friends)¹²⁸, relationship diversity¹²⁹, marital status and quality¹³⁰⁻¹³², closeness and intimacy^{133,134}, homophily^{135,136} and their perceived valence (i.e., positive, negative, ambivalent)¹³⁷.

Properties of social Interactions, which may include perceived and received support¹³⁸⁻¹⁴⁰, companionship^{141,142}, negative interactions^{143,144} and their geospatial distribution^{145,146}.

Individual position within social structures such as centrality and periphery¹⁴⁷, brokerage¹⁴⁸, and belonging to specific subgroups¹⁴⁹

Indicators of complex process such as social isolation^{150,151} bonding and bridging capital^{152,153}, social participation¹⁵⁴, social inclusion and exclusion¹⁵⁵.

International and intra-national comparison of individual-level social capital according, not exclusively, to ethnic groups¹⁵⁶, welfare regime¹⁵⁷, regional economic growth¹⁵⁸, or socio-economic status¹⁵²

Community-level social properties such as centrality^{159,160}, clustering¹⁶¹⁻¹⁶³ dyadic distances^{159,161}, social connectedness^{164,165} or components and cyclical structures¹⁶⁶

NA

768

769

770 **Table S2: Metrics from social network analysis to measure the components of social capital.** We define usual metrics used in social network analysis and
 771 give non-exhaustive example of their possible use in diverse systems to assess the components of social capital cited above in Table S1. We call network, the
 772 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
 773 individual B within a given group. The shortest path is the one that minimizes the number of necessary connections. We use the term 'resources' in a broad
 774 sense that can include, depending on the model studied: information, food, sexual partner...

Social metrics	Scale	Definition	Practical examples of the social network metrics to study social capital
degree	individual	* The number of connections (neighbors) of an individual * This metrics can be undirected or directed, in this latter case we distinguish the case where individuals <i>emit</i> interaction towards their neighbors (<i>out-degree</i>) from the ones where individuals <i>receive</i> interactions (<i>in-degree</i>).	* Studying the individual degree highlights social immunity in eusocial insects. ¹⁶⁷ * Chicks' degree in cooperative breeders is a proxy for the intensity of parental care they can get. ¹⁶⁸ * Humans live a longer and healthier life, when maintaining numerous positive social relationships. ^{169,170}
strength	individual	* The interaction number in which an individual is involved. * This metrics can be undirected or directed, in this case we distinguish the interactions <i>given</i> (<i>out-strength</i>) from the ones <i>received</i> (<i>in-strength</i>).	* The number of given and emitted aggressions between conspecifics affect the individual physiology, especially triggers oxidative stress. ¹⁷¹ * Duration and number of trophallaxes vary according to social role in black garden ants. ⁵⁸ * Lower-rank individuals may benefit from higher-rank ones' protection through an intensive grooming behavior. ¹⁷²
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. ¹⁷³
eigenvector	individual	This metrics adds the neighbor amount of an individual to the neighbor amount of those neighbors. 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. ¹⁷⁴
closeness	individual	Gives the average distance (number of connections) necessary to reach all other members of the groups. So, counterintuitively, a high closeness coefficient reflects social isolation.	* Closeness coefficients reliably predict hierarchy and dominance patterns, <i>e.g.</i> in pigs. ¹⁷⁵ * Social isolation is proved to be a major health issue in humans and non-human animals. ¹⁷⁶
modularity and clustering coefficient	network	These two metrics are based on different formula, but both assess whether individuals tend to cluster into modules characterized 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. ^{177,178}
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. ⁹¹
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. ¹⁷⁹

775