The co-evolution of longevity and social life

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Abstract

1. Living in social groups could influence the evolution of senescence and longevity by affecting key life history parameters such as extrinsic mortality and the cost of reproduction. For example, a decrease in extrinsic mortality as a result of social life is predicted to lead to the evolution of increased longevity.

2. We argue that benefits of social life in terms of increased survival are common only in species in which life in large groups is already the norm, most likely because these species have adapted to depend on social groups. By contrast, species with smaller social groups tend to show no clear association between survival and social group size.

3. This lack of a consistent benefit of social life on survival casts doubt on the idea that extended longevity should follow the evolution of sociality. In line with this, most rigorous cross-taxonomic studies failed to find an association between sociality and longevity, suggesting that a social mode of life does not systematically lead to the evolution of extended longevity.

4. The only effect of sociality on longevity that has been convincingly demonstrated is increased longevity in high-ranking individuals from co-operatively breeding vertebrates and social insects, who benefit from the protection and support of their non-breeding helpers. In contrast, helpers in these species usually do not show evidence of increased longevity, with the exception of naked mole rats where both breeders and helpers live much longer than related solitary species.

5. Where long-lived phenotypes exist in highly social species, such as social insect queens and naked mole rats, the scale of longevity increase is often striking. The means by which increased longevity is achieved are still poorly understood, but both social and physiological mechanisms are involved in reducing the burden of disease, including cancer, thus increasing the chances of

32 surviving to old age.

33 Thoughts on sociality and longevity are pervasive in human consciousness because of our strong

34 social bonds and our fear of death. Furthermore, we understand that sociality and longevity are

35 linked, because we inherently recognise the risks that social isolation poses to a long and healthy

36 life. What is less widely appreciated is that sociality and longevity may not only affect each-

37 other at the scale of an individual's life, but also throughout the evolution of species. For

38 example, because our species is both social and long-lived relative to most other mammals, it has

39 been proposed that our longevity may be due at least in part to our social mode of life (Carey &

40 Judge 2001, Hill & Kaplan 1999). This realisation has led to a wealth of theoretical and

41 empirical research to better understand the co-evolution of longevity and social life.

42 Sociality and longevity are key aspects of the life history of a species (Bourke 2007, Kirkwood

43 & Holliday 1979). Because of this, each can affect the evolution of the other either directly or

44 indirectly through the social environment, leading to the proposal of a wide range of interacting

45 and non-mutually exclusive selective forces causally linking the two. The first section of this

46 review will give a brief overview of the three main ways in which sociality may extend longevity

47 and, in turn, how longevity may promote sociality.

48 The large interspecific variation in social behaviour found in the animal kingdom, ranging from

49 simple allo-parental care to colonies of millions of cooperative individuals, provides ample

50 opportunity to test the association between longevity and social life. Within-species studies can

51 be used to understand the costs and benefits of sociality, and thus how longevity is expected to

52 evolve in a social context, while inter-specific comparisons can address whether the predicted

53 evolutionary trends are indeed observed. In the second part of this review, we draw from both

54 intra- and inter-specific studies to explore the empirical evidence for the predicted associations

55 between sociality and longevity.

56 Because longevity can be extremely plastic, with increases greater than tenfold being associated

57 with the evolution of social life (Keller & Genoud 1997), this raises the question of the

58 mechanisms regulating longevity and whether a better understanding of them could have medical

59 applications. For example, some social mammals have apparently developed effective ways of

60 evading cancer, attracting widespread attention (Edrey et al. 2011). The final part of this review

61 will therefore summarise what is known about these longevity-extending mechanisms in highly

62 social species.

1 Why should longevity be associated with sociality?

Extrinsic mortality

65 The first reason why sociality could affect longevity is that social life may reduce the rate of

66 extrinsic mortality, that is, mortality due to external factors such as disease or predators. True

67 extrinsic mortality is extremely difficult to measure because it cannot be disentangled from

68 internal factors such as frailty that increase vulnerability to external factors like predation.

69 Nevertheless, the fact that mortality never reaches zero, regardless of the amount of investment

70 into body maintenance and survival, is fundamental to the evolution of senescence. This is

71 because elevated mortality decreases average life expectancy, thus providing lower selective

72 pressure to remain fit and healthy up to an age which very few individuals reach and where a

73 substantial amount of reproduction has already been achieved (Hamilton 1966, Medawar 1952,

74 Williams 1957). It broadly follows that low extrinsic mortality should favour the evolution of

75 decreased rates of senescence (although this has been debated, see Box 1), a prediction which

76 has been largely supported by cross-species studies (Gaillard & Lemaître 2017). The age-

77 associated decline described by the term "senescence" can refer to different functions or

78 components of fitness, such as immunity, fertility and survival. Thus, all other things being

79 equal, lower extrinsic mortality leading to slower senescence in survival will also result in

80 greater longevity. Most arguments concerning ecological correlates of longevity therefore focus

81 on the consequences of those correlates on extrinsic mortality. For example, flight, fossoriality

82 and the possession of natural protective armour are predicted to lead to increased longevity

83 because they reduce predation risk (Healy et al. 2014, Williams 1957). To understand how

84 sociality affects the evolution of longevity, it is therefore crucial to understand how it affects

85 extrinsic mortality.

86 The predicted costs and benefits of sociality in terms of extrinsic mortality largely depend on the

87 nature of the social group. Groups that are little more than aggregations of individuals primarily

88 offer protection from predation by reducing the probability of being targeted by a predator

89 (Hamilton 1971). More cooperative social groups further provide benefits through improved

90 foraging efficiency and resource defence (Alexander 1974, Wrangham 1980), reducing the

91 chances of starvation. Dominant breeders will particularly benefit from cooperative social

92 groups, as the help they receive in rearing their young can reduce their energetic burden and

93 extend their life (Crick 1992). Thus, the greatest extensions to longevity should be seen in

94 breeders of species with high levels of cooperative brood care and reproductive division of

95 labour ("eusocial" species), while workers in these species, which bear the burden of work and

96 colony defence, may have substantially shorter lives. However, group living also incurs costs

97 through competition among group members and exposure to infectious diseases by social contact

98 (Alexander 1974). Thus, the balance of costs and benefits provided by group living will

99 determine its effects on longevity and the expected direction of this relationship is not clear *a*

100 *priori*.

101 **Species pace of life and life-history trade-offs**

102 The second reason why longevity might be associated with sociality is that social life may slow

103 the rate of development and delay the age of first reproduction. Because of the trade-off between

104 growth, reproduction and longevity (Lemaître et al. 2015), this slowing of the pace of life could

105 lead to increased longevity. Delayed reproduction is particularly likely to apply to cooperative

106 breeders, where young adults may become helpers while queuing for a breeding position

107 (Downing et al. 2015), but could also apply in dense colonies where breeding opportunities are

108 limited (Møller 2006). Importantly, the slowing of the pace of life is intrinsically linked to a

109 reduction in extrinsic mortality, since delaying maturity is not a viable strategy if high mortality

110 rates prevent most individuals from reaching the age of reproduction. Another process affecting

111 the trade-off between reproduction and longevity may apply in breeders of cooperative breeding

112 species, where the energetic allocation needed for reproduction is reduced because of the work

113 provided by helpers (Berger et al. 2015, Berger et al. 2018). Breeders are then able to allocate

114 more resources to survival and body maintenance, thereby promoting their longevity.

Kin selection

116 The third reason why longevity may be associated with sociality is that sociality is often

117 associated with preferential interactions between kin (Bourke 2007). As a result, life history

118 evolution will be influenced by inclusive fitness effects, as the length of an individual's life may

119 positively or negatively affect the fitness of its relatives, creating additional selective pressures

120 on longevity (Bourke 2007). For example, in the case of parental care, the dependence of

121 offspring on their parents may create pressures to extend parental life to ensure offspring survival

122 (Pavard et al. 2007), and will shape the age-dependent mortality pattern (Lee 2003).

123 Kin selection pressures may also lead to reduced longevity of workers in eusocial species

124 because workers obtain inclusive fitness by helping to raise the brood of relatives without having

125 to wait to reach reproductive maturity. This means that workers begin to accrue inclusive fitness

126 (through helping) at a younger age than queens or individuals in solitary species. Since the age at

127 which individuals begin to accrue fitness is theoretically linked to the start of senescence

128 (Hamilton 1966), helping at a young age could lead to a reduction in longevity (Alexander et al.

129 1991, Bourke 2007). Effectively, the early accrual of inclusive fitness accelerates the workers'

130 pace of life.

7

Longevity may promote sociality

While sociality is expected to influence the evolution of longevity for the reasons presented above, it is also possible that variation in longevity can affect the evolution of sociality (Ross et al. 2015). This is because cooperation is most likely to occur between kin, and kin are more likely to interact in a context of extended parental care, particularly when overlapping adult generations allow parents and their adult offspring to co-habit (Carey 2001). Extended parental care and overlapping adult generations require long-lived parents, and longevity therefore creates more opportunities for cooperative interactions between kin. Furthermore, in habitats where breeding sites become available only after the death of existing breeders, extended longevity may lead to higher population density and saturation of breeding opportunities, further selecting for young adults to stay in their parental nest and care for their siblings (Arnold & Owens 1998).

The evolutionary processes described in this section are likely to interact in complex ways (Fig. 1), and the reciprocal causality between longevity and sociality could create a self-reinforcing cycle whereby longevity promotes sociality, which in turn promotes further increases in longevity (Carey & Judge 2001). For example, sociality could reduce extrinsic mortality and extend life, leading to increased overlap of generations and higher levels of parental care, which could then favour the evolution of delayed reproduction, a slower pace of life and further delay of senescence. These various causal relationships between longevity and sociality complicate analyses of the influence of sociality on longevity, requiring to either disentangle the direction of causality or critically evaluate the most likely interpretation where a significant correlation is found. Since it is rarely possible to distinguish between the different possible causal relationships, in Section 2 we will focus on two main questions. Firstly, whether there is any evidence within species that extrinsic mortality is reduced by social life, either in terms of group size or social connectedness. Second, whether there is evidence at the inter-specific level that sociality influences the evolution of longevity.

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157 **The concept that increased extrinsic mortality should necessarily lead to faster senescence**
158 **has been the subject of valid criticisms (Abrams 1993, Moorad et al. 2019). The argument is**
159 **that increased extrinsic mortality will not only reduce survival, but also reduce population**
160 **growth, which has an opposite effect on the evolution of senescence and cancels out the**
161 **effect of reduced survival. As shown by Abrams (1993), one way in which increased**
162 **extrinsic mortality can occur without affecting population growth is if elevated death rate**
163 **is accompanied by a higher rate of fertility (or recruitment of adults into the breeding**
164 **population). Reduced extrinsic mortality in social species could therefore lead to a slowing**
165 **of senescence if the developmental period is extended, or if fertility is reduced compared to**
166 **solitary species. A special case applies to cooperative breeders where dominant breeders**
167 **but not subordinate helpers have reduced extrinsic mortality. In this case, the effect of**
168 **mortality on the growth rate of the "population" of breeders should be balanced by the**
169 **rate of recruitment to the dominant position, rather than by the overall fertility rate. For**
170 **example, in a system where breeders are replaced after their death, the breeder**
171 **recruitment rate is effectively equal to the breeder death rate, and thus a reduction in**
172 **extrinsic breeder mortality is compensated by reduced recruitment. This could allow the**
173 **evolution of a plastic system of reduced senescence for individuals attaining the breeding**
174 **position. In species such as ants and honeybees, where reproductive roles are determined**
175 **during development, the recruitment rate of queens is low compared to workers due to**
176 **fewer brood developing as queens and / or a high death rate of queens at the colony**
177 **founding stage. This means that the low extrinsic mortality of established queens does not**
178 **translate to a higher growth rate in the "population" of queens compared to workers. Thus,**
179 **the lower extrinsic mortality of queens could create selective pressure for their extended**
180 **longevity.**

181 ## 2 Is longevity associated with sociality?

182 **Intraspecific studies of sociality and survival**

183 As we have seen, delayed senescence and extended longevity in social species could evolve if

184 social life leads to reduced extrinsic mortality. An important question to address is therefore

185 whether individuals in larger groups or with more social partners do indeed live longer than more

186 solitary individuals. Several studies have investigated how intraspecific variation in longevity is

187   associated with various measures of sociality, such as the size of the social group or the number

188   of group members with which individuals interact. Overall, these studies found benefits of

189   increased group size on survival in species living in relatively large groups, suggesting that

190   sociality may be primarily important for longevity in species that have already adopted a social

191   mode of life. In our own species, there is a strong association between sociality and the rate of

192   survival that is consistent across age and gender (Holt-Lunstad et al. 2010), and social

193   integration has been shown to be associated with a wide range of health benefits such as reduced

194   obesity, hypertension and inflammation (Yang et al. 2016), as well as improved mental well-

195   being (Kawachi & Berkman 2001). Much like the dependence on parental care that has evolved

196   in many species, we have evolved to become partly dependent on the social networks that are

197   typically part of our environment.

198   A similar picture emerges from studies in insects and vertebrates, where species living in

199   relatively large groups are typically characterized by a positive association between the size of

200   the social group and either longevity or adult mortality (Supplementary Table 1). In carpenter

201   ant*s* and the termite *Nasutitermes aquilinus*, workers isolated from their colonies survive longer

202   when kept together in larger numbers (Koto et al. 2015, Miramontes & DeSouza 1996). In rhesus

203   macaques, which live in large groups of dozens or hundreds of individuals, young females with

204   larger family social networks have higher survival rates than those with smaller networks (Brent

205   et al. 2017). Similarly, in a group of chacma baboons with a mean group size of 27 over the study

206   period, stronger and more stable relationships were associated with greater female longevity

207   (Silk et al. 2010), and in yellow baboons (where the mean group size has been reported as 39

208   individuals, Samuels & Altmann 1991), social connectedness was positively associated with

209   survival (Archie et al. 2014). In a population of bighorn sheep, with mean group sizes of 21

210   females or 19 males, social network centrality (a measure of the number of social connections)

211   was positively correlated with survival (Vander Wal et al. 2015). In killer whales, measures of

212   social network centrality were also positively correlated with survival in males, but not in

213   females (Ellis et al. 2017). The study was in a socially inter-connected population of 71 - 98

214   individuals, which formed temporary and changing groups with a mean size of 2.5. In blue

215   monkeys, where mean group size was around 14, female survival was higher in individuals

216   whose social bonds were weak but consistent between years, emphasising the importance of

217   stability in an individual's social network (Thompson & Cords 2018). Group size is positively

218   correlated with survival in meerkats, where the median group size was 7-11 individuals (Clutton-

219   Brock et al. 1999), and dwarf mongooses, where the mean group size was 9 individuals (Rood

220   1990). An experiment releasing prairie dogs in groups of 10 to 60 individuals found that survival

221   was higher in larger groups, although only in the first few months after release (Robinette et al.

222   1995). In birds, positive effects of group size on survival have been found in lesser kestrels,

223   where group size ranged from one to 43 breeding pairs (Serrano et al. 2005), cliff swallows,

224   where the mean colony size was 363 (Brown & Brown 2004) and weaver birds, where colony

225   sizes range from 10 to 200 individuals (Brown et al. 2003). The positive effects of sociality on

226   longevity in species with large social groups may be a result of these species having adapted to

227   life in social groups and thus requiring social interactions as part of their optimal environment.

228   In contrast, studies that have found little association between group size and longevity have

229   tended to be in species with smaller groups than those described above, perhaps because these

230   species are less dependent on social groups for survival. There was no association between

231   mortality and group size in degus (Hayes et al. 2009), African wild dogs (Gusset & Macdonald

232   2010) and Pallas's mastiff bats (Gager et al. 2016), three species with a mean group size of 6-8,

233   and there was a negative association with group size in Seychelles Warblers, where group sizes

234   ranged from 1 to 6 (Brouwer et al. 2006). In a study of social networks in yellow-bellied

235   marmots (mean group size of 6.4), five of the 11 studied measures of sociality were negatively

236   correlated with longevity, while none were positively correlated (Blumstein et al. 2018). Rock

237   hyraxes provide a slight exception to the trend, with longevity being negatively correlated with

238   group size and uncorrelated with an individual's position in the social network (Barocas et al.

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239 2011), yet the mean group size of 14 is in the range of those found in the species where sociality

240 and longevity are correlated.

241 The 20 studies presented above do not provide a sufficiently large and uniform dataset (in terms

242 of dependent and independent variables) for rigorous statistical testing. However, a crude non-

243 parametric test does reveal that species in which a positive correlation between sociality and

244 survival was found tend to live in larger groups than species where this was not the case

245 (Wilcoxon rank sum test, $W = 82$, $P = 0.001$, see Supplementary Table S1 for details of test).

246 There are also several examples of cooperative-breeding species where dominant breeders live

247 longer or senesce more slowly in the presence of helpers at the nest (Berger et al. 2018, Crick

248 1992, Paquet et al. 2015). However, where only the length of the breeders' life is considered, it

249 may not be social life *per se* that increases longevity, but rather the presence at the top of the

250 social hierarchy.

251 **Inter-specific studies of sociality and longevity**

252 Testing whether sociality affects longevity over evolutionary time is possible by conducting

253 interspecific comparisons (Supplementary Table 2), ideally accounting for phylogenetic non-

254 independence of species and controlling for confounding factors that are known to affect

255 longevity (e.g., body size, which is associated with longevity following an allometric

256 relationship, Peters 1983).

257 A difficulty of comparative studies is that there is no consensus on how the longevity and the

258 level of sociality of a species should be defined. To fully account for the age-dependence in

259 survival rates, the best metrics for longevity are those based on demographic data, such as the

260 rate or age of onset of senescence (Jones et al. 2008), but such data are often unavailable as they

261 require detailed records from a large number of individuals in a population. Many studies have

262 used adult mortality rates as a proxy, but this measure conflates intrinsic and extrinsic mortality,

263 meaning that sociality might be associated with reduced mortality because of direct protection

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264   from predators rather than through its effects on senescence. An alternative measure of longevity

265   to the rate of mortality is the maximum recorded lifespan, which intuitively should indicate how

266   long an individual can live in ideal conditions. The main drawback of this measure is that it is

267   correlated with sampling effort, since a larger dataset is likely to contain a larger maximum

268   recorded lifespan (Moorad et al. 2012), making it important for studies of maximum lifespan to

269   control for sampling effort.

270   One possible measure of sociality is group size. While this is relatively crude, it is nevertheless

271   an informative measure because solitary species are less social than species forming breeding

272   pairs, which are less social than species living in groups. Also, within a given social mode of life,

273   the size of the social group is likely to indicate the level of dependence on sociality. For example,

274   an ant species with a colony size of several thousand workers is likely to be more reliant on these

275   helpers than a species with just a handful of helpers.

276   In mammals and birds, there is little evidence that larger group size leads to the evolution of

277   longer life, with only one taxon, out of the seven for which we found information, showing a

278   positive association between group size and longevity. While a study of 100 bovid species found

279   a positive correlation between longevity and group size (Bro-Jørgensen 2012), there was no

280   significant correlation in bats (Wilkinson & South 2002), primates or rodents (Kamilar et al.

281   2010). Moreover, there was a negative association between longevity and group size in

282   artiodactyls (Kamilar et al. 2010). Overall, an analysis combining 253 species from multiple

283   order of mammals, controlling for phylogeny and other factors such as body size, found that

284   there was overall no effect of group size on longevity (Kamilar et al. 2010). Similarly, in birds, a

285   study controlling for body size, phylogeny and sampling effort, found no effect of colony size on

286   maximum longevity (Møller 2006).

287   Another measure of the level of sociality is to categorise species according to their social mode

288   of life, usually comparing cooperative breeders, where some individuals temporarily or

289 permanently forgo reproduction to help raise the brood of others, with other species such as

290 colonial or solitary breeders. The most extreme levels of cooperative brood care and reproductive

291 division of labour, including permanently sterile helpers, are found among eusocial insects,

292 where the queens can be extremely long-lived (up to 30 years in some species, Keller 1998).

293 Early work showed that the evolution of eusociality in insects was accompanied by a 100-fold

294 increase in lifespan (Keller & Genoud 1997). This increase specifically relates to social insect

295 queens, since workers have considerably shorter lives. In honeybees, for example, while the

296 queen can live several years, workers live only a few weeks (or a few months when over-

297 wintering), a value much more in line with the longevity of solitary species. This difference

298 between queens and workers makes it likely that eusociality promoted queen longevity rather

299 than the converse, since the social differentiation between queens and worker must first exist

300 before longevity differences can appear between them. The effects of eusociality on worker

301 longevity have never been formally studied, but a cross-species study of queen and worker ants

302 revealed no correlation between colony size and worker lifespan, while the lifespan of queens

303 increased slightly with colony size (Kramer & Schaible 2013). It would be interesting to

304 compare the longevity of social insect workers to solitary species while controlling statistically

305 for the fossorial mode of life in ants and termites, since fossoriality itself could be associated

306 with increased longevity due to increased protection from predators. In the meantime, it appears

307 that the longevity benefits of eusociality primarily apply to queens, rather than to eusocial

308 species as a whole.

309 In wasps, few data on longevity are available, making rigorous tests difficult. One study

310 investigated the association of sociality with wasp longevity and found that, as in ants,

311 honeybees and termites, queens live longer than workers (Toth et al. 2016). A limitation of this

312 study, however, is that many estimates of wasp longevity come from the field. Because workers

313 spend much more time foraging than queens, they are exposed to higher levels of extrinsic

314 mortality, which confounds measurements of longevity. Notwithstanding this limitation, worker

315 lifespan was found to decrease with colony size (Toth et al. 2016), again suggesting that sociality

316 selectively favours increased queen longevity rather than the longevity of workers. To our

317 knowledge, there is not yet any study on the association between level of sociality and longevity

318 in bees, which would be an interesting group given their extensive variation in levels of sociality.

319 However, as with wasps, the difficulty of keeping most species in captivity makes it difficult to

320 obtain estimates of longevity unaffected by predation.

321 In birds, there have been conflicting results, but the most rigorous studies indicate a lack of

322 association between longevity and sociality. Two phylogenetically-controlled studies have found

323 a negative association between the extent of cooperative breeding and mortality, initially

324 suggesting that sociality may promote longevity (Arnold & Owens 1998, Downing et al. 2015).

325 However, both studies looked at adult mortality / survival rates, rather than maximum longevity.

326 Furthermore, both studies found evidence that it was high survival that favoured cooperative

327 breeding, rather than cooperative breeding leading to increased survival. The study by Arnold &

328 Owens (1998) found that families with high proportions of cooperative species had low mortality

329 rates even in non-cooperative species, suggesting that low rates of mortality in a family increases

330 the chances that a species in that family adopts a social mode of life. Similarly, the study by

331 Downing et al. (2015) mapped cooperative breeding and survival onto a phylogeny and found

332 that cooperative breeding was more likely to evolve in ancestral species with high survival. A

333 study using a broader definition of sociality, including both co-operative breeding and colonial

334 nesting, and controlling for body size, found that social species had higher maximum longevity

335 than non-social species (Wasser & Sherman 2010), but this study did not control for sampling

336 effort and only partly for phylogeny by performing an analysis at the family-level (which does

337 not control for phylogenetic relationships between families). In contrast, a study in North

338 American birds that controlled for phylogeny, body size and sampling effort found no effect of

339 cooperative breeding on maximum longevity (Blumstein & Møller 2008). Furthermore,

340 illustrating the importance of distinguishing between survival and maximum lifespan, a study of

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341 cooperative / non-cooperative species pairs, which controlled for body size, found that while

342 annual survival was higher in cooperative than non-cooperative breeders, there was no difference

343 in maximum lifespan (Beauchamp 2014). Taken together, the evidence therefore points to there

344 being no effect of sociality on longevity in birds.

345 Interestingly, as with social insects, there does seem to be a positive association in mammals

346 between a eusocial / cooperative breeding mode of life and the maximum longevity that a species

347 can achieve. An analysis of 440 ground-dwelling mammals, of which 17 were classified as

348 eusocial cooperative breeders, showed that eusocial species have a higher maximum lifespan

349 than non-eusocial species (Healy 2015, Williams & Shattuck 2015). The highest level of

350 sociality in mammals occurs in the eusocial mole rats which, like social insects, exhibit large

351 differences in longevity between reproductives and non-reproductives (Dammann et al. 2011,

352 Dammann & Burda 2006, Schmidt et al. 2013), and the same may be true of other eusocial

353 mammals. Records of maximum lifespan in eusocial mammals are therefore likely to reflect the

354 longevity of reproductives rather than helpers and, as with insects, it remains to be tested

355 whether non-reproductive helpers live longer than individuals from non-eusocial species.

356 In both insects and mammals, therefore, it may not be sociality itself that is important in

357 promoting longevity, but rather the position at the top of the social hierarchy, because

358 reproductively dominant individuals receive care from others and are protected from many

359 causes of extrinsic mortality. Cooperative brood care and reproductive division of labour

360 together create a context in which the brunt of predation and disease is borne by a sub-group of

361 individuals, freeing the reproductive caste from the selective constraints on longevity imposed by

362 extrinsic mortality. Alternatively, a fundamental difference in helper longevity may exist between

363 taxa such as ants, where helpers are obligately sterile, and cooperatively breeding birds and

364 mammals, where helpers may attain a breeding position. In the former case, helping represents

365 the only form of fitness that workers can obtain, and they begin helping as soon as they emerge

366 as adults, thus reproduction is in no way delayed (Bourke 2007). In the latter case, delayed

367 opportunity for reproduction may instead select for increased longevity. In order to better

368 understand these two effects, studies should consider the longevity of helpers and account for the

369 likelihood for helpers to become breeders.

370 One salient exception to the longevity difference between workers and reproductives comes from

371 the naked mole rat, where the workers also have extremely high longevity in captivity, similar to

372 that of reproductives (Buffenstein 2008). Whether extended longevity of both queens and

373 workers in this species is due to eusociality is difficult to determine. The fossorial mode of life of

374 naked mole rats may also contribute to their long lives, although across mammals there is no

375 effect of fossoriality on longevity once sociality is accounted for (Healy 2015). Whatever its

376 evolutionary cause, the striking longevity of eusocial reproductives, and of naked mole rats,

377 provides valuable opportunities to study the physiological mechanisms of life extension (Edrey

378 et al. 2011, Lucas & Keller 2017).

379 3   How is longevity extended in social species?

380 The difference in longevity between reproductives and workers in most eusocial species makes

381 them powerful study organisms for ageing research because they provide contrasting phenotypes

382 that do not differ genetically. For this reason, studies in eusocial insects typically compare

383 queens and workers to identify key features of their physiology that could explain their different

384 longevities. Because naked mole rats do not show differences in longevity between queens and

385 workers, they are instead compared with mice, which are similar-sized rodents with markedly

386 shorter lives (whereas naked mole rats live up to 30 years (Edrey et al. 2011), the maximum

387 recorded lifespan of mice is only around four years (Miller et al. 2002)).

388 Senescence

389 In species where reduced extrinsic mortality selects for delayed senescence, this could be

390 achieved by greater allocation of resources into physiological processes that slow the age-

391 associated accumulation of physiological damage. The mechanisms by which senescence is

392 delayed in long-lived social organisms have so far proven difficult to determine. A prominent

393 proximate theory proposes that ageing is the result of accumulation of unrepaired molecular

394 damage, caused in part by oxidative stress (Finkel & Holbrook 2000). If such damage is a

395 primary cause of ageing, then mechanisms should be in place that slow its accumulation in long-

396 lived organisms. Surprisingly, few studies have investigated whether oxidative damage

397 accumulation is lower in queens than workers. One study in the termite *Reticulitermes speratus*

398 found that queens have less oxidative damage than workers (Tasaki et al. 2018). However,

399 damage was measured in whole bodies and therefore did not account for the drastically different

400 body plans of queens and workers. Most of the tissue in termite queens consists of the abdomen,

401 full of egg-laying organs, while workers have much smaller abdomens and are reproductively

402 inactive. If the germline contains less oxidative damage and higher expression of maintenance

403 genes than the soma (a likely possibility if eggs need to be free of oxidative damage), this would

404 confound any whole-body comparison between queens and workers. Similarly, markers of

405 oxidative damage were lower in reproductive Damaraland mole rats compared to non-

406 reproductives (Schmidt et al. 2014), but this study did not control for possible age differences

407 between reproductives and non-reproductives.

408 A tissue- and age-controlled study in the ant *Lasius niger* found that while double-stranded

409 breaks in DNA increased with age, this increase was similar in both queens and workers (Lucas

410 et al. 2017). Similarly, levels of oxidative damage seem higher in naked mole rats than mice

411 (Andziak & Buffenstein 2006, Andziak et al. 2006), showing that longer-lived phenotypes do not

412 have reduced levels of damage. However, interestingly, naked mole rats show slower increases in

413 oxidative protein damage with age compared to mice (Pérez et al. 2009). Slower increase of

414 damage with age may be the result of delayed ageing, rather than its cause, but naked mole rats

415 also show much higher rates of fidelity during protein translation than do mice (Azpurua et al.

416 2013), suggesting that they may maintain consistently high levels of protein homeostasis and that

417   this may partly explain their longer lives.

418   Several studies have also investigated the role of pathways preventing or repairing molecular

419   damage. Potentially important pathways include ones which can repair damage when it occurs,

420   such as those involved in DNA repair (Lombard et al. 2005). DNA repair gene expression is

421   higher in queens than workers in *L. niger* (Lucas et al. 2016) and in naked mole rats compared to

422   mice (MacRae et al. 2015), indicating an association between DNA repair and longevity.

423   However, this up-regulation of DNA repair pathways contrasts with the lack of difference in

424   DNA damage accumulation between queen and worker described above. One possibility is that

425   DNA damage does accumulate differently in queens and workers, but not in the form of double-

426   stranded breaks. Nucleotide substitutions, leading to protein sequence errors, may be more

427   crucial, and avoidance of this type of damage would provide an interesting parallel to the

428   increased translation fidelity identified in naked mole rats (Azpurua et al. 2013).

429   Another class of damage prevention gene which has been extensively studied is antioxidant

430   enzymes such as Superoxide Dismutase (SOD) and catalase (CAT), which can remove reactive

431   oxygen species and prevent molecular damage. It is however difficult to say whether anti-

432   oxidants are involved in increased longevity in eusocial species, as results from various species

433   have been equivocal. In *L. niger*, an early study found no difference in expression of SOD1

434   between queens and workers (Parker et al. 2004), but it has recently been shown that another

435   SOD enzyme, SOD3, has the most significantly queen-biased expression in the entire brain

436   transcriptome (Lucas & Keller 2018). In the ant *Harpegnathos saltator*, SOD and glutathione

437   peroxidase activity do not differ between queens and workers, while catalase activity is lower in

438   queens (Schneider et al. 2011), although this study did not control for age. In honeybees,

439   antioxidant genes are up-regulated in queens compared to workers in 1-day-old individuals, but

440   the opposite is true in 1-month old individuals (Corona et al. 2005). Finally, in naked mole rats,

441   the difference in anti-oxidant activity relative to mice was highly dependent on the anti-oxidant

442   being studied, with SOD activity being higher in naked mole rats than in mice, but glutathione

443   peroxidase activity being nearly 100-fold lower in naked mole rats (Andziak et al. 2005).

Immunity

445   As part of extending their longevity, organisms need to reduce their burden of disease. This can

446   be achieved directly by up-regulating immune processes, or indirectly by delaying senescence to

447   avoid the deterioration of immune functions with age (Doums et al. 2002, Simon et al. 2015).

448   Additionally, disease avoidance can be achieved either behaviourally by avoiding contact with

449   infectious agents, or physiologically by boosting the immune system to prevent the infection

450   from taking hold. Social insect queens employ both physiological and behavioural mechanisms

451   to protect themselves from disease.

452   For queens living in enclosed nests, behavioural resistance is achieved by remaining in the nest,

453   where infectious agents can only reach her via her workers. The social structure of ant and

454   honeybee colonies minimises queen exposure to pathogens, since queens are largely isolated

455   from direct contact with the workers that are most likely to be infectious (Stroeymeyt et al. 2014,

456   Stroeymeyt et al. 2018). Disease progression through the ant colony is also minimised through

457   sanitary behaviours such as grooming, cleaning, and the ejection of sick individuals, ensuring

458   that diseases rarely persist in the nest long enough to reach the queen (Cremer et al. 2018).

459   Several studies also revealed that queens up-regulate genes involved in immunity pathways to

460   further protect themselves against disease. A crucial facet of insect immunity is the melanisation

461   response, activated by the enzyme phenoloxidase (PO) (González-Santoyo & Córdoba-Aguilar

462   2012), the molecular pre-cursor of which is pro-phenoloxidase (PPO). Social insect queens up-

463   regulate the melanisation pathway compared to workers. Queen expression of PPO is higher than

464   workers in *L. niger* (Lucas & Keller 2018) and higher than in the very short-lived males in the

465   ant *Formica exsecta* (Stucki et al. 2017), while PO activity is higher in queens than workers in

466   honeybees (Schmid et al. 2008). More broadly, a transcriptome-wide study of queen and worker

467   gene expression in *L. niger* revealed an enrichment of immune genes among genes that are

468 queen-biased in 1-day-old individuals (an age at which queens do not yet head a colony and thus

469 may not benefit from social immunity any more than workers do, Lucas & Keller 2018).

Cancer

471 One remarkable finding in ageing studies on naked mole rats is that they suffer almost negligible

472 rates of cancer (Buffenstein 2008, Taylor et al. 2017). Cancer is particularly important in the

473 context of the evolution of extended longevity because it is an age-related pathology and is thus

474 directly associated with senescence (Lemaître et al., this issue). Long life therefore requires

475 delay or reduction of cancer incidence alongside the avoidance of other symptoms of ageing. The

476 cellular mechanisms underlying resistance of naked mole rats to one of the most pervasive

477 causes of mortality in modern day humans has yet to be fully elucidated, but promising inroads

478 have been made in recent years. A key observation has been that, even in the presence of

479 oncogenic mutations, naked mole rat fibroblasts are less likely than those of mice to develop

480 tumours (Liang et al. 2010, Miyawaki et al. 2016), due at least in part to their tendency to arrest

481 duplication at lower densities than in mice (Seluanov et al. 2009). This inhibition of cell division

482 is caused by the production of extremely high-molecular-mass hyaluronan, inducing the cyclin-

483 dependent kinase inhibitor p16, which in turn arrests the cell cycle by acting on the p53 and pRb

484 tumour suppressor pathways (Seluanov et al. 2009, Tian et al. 2013). The striking differences

485 between naked mole rats and mice in tumour formation may provide a good opportunity to better

486 understand the pathways regulating cancer.

Direct association between accelerated development and longevity

488 The possibility that longevity may be extended in social species as a result of reduced pace of

489 life and a resulting slowing of development presents an intriguing parallel with another theory of

490 ageing. The hyperfunction theory suggests that senescence is a direct result of processes involved

491 in growth and development to reproductive maturity, which then continue unchecked in later life,

492 causing harm (Blagosklonny 2012, Gems & Partridge 2013). To our knowledge, this theory has

not been explicitly tested in eusocial species. Distinguishing between this possibility and, for example, senescence caused by the accumulation of molecular damage, requires identifying the changes that cause the deterioration of old individuals to establish whether these changes are inherently deleterious (supporting the damage accumulation theory) or necessary in early life but allowed to continue beyond healthy levels (supporting the hyperfunction theory).

4 Conclusion

Overall, there is currently little evidence that sociality increases survival or longevity as a general rule. Intra-specific studies only reveal a correlation between survival and social group size in species that have already adapted to life in large groups, and inter-specific studies to date suggest that social life promotes the evolution of extended longevity only for the few individuals that benefit from the protection and support of others. Further research should seek to establish whether increased longevity is found also in helpers of eusocial species, and whether this differs between species with facultative and obligate helpers. Given the confounding factor of possibly heightened exposure to predation and disease that workers face compared to solitary species, such studies will ideally use data obtained in laboratory conditions. Where this is not possible, data on the maximum lifespan of helpers in the wild (i.e., excluding breeders from the data) could be used instead.

More research is also needed to understand whether living in groups provides survival benefits in species that facultatively live in groups, or that live in small groups, to establish the contexts in which social life increases survival. Such data would allow a more rigorous statistical analysis that the one we were able to perform here, controlling for phylogeny and other confounding factors, and could highlight the ecological and life-history factors that make living in groups valuable in terms of greater survival.

The physiological mechanisms that underlie the striking longevity of reproductive individuals in eusocial species remain poorly understood, despite important progress in understanding how

518 these long-lived phenotypes modulate physiological deterioration and disease. While the

519 selective pressure to extend longevity is similar across taxa as distant as ants and naked mole

520 rats, the way in which this extension is achieved is likely to differ, as the physiological

521 challenges to be overcome (such as cancer) will vary. Particularly in insects, very little is still

522 known about the pathologies that cause death in aged individuals, both workers and

523 reproductives, and this should be established before the physiological failures that cause these

524 pathologies can be fully understood. Such studies will provide valuable insights into the

525 mechanisms of ageing and the means by which they can be avoided.

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Author contributions

532 ERL and LK wrote the manuscript.

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840 Figure legends

Figure 1: Primary ways in which sociality influences the evolution of longevity and vice versa. + indicates a promoting effect and – indicates a suppressing effect.