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Ageing red deer alter their spatial behaviour and become less social

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Abstract

Social relationships are important to many aspects of animals' lives, and an individual's connections may change over the course of their lifespan. Currently, it is unclear whether social connectedness declines within individuals as they age, and what the underlying mechanisms might be, so the role of age in structuring animal social systems remains unresolved, particularly in non-primates. Here, we describe senescent declines in social connectedness using 46 years of data in a wild, individually monitored population of a long-lived mammal (European red deer, *Cervus elaphus*). Applying a series of spatial and social network analyses, we demonstrate that these declines occur due to within-individual changes in social behaviour, with correlated changes in spatial behaviour (smaller home ranges and movements to lower-density, lower-quality areas). These findings demonstrate that within-individual socio-spatial behavioural changes can lead older animals in fission-fusion societies to become less socially connected, shedding light on the ecological and evolutionary processes structuring wild animal populations.

Introduction

Identifying the drivers of a wild animal's social connectedness is important for understanding diverse processes like pathogen transmission¹⁻³, information acquisition^{4,5}, and fitness^{6,7}. In particular, individual ageing provokes broad phenotypic changes, and is therefore likely to impact sociality through a range of mechanisms⁸ (Table 1). Despite growing knowledge concerning senescent changes in wild animals^{9,10}, including several examples of senescing behavioural traits¹¹⁻¹³, relatively little is yet known about the mechanisms underlying age-related declines in sociality ("social senescence"). In recent years, the popularity of social network analysis has facilitated a profound growth in our knowledge of the ecology and evolution of sociality in wild animals^{14,15}. Similarly, a recent deeper understanding of senescence in the wild has allowed researchers to identify within-individual declines separate from other demographic processes^{9,10}. Combining these two knowledge bases (social networks and senescence in the wild) could lend useful insights into the role of ageing in shaping animal behaviour and structuring wild animal societies, thus informing a wide range of ecological and evolutionary phenomena¹⁶.

Social senescence might occur for many reasons, ranging from individual- to population-level in scale (Table 1)¹⁶. At the individual level, physiological changes may render older individuals less competitive¹⁷; they may therefore avoid associating with (younger) conspecifics to avoid being

42 outcompeted, or they may be actively excluded. Similarly, ageing individuals may show increased
43 "social selectivity," replacing disadvantageous or aggressive interactions over the course of their lives
44 with fewer, more positive interactions¹². In humans, age-related physiological declines (and resulting
45 healthcare requirements) are associated with friends being replaced with family members in the
46 ageing individual's social network¹⁸. Alternatively, rather than being driven by physiological decline,
47 such changes could be driven by changing motivations with age – for example, where sociality is
48 beneficial in earlier life but not in old age^{19–21}.

49 In species with relatively fluid social systems, an individual's observed sociality can be influenced by
50 its movement within its environment; in such systems, age-related changes in spatial behaviours
51 could be associated with concurrent changes in observed social connectedness, without actually being
52 driven by a reduction in social behaviour *per se*^{14,22}. As such, providing evidence for social senescence
53 may require demonstrating that the observed changes are robust to changes in spatial behaviour. For
54 example, if older individuals have smaller home ranges, they will likely also make fewer unique
55 contacts²². Further, ageing individuals may select less desired habitats or prefer areas that other
56 individuals tend to avoid (and which therefore host lower conspecific densities), both of which will
57 likewise reduce social connections^{3,14,23}. The relevance of each of these processes will likely depend
58 on the social system of the animal in question: for example, in species with highly stable social
59 groups that move and forage together, it may be unlikely that age-related changes in spatial
60 behaviours underlie changes in sociality.

61 Notably, observed age-related patterns may not originate from within-individual changes: if certain
62 individuals have higher mortality rates than others, then an apparent age-related pattern might
63 emerge at the population level (i.e., "selective disappearance")^{9,10}. For example, if more social
64 individuals are more likely to die because of greater levels of competition, a population-level pattern
65 of decreasing sociality with age would emerge without requiring any within-individual decline in
66 sociality. Identifying and differentiating selective disappearance from within-individual senescence
67 requires longitudinal analyses following known individuals^{9,10}. Similarly, because an animal's observed
68 sociality depends on surrounding population structure^{22,24,25}, demographic changes could produce
69 apparent age-related social declines. For example, if an animal forms relationships when it is young
70 which are not replaced when those contacts die^{26,27}, then older animals will be less socially connected
71 as a result. Social connectedness has recently been shown to correlate with age in chimpanzees,
72 macaques, ibex, and marmots^{12,28–31}, but the relative roles of these spatial, demographic, and within-
73 individual drivers have yet to be investigated. Untangling these processes could shed a light on the
74 relative importance of within-individual age-related behavioural changes (compared to physiological
75 or demographic processes) in determining population structure in wild animals. Ultimately, doing so
76 will help to inform the role that ageing individuals play in a system's ecology through processes like
77 pathogen transmission, cooperation, or competition with its associates.

78 We investigated age-related declines in social behaviour using a wild, long-term study population of
79 individually monitored red deer (*Cervus elaphus*)³². The deer, which have been studied since 1973,
80 inhabit a ~12km² area in the north block of the Isle of Rum, Scotland. They are individually followed
81 from birth, and exhibit a fission-fusion social system characterised by substantial mixing but with
82 repeatable social phenotypes based on spatiotemporal grouping patterns²². The deer are well-suited
83 to studying social senescence: they experience strong age-related declines in ranging behaviour¹¹ and
84 fitness³³, and they have well-characterised spatially structured social networks structured by a
85 combination of spatiotemporal drivers and individual phenotypes²². Importantly, these data are
86 observational, and are not able to differentiate between all the hypothetical drivers of social decline
87 that we outline in Table 1. Nevertheless, by fitting a series of spatially explicit network models, we
88 examine how age-related declines in social behaviour could arise through within-individual

89 senescence, changes in spatial behaviour, and demography, beginning to untangle the potential
90 causes of age-related social changes in wild mammals.

91 Results

92 **Evidencing social declines.** Using 46 years of census data containing over 200,000 observations of
93 spatiotemporal grouping patterns in 712 individually known female deer, we fitted generalised linear
94 mixed models (GLMMs) to investigate the phenotypic drivers of three correlated annual measures of
95 social connectedness: mean group size, degree centrality, and connection strength. Although
96 representing slightly different elements of sociality, these metrics are all taken to be broadly
97 descriptive of general social connectedness, and are used throughout the literature for this³⁴. We
98 uncovered age-related declines in all three measures when accounting for a range of other intrinsic
99 and extrinsic drivers (**Model Set 1**; Fig. 1A-C). Older females had smaller groups, fewer contacts,
100 and weaker social connections (Fig. 1A-C). Ageing 1 year came with a reduction in average group size
101 of 0.24 individuals (CI -0.29, -0.19; $P < 10^{-6}$; Fig. 1A), 0.65 fewer unique contacts (CI -0.82, -0.50;
102 $P < 10^{-6}$; Fig. 1B), and 0.05 weaker network connection strength (CI -0.07, -0.04; $P < 10^{-6}$; Fig. 1C).

103 **Testing selective disappearance.** An age-related decline in social connectedness could be
104 produced if highly social individuals are more likely to die (i.e., "selective disappearance"), creating an
105 apparent population-level decline in sociality. To test this possibility, we sequentially added individual
106 identity and longevity (age at death) to a model constructed on the subset of individuals with known
107 death year (90% of individuals; **Model Set 2**). Longevity was positively associated with group size
108 (0.09; CI 0.03, 0.16; $P = 0.002$), degree centrality (0.08; CI 0.03, 0.13; $P < 0.001$) and connection
109 strength (0.08; CI 0.03, 0.13, $P = 0.002$), indicating that individuals with more and stronger contacts
110 were likely to live longer (Fig. 1D). However, incorporating individual identity and longevity did not
111 notably change or remove the negative age effect estimates, demonstrating that the observed
112 senescence did not originate from selective disappearance of more-social individuals ($P < 10^{-6}$; Fig.
113 1D).

114 **Testing demographic drivers.** We tested whether the death of associates could be driving age-
115 related social declines by examining the relationship between an individual's summed social
116 connections to individuals that had died in the preceding year, and her own sociality in the focal year
117 (**Model Set 3**). We found that the death of associates was not predictive of social metrics, regardless
118 of whether these associates had died naturally or had been shot; although the strength of
119 associations with dead individuals improved the group size model, and shot friends the strength
120 model (Supplementary Table 1; $\Delta\text{DIC} > 2$), the 95% credibility intervals for both effect estimates
121 overlapped with 0. This finding implies that mortality-associated loss of associates is offset by the
122 acquisition of new connections with surviving individuals.

123 **Examining spatial autocorrelation.** Accounting for spatial positioning is important in social
124 network ecology because spatial autocorrelation may produce confounding between response and
125 explanatory variables, potentially rendering analyses less conservative³⁵. Specifically, in social network
126 analyses, individuals that live in closer proximity to one another may exhibit more similar social
127 phenotypes because they experience similar environments, and they socialise with each other more
128 frequently²². We fitted Stochastic Partial Differentiation Equation (SPDE) effects to consider spatial
129 autocorrelation by accounting for spatial variation in the response variable across the landscape (see
130 Methods). We found that fitting the SPDE effect substantially improved the fit of our models
131 ($\Delta\text{DIC} > 462$) and reduced age effect estimates in **Model Set 1-2** (Fig. 1); the age effects remained
132 significant for group size ($P = 1.2 \times 10^{-5}$) and strength ($P = 0.0009$), while degree centrality became
133 nonsignificant ($P = 0.10$). The SPDE effect also removed the effect of longevity on group size in **Model**
134 **Set 2** ($P = 0.5$; Fig. 1; See Supplementary Table 2 for full effect estimates). Age was heavily spatially
135 structured ($\Delta\text{DIC} = 299$): individuals with more similar ages lived in closer proximity, with younger

136 individuals in the centre of the study area, and with age increasing to the fringes of the population
137 (Fig. 2A). This trend implied that age-dependent changes in spatial behaviour could be contributing to
138 the observed declines in social connectedness.

139 **Evidencing declines in spatial behaviour metrics.** We quantified age-related changes in a
140 correlated suite of eight annual spatial behaviour metrics, to provide a general assessment of changes
141 in individuals' spatial behaviour through their lives (**Model Set 4**; Fig. 3; See Supplementary Table 3
142 for full effect estimates). These metrics included: local population density; distance between annual
143 centroids (i.e., mean X and Y coordinates); distance from the population centroid; home range area;
144 proportional overlap with prior annual home range; and average grazing quality. Older deer occurred
145 in lower-density areas (-0.049; CI -0.069, -0.029; $P=2\times 10^{-6}$; Fig. 3A), further from the centre of the
146 study area (0.123; CI 0.101, 0.146; $P<10^{-6}$; Fig. 3C), and moved their annual centroids slightly less
147 between years (-0.032; CI -0.061, -0.003; $P=0.03$; Fig. 3B). Older individuals also had smaller home
148 ranges (-0.032; CI -0.056, -0.007; $P=5\times 10^{-4}$; Fig. 3D). There was no age trend in the degree of
149 overlap between consecutive annual home ranges (0.021; CI -0.01, 0.052; $P=0.19$; Fig. 3E), implying
150 that home ranges do not shrink within themselves. Older individuals were less likely to be observed
151 on high quality grazing (-0.049; CI -0.074, -0.024; $P<10^{-5}$; Fig. 3F), which was likewise spatially
152 distributed (Fig. 2B).

153 **Testing selective disappearance for spatial behaviours.** Following our protocol for social
154 metrics (**Model Set 2**), we added longevity to investigate how selective disappearance could affect
155 observed spatial metrics' relationships with age (**Model Set 5**; Extended Data Fig. 1). Longer lifespan
156 was associated with those individuals that: inhabited areas of higher density (0.139; CI 0.07, 0.21;
157 $P<0.001$; Extended Data Fig. 1A); moved less far between annual centroids (-0.08; CI -0.14, -0.02;
158 $P=0.009$; Extended Data Fig. 1B); lived closer to the population centre (-0.193; CI -0.27, -0.12;
159 $P<0.001$; Extended Data Fig. 1C); and had smaller home ranges (-0.16; CI -0.24, -0.09; $P<0.001$;
160 Extended Data Fig. 1F). Neither home range overlap nor grazing quality were associated with
161 longevity ($P>0.3$; Extended Data Fig. 1D-E). Notably, controlling for selective disappearance did not
162 decrease or remove any age effects except that of graze quality ($P>0.05$; Extended Data Fig. 1F).

163 **Testing spatial explanations for social declines.** We then fitted spatial metrics as explanatory
164 covariates to test whether they could explain age-related declines in social metrics (**Model Set 6**).
165 We found that social metrics were positively associated with local density and home range area,
166 agreeing with previous findings²². Additionally, social metrics were negatively associated with distance
167 from the population centre ($P\text{ Value}<10^{-6}$). Fitting these effects as explanatory variables in the
168 GLMMs did not fully supplant the negative effects of ageing ($P<0.001$; Extended Data Fig. 2;
169 Supplementary Table 4), although it did substantially reduce the size of the estimated effects
170 (Extended Data Fig. 3). Including the SPDE effect alongside these three spatial covariates likewise did
171 not remove these effects ($P\text{ Value}<0.03$; Extended Data Fig. 2B; Extended Data Fig. 3).

172 Discussion

173 These observations demonstrate senescent declines in social connectedness in a wild ungulate, while
174 providing much-needed insights into the potential underlying drivers. We uncovered no evidence for
175 selective disappearance or demographic mechanisms governing age-related declines in social
176 connectedness; instead, our results suggest that such declines occurred at the within-individual level.
177 We found that generalised spatial phenotypes also changed with age, as represented by a correlated
178 suite of spatial metrics: older individuals were generally found with smaller home ranges, farther from
179 the centre of the population, in areas of lower density, and with lower-quality grazing. This altered
180 spatial behaviour did not fully explain age-related declines in social connectedness, implying the
181 partial involvement of a non-spatial driver of social senescence. Moreover, due to the reciprocal

182 relationships between spatial and social behaviour^{14,36,37} and our use of an observational dataset, it is
183 possible that the changes in spatial behaviour arose from the changes in social connectedness, rather
184 than *vice versa*. Nevertheless, these observations support the value of examining spatial context
185 when considering the intrinsic drivers of social network structure^{3,14,22}, particularly when combining
186 long-term data with spatially explicit network models.

187 Social senescence could emerge from generalised reductions in spatial activity caused by physiological
188 decline and inhibited movement ability^{11,16}. This mechanism would be supported if older individuals'
189 ranges gradually shrank within themselves, while moving less in space. This explanation was not
190 supported for several reasons: first, although an age-related decline in home range area was evident
191 (supporting earlier findings¹¹), it was not robust to controlling for spatial autocorrelation, which
192 implies that this finding could originate from age-related changes in spatial locations or spatially
193 structured observation effort rather than smaller home ranges *per se*. Second, older individuals' home
194 ranges did not increasingly fall within their previous home ranges, implying that they inhabited
195 different areas rather than smaller subsets of the same area. Third, age-related declines in shifts in
196 average annual location were very weak and not robust to controlling for spatial autocorrelation,
197 demonstrating that home ranges shifted at a relatively constant rate across the landscape through an
198 individual's life rather than notably slowing down in old age. Taken together, these observations imply
199 that ageing females exhibit similar spatial activity levels but in different areas of the landscape.

200 Although reduced activity did not appear to be responsible, altered spatial behaviour did contribute to
201 age-related declines in social connectedness. Ageing individuals were less social partly because they
202 preferred to inhabit lower-density, lower-quality areas at the edge of the study area which offer fewer
203 social opportunities. They may ultimately inhabit these areas because physiological changes cause
204 ageing individuals to alter their habitat selection. Red deer teeth are worn down as they age^{38,39},
205 reducing their ability to ingest food as efficiently. Older deer may accommodate these physiological
206 changes by moving to areas that allow them to feed on alternative vegetation (e.g. if longer grasses
207 are easier to crop with worn incisors), which also contain lower densities of conspecifics. In this way,
208 social declines could arise partly as a by-product of habitat selection based on physiological ageing
209 rather than being related to changes in social preferences itself.

210 Nevertheless, we found that social senescence was evident even when spatial factors were accounted
211 for: older individuals still had smaller groups even when considering their home range areas, local
212 population density, and location on the landscape, implying that alterations in spatial behaviour could
213 not be the only explanation for the deer becoming less social with age. Although we tested six spatial
214 metrics and three social metrics, these behaviours are extremely unlikely to be independent: for
215 example, moving away from the centre of the population, towards areas of lower density, and having
216 fewer social associates are all likely to be part of the same correlated selection of behaviours that are
217 very difficult to discern using observational data. Furthermore, while we fitted spatial behaviours as
218 explanatory variables in our models of social connectedness, social and spatial behaviour are part of a
219 bidirectional process involving a number of feedbacks^{36,37,40}. As such, although we formulate spatial
220 behaviours as being explanatory of changes in social connectedness, it is possible that changes in
221 spatial behaviour were themselves influenced by changes in social behaviour. Similarly, our measures
222 of sociality were based on "gambit of the group", which ultimately represents spatiotemporal
223 proximity⁴¹, rather than on observations of between-individual interactions (e.g. fights). The spatial
224 component of the gambit of the group metric could drive increased confounding with spatial
225 behaviours like range area. Future investigations could investigate such behaviours to examine and
226 compare their relationships with age and spatial behaviour. Our results should not necessarily be
227 interpreted as separate evidence for (absence of) changes in each spatial behaviour in isolation, but
228 to indicate that age is associated with generalisable within-individual changes in socio-spatial
229 behavioural syndromes and reduced social connectedness.

230 Social senescence could be a response to aggressive or competitive interactions with younger
231 individuals that may have greater resource demands: to give an example, reproductive female olive
232 baboons (*Papio anubis*) are more aggressive to other females for this reason⁴². Older female deer are
233 less likely to reproduce³³, but reproductive status was included in our models and is therefore unlikely
234 to be directly responsible for the observed social senescence. Alternatively, ageing deer may reduce
235 their connections to individuals with whom they have had more aggressive interactions in favour of
236 more positive interactions, thereby becoming more "socially selective" as they age¹². This tendency to
237 avoid aggressive interactions could also cause them to have reduced grazing quality (as we observed)
238 if younger individuals monopolise the higher quality resources, or if the younger individuals are more
239 competitive and older individuals avoid this competition by moving to less-favoured areas (i.e.,
240 competitive exclusion). Inferring such competitive or aggressive interactions would likely require high-
241 resolution methods like direct behavioural observation in combination with telemetry, which provide
242 detailed information on fine-scale movement patterns but which often currently come with important
243 restrictive tradeoffs in terms of how many individuals are GPS-tagged or observed and for how
244 long^{43,44}. Telemetry- or behavioural observation-based approaches may not be feasible to run for the
245 duration necessary to detect the subtle, life-long patterns of social senescence we observed.
246 Crucially, our long-term longitudinal data (complete with high-certainty life history measures) were
247 also able to differentiate selective disappearance and changes in demographic network structure from
248 within-individual declines, which may be important for producing age-related social changes in other
249 populations (e.g. ibex³⁰). These findings therefore imply a tradeoff between the resolution and
250 breadth of behavioural data, while supporting the value of individual-based long-term studies of wild
251 animals for identifying senescence⁹ and behavioural changes³⁰.

252 Older individuals may decrease their social connectedness due to changing motivations as they age –
253 for example, if it is advantageous to be well-connected when young (e.g. to gain social information)
254 but less so when older (e.g. due to previously accumulated knowledge)^{19–21}. Alternatively, if older
255 individuals undergo immunosenescence⁴⁵ they may reduce social connections as a compensatory
256 measure to avoid parasite exposure. Identifying these kinds of mechanisms would require
257 investigating the fitness- and disease-related consequences of sociality, asking whether the fitness of
258 younger individuals holds a different relationship to social connectedness than the fitness of older
259 individuals does. Importantly, such sociality-fitness relationships are likely to depend on a species'
260 social system; because the deer exhibit a loose, fission-fusion system, our results may be less
261 applicable to species with tight, consistent social groups that move and forage together. Investigating
262 demographic structuring, selective disappearance, and spatial behaviours in primate populations
263 (e.g.^{12,28,46}) may shed an important light on the different drivers of age-related changes in sociality
264 across mammals and other taxa. Ultimately, broadening the selection of study organisms for age-
265 sociality interactions to include those a wider variety of fluid and rigid social systems could help to
266 develop generalisable insights about the causes and consequences of social ageing across the tree of
267 life.

268 In sum, we provide evidence of social senescence in wild deer, and show that this senescence could
269 be explained partly by altered spatial behaviour. Although experiments might be necessary to fully
270 discern the specific drivers of social senescence, we were able to use long-term observational data to
271 successfully identify a within-individual decline (i.e., senescence) in social connectedness that was
272 robust to selective disappearance, demographic changes, and changes in spatial behaviours. As such,
273 these findings provide novel insights into the ecology and evolution of social behavioural changes and
274 the ecological role played by ageing individuals, forming a foundation for understanding how age
275 governs the structure of wild animal societies by shaping individual behaviour.

276

277

Methods

278 Data collection and study system

279 The study was carried out on an unpredated long-term study population of red deer on the Isle of
280 Rum, Scotland (57°N,6°20'W). The natural history of this matrilineal mammalian system has been
281 studied extensively³², and we focussed on females aged 5+ years, as these females have the most
282 complete associated census data, few males live year round in the study area, and nearly all females
283 have bred for the first time at the age of 5. These individuals are known to exhibit age-related
284 declines in a range of behavioural and life history traits^{11,33,47}. Individuals are monitored from birth,
285 providing substantial life history and behavioural data, and >90% of calves are caught and tagged,
286 with tissue samples taken³². Census data were collected for the years 1974-2019, totalling 201,746
287 census observations. Deer were censused by field workers five times a month, for eight months of
288 the year, along one of two alternating routes³². Individuals' identities, locations (to the nearest
289 100M), and group membership were recorded. Grouping events were estimated by experienced field
290 workers according to a variant of the "chain rule" (e.g.⁴⁸), where individuals grazing in a contiguous
291 group within close proximity of each other (under ~10 metres) were deemed to be associating, with
292 mean 204.5 groups observed per individual across their lifetime (range 1-853). If they breed female
293 deer on Rum give birth to a single offspring, typically in May, and we therefore consider their annual
294 cycle as running from May in one calendar year to May the next. All individuals are deemed to be age
295 "zero" in their first year, and all turn "one" on the first of May the following year, regardless of when
296 they were born. This age assignment continues throughout their lives (e.g., in the 2015 deer year, all
297 individuals that were born in 1994 were considered "21 years old"). Accordingly, we summarised
298 individuals' behaviours based on a "deer year", which runs from 1st May to 30th April; any female that
299 died in the course of this period was removed. Our full dataset included 4519 observations of 738
300 individuals. Previous work shows that gestation and lactation impose costs to subsequent survival and
301 reproduction^{49,50}. To characterise each female's investment in reproduction the previous year, we
302 used three categories based on field observations: None (did not give birth); Summer (the female's
303 calf died in the summer, before 1st October); and Winter (the female's calf survived past 1st October).

304 Deriving behavioural metrics

305 All code and data are available at <https://github.com/gfalbery/Lonely-Old-Deers>. Following previous
306 methodology²², we constructed a series of 46 annual social networks using "gambit of the group,"
307 where individuals in the same grouping event (as described above) were taken to be associating⁴¹.
308 Dyadic associations were calculated using the "simple ratio index"⁵¹ derived as a proportion of total
309 sightings (grouping events) in which the focal individuals were seen together:
310 $\text{Sightings}_{A,B} / (\text{Sightings}_A + \text{Sightings}_B - \text{Sightings}_{A,B})$. In this dyadic matrix, 0=never seen together and
311 1=never seen apart. Using the annual social networks, we derived three individual-level annual
312 network metrics that are commonly used across animal social networks and have been considered in
313 detail^{25,26,52,53}.

314 Our measures included three "direct" sociality metrics, which only consider an individual's connections
315 with other individuals:

- 316 1) Group Size – the average number of individuals a deer associated with per sighting;
- 317 2) Degree – the number of unique individuals she was observed with over the course of a year,
318 irrespective of how frequently she was observed with them;
- 319 3) Strength – the sum of all their weighted social associations to others, also known as
320 "weighted degree".

321 Each metric was fitted as a response variable in separate Model Sets. These metrics were well
322 correlated (Extended Data Fig. 4), and therefore should not be considered substantially different

323 phenotypes; instead, we present all three metrics under the expectation that they would all change in
324 similar directions, being highly correlated.

325 We derived 6 correlated metrics related to population structure and spatial behaviour, hereafter
326 referred to collectively as "spatial metrics". These metrics were to be used first as response variables
327 to identify the drivers of spatial behaviours (**Model Sets 4-5**), and as explanatory variables to
328 identify how spatial behaviours affect social metrics (**Model Set 6**).

- 329 1) Local population density (hereafter "**density**") was calculated based on an annual
330 population-level space use kernel derived in AdeHabitatHR⁵⁴ and using each individual's
331 annual centroids (i.e., mean X and Y coordinates), following previous methodology²². Briefly,
332 for each year, we took each individual's annual centroid and calculated the spatial density of
333 these centroids (i.e., individuals per KM²). Each individual was then assigned a local density
334 value based on their location on this annual kernel.
- 335 2) Distance between an individual's annual centroids was taken to indicate shifting in average
336 location from year to year, to identify whether individuals' locations move more in their later
337 years ("**Annual centroid distance**").
- 338 3) To detect long-term patterns of an individual's space use on the two-dimensional landscape,
339 and to identify whether ageing individuals move gradually outwards, we took distance from
340 the overall centre of the population, calculated by taking the mean of all annual centroids'
341 easting and northing ("**Population centroid distance**").
- 342 4) To examine changes in range size over the course of an individual's lifespan, we used the
343 70% isocline of an individual's space use kernel ("**Home range area**"). Based on each
344 individual's annual sighting locations and using the AdeHabitatHR package⁵⁴, this was
345 calculated using a density kernel estimator based on previous methodology^{11,22}.
- 346 5) To investigate the degree to which an individual's annual home range fell within its previous
347 home range, we used an asymmetrical measure of home range overlap from year to year,
348 using the space use kernels ("**Home range overlap**"). A value of 1 for this variable would
349 indicate that an individual's home range in year t fell entirely within its home range in year t-
350 1; a value of 0.5 indicates that half of its home range lay within its previous home range; and
351 a value of 0 indicates no overlap with its previous annual home range. Combined with the
352 "Annual centroid distance" metric, this home range overlap metric aimed to test whether an
353 individual's range generally shrunk to smaller areas within its known range, consistent with
354 physiological decline, rather than an active movement to areas outside its previous range.
- 355 6) To investigate changes in grazing quality, for each individual we calculated the proportion of
356 sightings that occurred on high-quality short or long greens each year ("**Grazing quality**").
357 A value of 1 denoted that an individual was only ever present on these high-quality grasses,
358 while a value of 0 denoted an individual was never seen grazing on them, and was instead
359 always seen on other land types like rock, sand, or lower-quality grazing like heather or
360 *Molinia*.

361 For metrics that represented year-to-year changes ("Annual centroid distance" and "Home range
362 overlap"), we only included observations that occurred in sequential years (year t and year t+1, year
363 t+1 and year t+2, etc). For example, if a female was only observed in two non-sequential years (year
364 t and year t+2), both timepoints were coded as missing. Importantly, because these variables were
365 well correlated (Extended Data Fig. 4), we choose not to interpret these results independently, but to
366 paint a general picture of age-related changes in spatial behaviours, with the caveat that the results
367 of these models are likely non-independent.

368 Statistical analysis

369 To investigate phenotypic associations with social behaviour, we fitted Generalised Linear Mixed
370 Models (GLMMs) using the Integrated Nested Laplace Approximation (INLA) in the R package R-
371 INLA^{55,56}. This method allows fitting of a Stochastic Partial Differentiation Equation (SPDE) random
372 effect to control for and quantify spatial autocorrelation^{57,58}. The SPDE effect models spatial
373 autocorrelation by estimating to what degree points that are closer to each other in space are more
374 similar than points that are further away³⁵. The model then accounts for this similarity, finding
375 sources of variation that occur over and above that expected given the spatial patterns of the
376 response variable. It does so using Matérn covariance, approximating the continuous Gaussian field of
377 the response variable using a triangulated mesh of connected discrete locations⁵⁵. The fits of
378 equivalent models with and without the SPDE effect were compared using the Deviance Information
379 Criterion (DIC) to investigate the importance of spatial autocorrelation. All P values are derived from
380 estimating the proportion of the marginal distribution for a given effect that overlapped with zero,
381 and multiplying it by 2. This can be thought of as being the probability of drawing a value greater
382 than or lower than zero (depending on the direction of the effect), per a two-tailed test.

383 All GLMMs used a Gaussian family specification. For all models, we used noninformative priors for the
384 SPDE effects; we assessed covariance of our explanatory variables and their variance inflation factor
385 (VIF) to ensure models fit well and without being overwhelmed by correlations among our predictors
386 (all VIF values < 2). We checked model fit by assessing correlations between predicted and observed
387 values and by ensuring even distributions of the model residuals.

388 We constructed 6 sets of models designed to test different mechanisms driving age-related changes
389 in sociality (see Model Set details below). All models included the following "base" fixed effects: Year
390 (continuous); annual Population Size (continuous, log-transformed); Number of observations per
391 individual (continuous); Reproductive Status (three categories: No Calf; Calf Summer Death; Calf
392 Survived to October 1st); Age in years (continuous). All continuous explanatory and response
393 variables were scaled (mean=0; standard deviation=1) to help model fitting. All models included
394 random effects of individual ID and observation year.

395 Before beginning the behavioural analysis, to investigate the spatial autocorrelation of age and to
396 examine its spatial distribution visually, we fitted a model with age as a response variable and with
397 only the SPDE effect as an explanatory variable.

398 Model Set 1: Social metrics and age

399 Our first Model Set examined whether our sociality metrics changed over individuals' lifespans, using
400 mean annual measures (N=4203 female years), and including only the base covariates outlined
401 above. We then added a spatial autocorrelation term using an SPDE random effect in INLA, to
402 investigate whether the models were robust to spatial structuring. Comparing the effect of the base
403 model with the spatial model would indicate whether the response variable is spatially structured, and
404 comparing the effect estimates would reveal whether this changed our conclusions. We used the
405 Deviance Information Criterion (DIC) as a measure of model fit; we chose a change in DIC (Δ DIC) of
406 10 to identify whether the spatial autocorrelation effect improved the model.

407 Model Set 2: Social metrics and selective disappearance

408 To investigate whether selective disappearance of individuals may influence estimates of age-related
409 social changes (e.g. if more social individuals were selectively lost), we sequentially added a selection
410 of variables into the models. Because these models only used individuals with a known death year,
411 they used a slightly smaller dataset (N=3873 female-years). We first fitted a base model without
412 individual identity as a random effect, and we then sequentially added individual identity as a random
413 effect, and then longevity as a fixed effect (i.e., age at death). An explanation of the test for selective

414 disappearance can be found in Van de Pol and Verhulst¹⁰. Briefly, fitting both longevity and age in the
415 model isolates the effect of within-individual ageing from that of between-individual selective
416 disappearance. If fitting longevity as a covariate altered the size of the age effects, particularly by
417 rendering them insignificant, it would imply important selective disappearance effects (i.e., between-
418 individual differences) rather than within-individual changes^{10,11}. Finally, we included the SPDE effect
419 to examine whether longevity effects were robust to spatial structuring.

420 **Model Set 3: Investigating demographic associations**

421 Because the social phenotype of any individual is dependent upon not just itself but also on the other
422 individuals within the population, demographic processes, particularly the loss of an individual's social
423 associates over time, may passively contribute to age-related changes in remaining individuals'
424 sociality (e.g. through reducing the potential for encounters with previous associates). To investigate
425 whether these loss processes could drive age-related declines, we tested whether social network
426 positions were predicted by the death of the female's connections the previous year. We fitted this
427 value as an explanatory variable in the models from Model Set 1, using either 1) connections to
428 individuals that were shot, or 2) those that died for any reason. A negative estimate for this effect
429 would imply that age-related declines could be explained by the death of a deer's previous
430 connections, rather than solely individual-level change.

431 **Model Set 4: Spatial metrics**

432 We investigated how age altered spatial behaviour, using our six spatial metrics as response variables
433 (described above). These models included the same covariates as the social behaviour models (Model
434 Set 1). For annual movement and the home range area and overlap metrics, we also fitted the SPDE
435 effect; for density and population centroid distance, the response variables were explicitly spatially
436 distributed on the landscape, so fitting the SPDE effect would be misleading.

437 **Model Set 5: Spatial metrics and selective disappearance**

438 We then repeated the selective disappearance protocol used for social metrics (Model Set 2) on our
439 spatial metrics, to investigate whether any estimated age-related changes in spatial behaviour were
440 altered by selective disappearance of certain individuals.

441 **Model Set 6: Investigating how spatial behaviour affects the ageing of sociality**

442 Finally, we investigated whether social metrics were driven by variation in spatial behaviour, and
443 whether age-related declines were robust to these spatial drivers. Because several of our spatial
444 measures were well-correlated, we used a model addition procedure to identify which spatial
445 measures best explained social network metrics. We used the Deviance Information Criterion (DIC) as
446 a measure of model fit. Beginning with the base model, we sequentially added each spatial metric
447 and then compared the DIC of these models. The best-fitting variable (i.e., the one that reduced DIC
448 by the most) was kept, and then the process was repeated, until all variables were fitted or no
449 remaining variables improved the model. We used a change in DIC of 10 to identify variables that
450 improved model fit.

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461 Author Contributions

462 GFA, DHN, and JAF devised the analysis; GFA carried out the analysis and wrote the manuscript. AM
463 and SM collected behavioural data. THC-B, JMP, DHN, and JAF commented on the manuscript. THC-B
464 and JMP oversaw wider running of the project.

465 Code Availability

466 All code are available at <https://github.com/gfalbery/Lonely-Old-Deers>.

467 Data Availability

468 All data are available at <https://github.com/gfalbery/Lonely-Old-Deers>.

469 Competing Interests

470 We declare no competing interests.

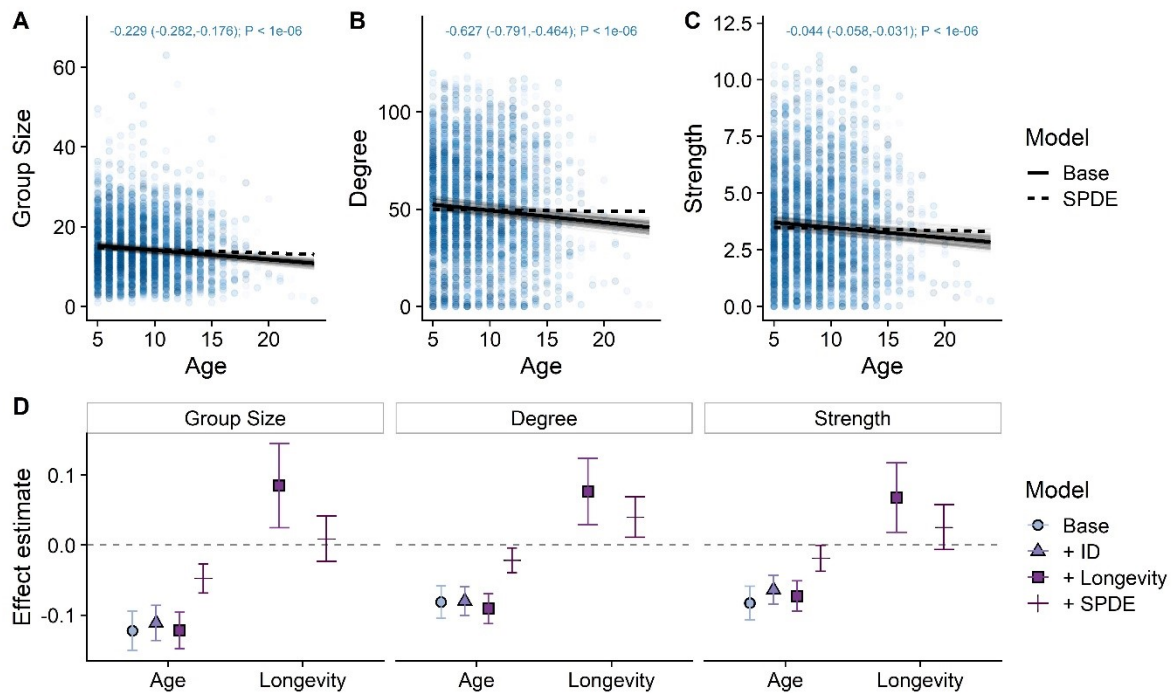
471 Table Captions

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Mechanism	Explanation
Competition avoidance*	Older individuals are less competitive (e.g. due to physiological changes), motivating them to avoid conspecifics.
Exclusion*	Older individuals are excluded by younger or more competitive individuals.
Spatial behaviour changes*	Older individuals alter spatial behaviours like habitat selection, with their social positions changing as a result. Tested using the SPDE extensions of all model sets, and using the spatial behaviour metrics in model sets 4-6.
Selective disappearance	More social individuals are more likely to die earlier (e.g. through competition), creating an apparent age-related decline. Tested using model sets 2 and 5.
Demographic changes	Older individuals' associates die as they age, and are then not replaced. Tested using model set 3.

473 Table 1. Potential non-exclusive explanations causing animals to reduce social behaviour as they age. Asterisks
474 denote within-individual changes – i.e., processes that drive “social senescence” *per se* – while mechanisms
475 without asterisks are processes that could drive apparent age-related changes but without necessitating any
476 within-individual changes. NB our data were not able to identify roles of competition avoidance or exclusion.

Figure Captions



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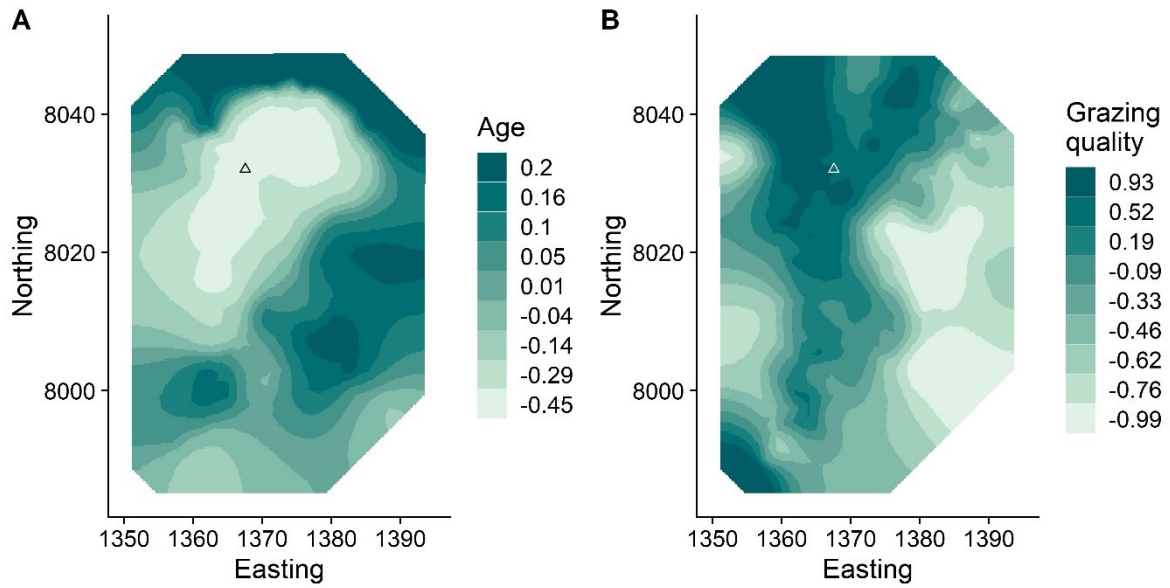
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Fig. 1: **Ageing was associated with reduction in social connectedness.** Panels A-C display age-related declines based on 4203 annual observations of 712 individuals, where each point is an observation, with point shading denoting individual age (lighter=older). The text at the top of panels A-C displays the effect estimate (expressed in units per year), with 95% credibility intervals in brackets, and the P value. Opaque black lines are derived from linear model fits from **Model Set 1**, taking the mean of the posterior distribution. Transparent grey lines represent 100 fits drawn randomly from the posterior estimate distributions of each model, to demonstrate error in the slope and intercepts. Dotted black lines display the effect for the SPDE model, demonstrating the result's robustness to controlling for spatial autocorrelation. Panel D displays the model effect estimates taken from **Model Set 2** (N=3873; effects expressed in units of standard deviations) for age and longevity effects for each social behaviour trait with increasingly complex model formulations, demonstrating that selective disappearance was not responsible for the age-related declines in social connectedness. Dots represent the mean of the posterior effect estimate distribution; error bars denote the 95% credibility intervals of the effect. NB each additional model includes the variables of the models above it (e.g., the longevity model also includes the ID random effect). See Supplementary Table 2 for full effect estimates.



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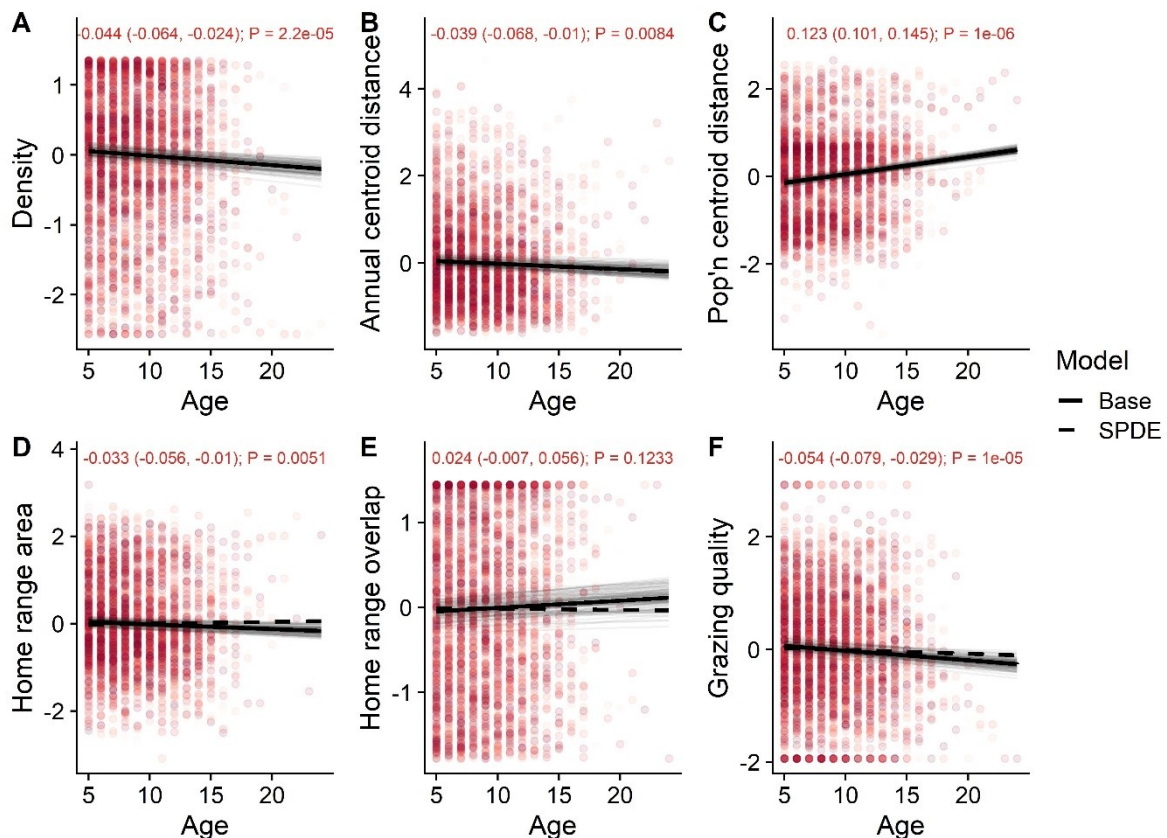
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Fig. 2: The spatial distributions of age of mature females (A) and grazing quality (B) within the study area. Darker colours relate to greater age or grazing quality. Both figures were obtained by plotting the two-dimensional distribution of the SPDE random effect in INLA GLMMs (N=4203), with age and grazing quality as response variables respectively. Triangle points represent the population's centroid, obtained by taking the average location of all individuals' annual centroids. Ten axis units = 1KM.



501

502 Fig. 3: **Ageing was associated with changes in a range of socio-spatial behaviours.** Each point
 503 represents an annual observation of an individual, with point shading denoting individual age (lighter=older). The
 504 text at the top of the panels displays the effect estimate for the Base models, with 95% credibility intervals in
 505 brackets, and the P value, taken from **Model Set 4** (N=4203). Opaque black lines are derived from linear model
 506 fits, taking the mean of the posterior distribution. Transparent grey lines represent 100 fits drawn randomly from
 507 the posterior estimate distributions of each model, to demonstrate error in the slope and intercepts. Dotted black
 508 lines display the effect for the SPDE model, demonstrating the result's robustness to controlling for spatial
 509 autocorrelation. The y axes are in units of standard deviations, and were centred around the mean.

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511 References

- 512 1. White, L. A., Forester, J. D. & Craft, M. E. Using contact networks to explore mechanisms of
 513 parasite transmission in wildlife. *Biol. Rev.* **92**, 389–409 (2017).
- 514 2. Silk, M. J. *et al.* Using Social Network Measures in Wildlife Disease Ecology, Epidemiology, and
 515 Management. *Bioscience* **67**, 245–257 (2017).
- 516 3. Albery, G. F., Kirkpatrick, L., Firth, J. A. & Bansal, S. Unifying spatial and social network
 517 analysis in disease ecology. *J. Anim. Ecol.* **90**, 1–17 (2021).
- 518 4. Evans, J. C., Silk, M. J., Boogert, N. J. & Hodgson, D. J. Infected or informed? Social structure
 519 and the simultaneous transmission of information and infectious disease. *Oikos* **129**, 1271–
 520 1288 (2020).
- 521 5. Aplin, L. M., Sheldon, B. C. & Morand-Ferron, J. Milk bottles revisited: Social learning and
 522 individual variation in the blue tit, *Cyanistes caeruleus*. *Anim. Behav.* **85**, 1225–1232 (2013).

- 523 6. Silk, J. B. The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **362**, 539–559 (2007).
524
- 525 7. Snyder-Mackler, N. *et al.* Social determinants of health and survival in humans and other
526 animals. *Science (80-.)*. **9553**, (2020).
- 527 8. Machanda, Z. P. & Rosati, A. G. Shifting sociality during primate ageing. *Philos. Trans. R. Soc. B Biol. Sci.* **375**, (2020).
528
- 529 9. Nussey, D. H., Coulson, T., Festa-Bianchet, M. & Gaillard, J. M. Measuring senescence in wild
530 animal populations: Towards a longitudinal approach. *Funct. Ecol.* **22**, 393–406 (2008).
- 531 10. van de Pol, M. & Verhulst, S. Age-dependent traits: a new statistical model to separate within-
532 and between-individual effects. *Am. Nat.* **167**, 766–73 (2006).
- 533 11. Froy, H. *et al.* Declining home range area predicts reduced late-life survival in two wild
534 ungulate populations. *Ecol. Lett.* **21**, 1001–1009 (2018).
- 535 12. Rosati, A. G. *et al.* Social selectivity in aging wild chimpanzees. *Science (80-.)*. **370**, 473–476
536 (2020).
- 537 13. Kim, S.-Y., Torres, R., Rodriguez, C. & Drummond, H. Effects of breeding success, mate
538 fidelity and senescence on breeding dispersal of male and female blue-footed boobies. *J. Anim. Ecol.* **76**, 471–479 (2007).
539
- 540 14. Webber, Q. M. R. & Vander Wal, E. An evolutionary framework outlining the integration of
541 individual social and spatial ecology. *J. Anim. Ecol.* **87**, 113–127 (2018).
- 542 15. Webber, Q. M. R. & Vander Wal, E. Trends and perspectives on the use of animal social
543 network analysis in behavioural ecology: a bibliometric approach. *Anim. Behav.* **149**, 77–87
544 (2019).
- 545 16. Siracusa, E. R., Higham, J. P., Snyder-mackler, N. & Brent, L. J. N. Social ageing: exploring the
546 drivers of late-life changes in social behaviour in mammals. *Biol. Lett.* **18**, 20210643 (2022).
- 547 17. Elliott, K. H. *et al.* Ageing gracefully: Physiology but not behaviour declines with age in a
548 diving seabird. *Funct. Ecol.* **29**, 219–228 (2015).
- 549 18. Aartsen, M. J., Van Tilburg, T., Smits, C. H. M. & Knipscheer, K. C. P. M. A longitudinal study
550 of the impact of physical and cognitive decline on the personal network in old age. *J. Soc. Pers. Relat.* **21**, 249–266 (2004).
551
- 552 19. Brent, L. J. N., Ruiz-Lambides, A. & Platt, M. L. Family network size and survival across the
553 lifespan of female macaques. *Proc. R. Soc. B Biol. Sci.* **284**, (2017).
- 554 20. Turner, J. W., Robitaille, A. L., Bills, P. S. & Holekamp, K. E. Early-life relationships matter:
555 Social position during early life predicts fitness among female spotted hyenas. *J. Anim. Ecol.*
556 **90**, 183–196 (2021).
- 557 21. Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A. M. & Fischer, J.
558 Motivational Shifts in Aging Monkeys and the Origins of Social Selectivity. *Curr. Biol.* **26**, 1744–
559 1749 (2016).
- 560 22. Albery, G. F. *et al.* Multiple spatial behaviours govern social network positions in a wild
561 ungulate. *Ecol. Lett.* **24**, 676–686 (2021).
- 562 23. Sanchez, J. N. & Hudgens, B. R. Interactions between density, home range behaviors, and
563 contact rates in the Channel Island fox (*Urocyon littoralis*). *Ecol. Evol.* **5**, 2466–2477 (2015).
- 564 24. Shizuka, D. & Johnson, A. E. How demographic processes shape animal social networks.
565 *Behav. Ecol.* 1–11 (2019) doi:10.1093/beheco/arz083.
- 566 25. Krause, J., James, R., Franks, D. W. & Croft, D. P. *Animal social networks*. (Oxford University
567 Press, 2015).

- 568 26. Firth, J. A. *et al.* Wild birds respond to flockmate loss by increasing their social network
569 associations to others. *Proc. R. Soc. B Biol. Sci.* **284**, (2017).
- 570 27. Evans, J. C., Liechti, J. I., Boatman, B. & König, B. A natural catastrophic turnover event:
571 individual sociality matters despite community resilience in wild house mice. *Proc. R. Soc. B*
572 *Biol. Sci.* **287**, 20192880 (2020).
- 573 28. Rathke, E. & Fischer, J. Social aging in male and female Barbary macaques. *Am. J. Primatol.*
574 (2021) doi:10.1002/ajp.23272.
- 575 29. Kroeger, S. B., Blumstein, D. T. & Martin, J. G. A. A. How social behaviour and life-history
576 traits change with age and in the year prior to death in female yellow-bellied marmots. *Philos.*
577 *Trans. R. Soc. B Biol. Sci.* **376**, 20190745 (2021).
- 578 30. Brambilla, A., von Hardenberg, A., Sueur, C., Canedoli, C. & Stanley, C. Long term analysis of
579 social structure: evidence of age-based consistent associations in Alpine ibex. *bioRxiv* 1–42
580 (2021).
- 581 31. González, N. T. *et al.* Age-related change in adult chimpanzee social network integration. *Evol.*
582 *Med. Public Heal.* **9**, 448–459 (2021).
- 583 32. Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. *Red Deer: Behavior and Ecology of Two*
584 *Sexes*. vol. 15 (University of Chicago Press, 1982).
- 585 33. Nussey, D. H., Kruuk, L. E. B., Donald, A., Fowlie, M. & Clutton-Brock, T. H. The rate of
586 senescence in maternal performance increases with early-life fecundity in red deer. *Ecol. Lett.*
587 **9**, 1342–1350 (2006).
- 588 34. Croft, D. P., James, R. & Krause, J. *Exploring animal social networks*. (Princeton University
589 Press, 2008).
- 590 35. Tobler, W. R. A Computer Movie Simulating Urban Growth in the Detroit Region. *Econ. Geogr.*
591 **46**, 234 (1970).
- 592 36. Firth, J. A. & Sheldon, B. C. Social carry-over effects underpin trans-seasonally linked structure
593 in a wild bird population. *Ecol. Lett.* **19**, 1324–1332 (2016).
- 594 37. Spiegel, O., Leu, S. T., Sih, A. & Bull, C. M. Socially interacting or indifferent neighbours?
595 Randomization of movement paths to tease apart social preference and spatial constraints.
596 *Methods Ecol. Evol.* 971–979 (2016) doi:10.1111/2041-210X.12553.
- 597 38. Nussey, D. H. *et al.* The relationship between tooth wear, habitat quality and late-life
598 reproduction in a wild red deer population. *J. Anim. Ecol.* **76**, 402–412 (2007).
- 599 39. Loe, L. E., Mysterud, A., Langvatn, R. & Stenseth, N. C. Decelerating and sex-dependent tooth
600 wear in Norwegian red deer. *Oecologia* **135**, 346–353 (2003).
- 601 40. Peignier, M. *et al.* Space use and social association in a gregarious ungulate: Testing the
602 conspecific attraction and resource dispersion hypotheses. *Ecol. Evol.* **9**, 5133–5145 (2019).
- 603 41. Franks, D. W., Ruxton, G. D. & James, R. Sampling animal association networks with the
604 gambit of the group. *Behav. Ecol. Sociobiol.* **64**, 493–503 (2010).
- 605 42. Patterson, S. K., Strum, S. C. & Silk, J. B. Resource competition shapes female-female
606 aggression in olive baboons, *Papio anubis*. *Anim. Behav.* **176**, 23–41 (2021).
- 607 43. Kays, R., Crofoot, M. C., Jetz, W. & Wikelski, M. Terrestrial animal tracking as an eye on life
608 and planet. *Science (80-.)*. **348**, aaa2478 (2015).
- 609 44. Gilbertson, M. L. J., White, L. A. & Craft, M. E. Trade-offs with telemetry-derived contact
610 networks for infectious disease studies in wildlife. *Methods Ecol. Evol.* 2041–210X.13355
611 (2020) doi:10.1111/2041-210X.13355.
- 612 45. Froy, H. *et al.* Senescence in immunity against helminth parasites predicts adult mortality in a

- 613 wild mammal. *Science (80-.)*. **365**, 1296–1298 (2019).
- 614 46. Siracusa, E. R. *et al.* Familiar Neighbors, but Not Relatives, Enhance Fitness in a Territorial
615 Mammal. *Curr. Biol.* **31**, 438–445.e3 (2021).
- 616 47. Nussey, D. H., Kruuk, L. E. B., Morris, A. & Clutton-Brock, T. H. Environmental conditions in
617 early life influence ageing rates in a wild population of red deer. *Curr. Biol.* **17**, 1000–1001
618 (2007).
- 619 48. Castles, M. *et al.* Social networks created with different techniques are not comparable. *Anim.*
620 *Behav.* **96**, 59–67 (2014).
- 621 49. Froy, H., Walling, C. A., Pemberton, J. M., Clutton-brock, T. H. & Kruuk, L. E. B. Relative costs
622 of offspring sex and offspring survival in a polygynous mammal. *Biol. Lett.* **12**, 20160417
623 (2016).
- 624 50. Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. Fitness costs of gestation and lactation in
625 wild mammals. *Nature* **337**, 260–262 (1989).
- 626 51. Cairns, S. J. & Schwager, S. J. A comparison of association indices. *Anim. Behav.* **35**, 1454–
627 1469 (1987).
- 628 52. Brent, L. J. N. Friends of friends: Are indirect connections in social networks important to
629 animal behaviour? *Anim. Behav.* **103**, 211–222 (2015).
- 630 53. Whitehead, H. *Analyzing animal societies: quantitative methods for vertebrate social analysis.*
631 (University of Chicago Press, 2008).
- 632 54. Calenge, C. Home range estimation in R: the adehabitatHR package. [https://cran.r-](https://cran.r-project.org/web/packages/adehabitatHR/index.html)
633 [project.org/web/packages/adehabitatHR/index.html](https://cran.r-project.org/web/packages/adehabitatHR/index.html) (2011).
- 634 55. Lindgren, F. & Rue, H. Bayesian Spatial Modelling with R-INLA. *J. Stat. Softw.* **63**, 1–25
635 (2015).
- 636 56. Rue, H. & Martino, S. Approximate Bayesian inference for latent Gaussian models by using
637 integrated nested Laplace approximations. *Stat. Methodol.* **71**, 319–392 (2009).
- 638 57. Bakka, H. *et al.* Spatial modelling with R-INLA: A review. *WIREs Comput. Stat.* **10**, e1443
639 (2018).
- 640 58. Lindgren, F., Rue, H. & Lindstrom, J. An explicit link between Gaussian fields and Gaussian
641 Markov random fields: the stochastic partial differential equation approach. *J. R. Stat. Soc. B*
642 **73**, 423–498 (2011).
- 643