

1 Is degree of sociality associated with reproductive senescence? A
2 comparative analysis across birds and mammals

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21 Our understanding on how widespread reproductive senescence is in the wild and how the onset and
22 rate of reproductive senescence vary among species in relation to life histories and lifestyles is
23 currently limited. More specifically, whether the species-specific degree of sociality is linked to the
24 occurrence, onset and rate of reproductive senescence remains unknown. Here, we investigate these
25 questions using phylogenetic comparative analyses across 36 bird and 101 mammal species
26 encompassing a wide array of life histories, lifestyles and social traits. We found that female
27 reproductive senescence (1) is widespread and occurs with similar frequency (about two thirds) in
28 birds and mammals; (2) occurs later in life and is slower in birds than in similar-sized mammals; (3)
29 occurs later in life and is slower with an increasingly slower pace of life in both vertebrate classes;
30 and (4) is only weakly associated, if any, with the degree of sociality in both classes after
31 accounting for the effect of body size and pace of life. However, when removing the effect of
32 species differences in pace of life, a higher degree of sociality was associated with later and weaker
33 reproductive senescence in females, which suggests that degree of sociality is either indirectly
34 related to reproductive senescence via the pace of life or simply a direct outcome of the pace of life.

35 **Keywords:**

36 brain size, coloniality, cooperative breeding, life history, reproductive ageing, vertebrates

37 **Subject Areas:**

38 ecology, evolution

39 1. Introduction

40 Reproductive senescence (or reproductive ageing) – the decline in reproductive performance with
41 increasing age – is widespread in nature [1,2], except for species with indeterminate growth that
42 gain mass and thereby increase fecundity with age [3]. Recent studies have revealed that both the
43 timing and the strength of reproductive senescence is highly variable across species [4,5], although
44 our knowledge is still very limited about how ecological factors and species-specific life history
45 shape variation in either the onset or the rate of reproductive senescence [1,6]. Among these factors,
46 the possible role played by the species-specific degree of sociality has never been investigated.

47 Sociality is evolutionarily associated with a complex set of life-history traits. Most notably, social
48 species might have longer lifespan and decreased actuarial senescence (see [7–9] for reviews).

49 Indeed, social life in cooperative breeders and colonial species can buffer environmentally-driven
50 mortality risks and might ultimately slow down actuarial senescence (e.g. [10] for a case study on
51 cooperatively breeding Seychelles warblers, *Acrocephalus sechellensis*), even if the relationship
52 between sociality and actuarial senescence is likely to be complex and might differ both within and
53 among species [7]. However, the association between social life and the occurrence, onset and rate
54 of reproductive senescence has never been investigated so far, although similar relationship with the
55 intensity of senescence is expected for survival and reproduction. We aimed here to fill this
56 knowledge gap using the most comprehensive comparative analyses performed to date across bird
57 and mammal species.

58 Within populations, there is a large variation among individuals in their sociability. Even within
59 highly social species, some individuals are more connected to others, while some have few and
60 loose social interactions with conspecifics (e.g. variation according to social status and
61 environmental context in spotted hyena, *Crocuta crocuta* [11]; variation with age in yellow-bellied
62 marmots, *Marmota flaviventer* [12]; variation in early social development in bottlenose dolphin,
63 *Tursiops* sp. [13]). In cooperative breeders, most of the individuals are social during at least part of

64 their life [14]. Nevertheless, even within these populations, individuals are not equally social and
65 they differ in the amount of help they receive and provide. The evolutionary hypotheses explaining
66 why social individuals should display a weaker senescence than solitary ones [7] are rooted in the
67 principle of allocation [15]. This principle states that increased allocation of finite resources to a
68 given biological function (e.g. reproduction) compromises allocation to a competing function (e.g.
69 somatic maintenance that promotes survival) [16]. Increased allocation of resources to reproduction
70 early in life, which is favoured by natural selection in growing populations [17], is expected to have
71 detrimental consequences in terms of actuarial and/or reproductive senescence [6]. This trade-off is
72 predicted by both antagonistic pleiotropy and disposable soma theories of ageing [18,19], and is
73 well supported by current empirical evidence [20,21]. For instance, male red deer (*Cervus elaphus*)
74 allocating substantial resources to sexual competition during early life show a steeper rate of
75 reproductive senescence in late life ([22]; see also [23] for examples in birds). How social lifestyle
76 may buffer against such costs? For instance, helpers in cooperative breeders reduce the workload of
77 reproducers according to the load-lightening hypothesis [24]. Thus, the principle of allocation, a key
78 concept of life-history evolution [16,25], explains how senescence can either increase due to a
79 delayed cost of high performance during early life [20,26] or decrease thanks to a reduced
80 reproductive effort required under high degree of sociality (e.g. the presence of helpers [24]).
81 Assuming that these processes can explain the variance in senescence observed at the inter-specific
82 level, two main hypotheses can be proposed to expect a negative covariation between the degree of
83 sociality and reproductive senescence:

84 (H1) Given the inevitable costs of reproduction [27,28], a high reproductive effort observed
85 in a given species should lead to an earlier and/or faster reproductive senescence [20]. For a
86 given reproductive effort, a higher degree of sociality in a given species might facilitate the
87 reproductive duties of individuals and therefore reduce directly the costs of reproduction [7]
88 and ultimately shape the senescence patterns of that species [7,21]. Thus, the mitigation of

89 reproductive cost by a social mode of life should lead to postponed onset and/or decelerated
90 rate of reproductive senescence of a given species.

91 (H2) The degree of sociality can drive the evolution of reproductive senescence in a given
92 species indirectly through decreasing adult mortality risk, thereby slowing down the pace of
93 life. Life-history theory postulates that a decreased rate of environmentally-driven mortality
94 should favour slower growth rate, longer time to maturation, older age at first reproduction
95 and reduced allocation to reproduction by young adults [16], as well as later onsets and
96 slower rates of both actuarial and reproductive senescence [6,29]. Indeed, sociality has been
97 shown to mitigate multiple forms of environmentally driven mortality risks (e.g. starvation,
98 predation). Thus, the presence of social partners in a given species is associated with a
99 slowing down of the pace of life, which leads to delayed and decelerated reproductive
100 senescence in both mammals and birds [5].

101 Under both hypotheses, reproductive senescence should be less pronounced in species with a higher
102 degree of sociality by involving either a direct response to reproductive effort at each reproductive
103 attempt (H1) or indirectly through a slower pace of life selecting for a lower reproductive effort
104 early in life (H2). If the degree of sociality is directly associated with reproductive senescence (H1),
105 we predict a substantial effect of the degree of sociality even after the effects of allometry and pace
106 of life on reproductive senescence are accounted for. If the degree of sociality is indirectly
107 associated with reproductive senescence via the pace of life (H2), we predict no detectable effect of
108 the degree of sociality once the effects of allometry and pace of life are accounted for.

109 Here, we modelled age-specific changes in reproductive traits at the species level and tested
110 whether the degree of sociality accounts for the variation in the occurrence, onset and rate of
111 reproductive senescence observed across birds and mammals ($n = 36$ and 101 species, respectively).
112 The age when reproductive performance starts to decline marks the onset, while the slope of the
113 age-specific decline in reproductive performance fitted from the onset expresses the rate. We

114 followed strict statistical rules to assess whether reproductive senescence occurred (see Methods)
115 and estimated onset and rate only for species in which it did occur (i.e. species with a statistically
116 significant decrease of reproductive performance with increasing age). We accounted for the
117 confounding effect of phylogenetic inertia, allometric constraints and species' ranking on the slow–
118 fast continuum of life histories (i.e. pace of life) in our phylogenetic comparative analyses, as all
119 these processes are known to shape variation in senescence [5].

120

121 2. Methods

122 (a) Female reproductive senescence data

123 As age-specific reproductive output is easier to measure in females than in males (e.g. due to extra-
124 pair offspring often produced by males; [30]) and has been reported in a much higher number of
125 vertebrate species, we focus on the reproductive ageing of females in both birds and mammals.
126 Reproductive senescence parameters of 101 wild or semi-captive mammal species were taken from
127 [31]. This data set includes the presence/absence of reproductive senescence and, for species with
128 evidence of senescence, the age at onset and the rate of reproductive senescence. All those
129 parameters were estimated from age-specific birth rates (i.e. number of female offspring alive at
130 birth that are produced by a female of age x , tabulated as m_x in a life table) extracted from published
131 life tables or graphs using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>). The
132 acquisition of age-specific reproductive data for mammals is fully detailed in [31]. In cooperatively
133 breeding mammals, age-specific reproductive data were collected for dominant females (e.g. [32]),
134 as subordinate females generally have no access to reproduction.

135 In birds, we conducted a systematic literature search of age-specific changes in reproductive traits
136 in wild populations to extract data similar to those obtained for mammals (see Electronic
137 Supplementary Material, ESM for search methods). Unlike in mammals, age-specific birth rates

138 (i.e. the m_x parameter) were seldom reported in bird studies because the probability of breeding –
139 necessary for birth rate calculations – is often unknown. Therefore, to increase the number of
140 species, we also included studies that reported age-specific number of hatchlings or number of
141 fledglings per female when birth rates could not be extracted or computed. Some studies reported
142 standardized values (i.e. normalized values or residuals from models) instead of raw values of age-
143 specific reproduction. We included those studies in our analyses and controlled for the effect of
144 analysing standardized data (yes/no). When reproductive data were reported for multiple
145 populations of the same species, we only included the study with the largest sample size, as done in
146 mammals [31]. To estimate reproductive senescence parameters, we accounted for differences in
147 the age-specific sample sizes, as done in mammals [31]. We used the original age-specific sample
148 size when reported in the original studies, and we calculated the number of females expected to be
149 alive at age x from the observed age distribution of females when sample sizes were not reported.
150 We collected female reproductive data for 36 avian species (see ESM ‘Data set’).

151 Age-dependent reproductive traits in birds followed similar distributions to mammalian ones.
152 Hence, we computed reproductive senescence parameters in birds using the same methods as in
153 mammals. Briefly (see [31] for further details), four different age-dependent models (i.e. constant
154 model, linear model, threshold model with one threshold and two linear segments, and threshold
155 model with two thresholds and three linear segments) weighted by the age-specific sample size
156 were fitted on the reproductive data using the R package ‘segmented’ [33]. The final model was
157 selected using Akaike’s Information Criterion (AIC) (see the Methods in the ESM for model
158 selection procedure and ESM ‘Model selection’ for the AIC values associated to each alternative
159 senescence models; see also ESM ‘Segmented’ for the segmented fits of the selected models plotted
160 separately for each bird species; similar table and plots for mammals can be found in [31]). Based
161 on the selected model, different procedures were used to infer reproductive senescence from the
162 slope of the different linear segments and their associated standard error. When reproductive
163 senescence occurred (i.e. slope of one of the segments < 0), the rate and the onset of reproductive

164 senescence were reported as the slope of the linear segment and the age corresponding to the
165 beginning of the segment, respectively. Using this procedure, we detected reproductive senescence
166 for most of the bird species for which it was observed in the original studies from which the data
167 were extracted. Only minor discrepancies were found mostly due to the use of different statistical
168 methods (see ESM ‘Occurrence’ for a comparison of the results found on reproductive senescence
169 using our standardized procedure against the results found in the original studies; a similar
170 comparison for mammals can be found in [31]).

171

172 (b) Life-history traits

173 To assess the relationship between the degree of sociality and reproductive senescence, we first had
174 to account for inter-specific differences in body size and biological time [34], which structure most
175 life-history variation across vertebrates [35]. Body mass is a reliable measure of species-specific
176 size that shapes age-specific reproductive and survival rates via allometric effects. Thus, small bird
177 and mammal species display both earlier and steeper reproductive senescence than large ones [5].
178 Likewise, for a given size, slow-living species display both later and slower reproductive
179 senescence, an effect well illustrated by the comparison of similar-sized birds and mammals [5].
180 Generation time is the most appropriate metric to position species on the slow–fast continuum of
181 life histories [36]; however, data to accurately measure generation time were missing for many of
182 the species studied here [37]. Thus, instead of generation time, we used a compound of the age at
183 first reproduction and maximum longevity observed in the focal case study to measure species-
184 specific pace of life (see below). In birds, we collected data on female body mass from [38], age at
185 first reproduction and longevity from the same papers including age-specific reproduction data
186 (ESM ‘Data set’), while in mammals data of the same traits were retrieved from [31].

187

188 (c) Sociality traits

189 The social environment varies considerably across species and this diversity can have vast
190 evolutionary consequences [39]. We use four simple sociality traits (i.e. coloniality, parental
191 cooperation, cooperative breeding and relative brain size; see also [40,41]) to assess the species-
192 specific degree of sociality (table 1) and test whether these traits are associated or not with the
193 occurrence, rate and onset of reproductive senescence across birds and mammals. These four
194 proxies of sociality cover different ranges of degree of sociality. For instance, cooperative breeders
195 often live in social systems with more complex social interactions than colonial ones, and therefore
196 imply different costs and benefits to the individuals. The diversity of social traits we use in this
197 study makes possible to assess whether social lifestyle in general or specific social systems in
198 particular are associated with reproductive senescence, if any.

199 We used three sociality traits in birds (i.e. presence/absence of coloniality, parental cooperation and
200 relative brain size). Both the degree of sociality and the use of social information are higher in
201 species breeding in large and dense colonies of non-kin individuals as compared with solitarily
202 breeding ones [42]. Coloniality has been considered as a proxy of sociality degree in studies of
203 longevity across bird species [40]. We used parental cooperation as a metric of the degree of
204 sociality, which reflects whether female-only, male-only or shared female–male parental care is
205 typical for a given bird species [43]. Family, where individuals form short-term pair bonds during
206 breeding and raise their offspring cooperatively (i.e. have biparental care) is the simplest social
207 system, and species with biparental care display a higher degree of sociality than species in which
208 only females care for their young [41]. This metric is relevant in birds because it influences the
209 reproductive costs of females and thus is likely to modulate female reproductive senescence
210 parameters. Biparental care is the most common form of social behaviour between unrelated
211 individuals in birds, with over 90% of all living birds being biparental [44]. The presence of
212 cooperative breeding was not considered in birds due to the low number of species with regular
213 cooperative breeding in our data set.

214 We used two sociality traits in mammals (i.e. presence/absence of cooperative breeding and relative
215 brain size). The degree of sociality is considered high (i.e. implying frequent and complex social
216 interactions among individuals) in species living in small cooperative breeding groups with helpers
217 as compared with non-cooperatively breeding ones. Cooperative breeders have the most intense
218 social system among mammals [45]. Because coloniality cannot be defined with confidence in
219 mammals, but in a few species only (e.g. in black-tailed prairie dogs, *Cynomys ludovicianus* [46]),
220 we had to omit this sociality trait in this vertebrate class.

221 The relative brain size (i.e. brain size for a given body size) was used for both birds and mammals.
222 Relative brain size is higher in species with high degree of social bonding (e.g. primates and
223 whales/dolphins) or reproductive pair bonding (e.g. monogamous carnivores and ungulates, bats
224 and birds) [41], making possible its use to measure the degree of sociality [41,47]. Quantifying the
225 degree of sociality in comparative studies encompassing species with a large range of life-history
226 strategies is far from trivial, which leads most comparative studies to use only proxies of sociality
227 instead of accurate metrics.

228 **Table 1.** Sociality traits and their meaning in terms of degree of sociality.

sociality trait	degree of sociality	
	low	high
colonial breeding (birds)	no	yes
parental cooperation (birds)	female care	female & male care
cooperative breeding (mammals)	no	yes
relative brain size (birds and mammals)	small	large

229

230 In birds, we collected data on brain mass from [48], presence/absence of coloniality from [49] and
231 parental cooperation during breeding from [43] (see ESM ‘Data set’). In the latter source, parental
232 cooperation was separately quantified for the pre- and post-hatching periods, which are highly

233 correlated (Pearson correlation $r = 0.76$, $df = 29$, $t = 6.24$, $p < 0.0001$). We calculated the average of
234 these two periods (henceforth parental cooperation) reflecting the sex bias in parental care during
235 breeding. Values range from -1 (exclusive female care) to 1 (exclusive male care), with 0 reflecting
236 an equal share of parental duties between sexes. Coloniality had a perfect overlap with marine
237 environment in our bird data set, as all colonial species are seabirds and all solitary ones are
238 terrestrial, which reflects a strong phylogenetic bias and a limitation of our coloniality data (see
239 Discussion). In mammals, data on brain mass were obtained from [50], presence/absence of
240 cooperative breeding from [51] and we completed species with lacking information with additional
241 sources (see ESM ‘Data set’).

242

243 **(d) Statistical analyses**

244 All analyses were performed in R version 4.0.1 [52]. To make meaningful inferences about the
245 effect of body size, pace of life and degree of sociality on reproductive senescence, all models were
246 controlled for phylogenetic inertia. In birds we used a rooted, ultrametric consensus tree built using
247 the SumTrees Python library [53] based on 1,000 trees. These trees were obtained from birdtree.org
248 [54] using the Hackett backbone tree [55]. For mammals, we used a published phylogenetic super-
249 tree (see also [56]).

250 Female body mass, age at first reproduction, longevity and brain mass were highly correlated across
251 both bird and mammal species (table S1). Therefore, to avoid multicollinearity problems, we
252 conducted a phylogenetically-controlled principal component analysis (PPCA) as implemented in R
253 package ‘phytools’ [57] on the first three traits (all log-transformed) separately for birds and
254 mammals. We retained the first two phylogenetic principal components (PPCs), where the first PPC
255 is a size component (hereafter PPC size), which explained 69% and 79% of variation in birds and
256 mammals, respectively, and the second PPC is a pace of life component (hereafter PPC pace),
257 which explained additional 23% and 12% of variation in birds and mammals, respectively (table

258 S2). Larger values indicate larger body mass (PPC size) and slower pace of life (PPC pace),
259 respectively (table S2). PPC size and PPC pace were used in the subsequent analyses to control for
260 allometry and pace of life, respectively. Given that we were specifically interested in the effect of
261 relative brain size (a proxy measure of the degree of sociality) on reproductive senescence, we did
262 not include brain size in the PPCA. Nonetheless, to avoid collinearity of brain size with PPC size,
263 we estimated relative brain size as residuals of a standard major axis regression (as implemented in
264 R package ‘lmodel2’) between log-transformed brain size and PPC size and used this measure in
265 the multifactorial models.

266 To explore variation in reproductive senescence patterns, we used phylogenetic logistic regressions
267 for evidence of reproductive senescence and phylogenetic linear regressions separately for onset
268 and rate of reproductive senescence as implemented in R package ‘phylolm’ [58]. Age at onset and
269 the absolute value of the rate of reproductive senescence were log-transformed prior to the analysis.
270 In birds, for each senescence metric, the reproductive trait used to assess reproductive senescence
271 (i.e. birth rate m_x , number of hatchlings or number of fledglings) and the presence/absence of
272 coloniality were tested as fixed factors, while PPC size, PPC pace, residual brain size and parental
273 cooperation were included as covariates. We did not need to account for either the hunting status
274 (because no bird species in the data set is hunted) or the data quality (because all bird studies were
275 based on longitudinal data and only included known-aged individuals). Similarly to analysis in
276 mammals (see [31]), we tested whether the probability to detect reproductive senescence in birds
277 was influenced by the sample size (i.e. total number of reproductive records in the population; log-
278 transformed in the analysis; ESM ‘Data set’). For the rate of reproductive senescence, the effect of
279 data standardization (yes/no) was also tested. In mammals, for each senescence metric, data quality
280 (transversal/longitudinal), hunting status (hunted/not hunted) and presence/absence of cooperative
281 breeding were included as fixed factors, while PPC size, PPC pace and residual brain size were
282 included as covariates. In both birds and mammals, the effect of age at onset of reproductive
283 senescence (log-transformed) was also tested in models of rate of reproductive senescence because

284 a negative correlation is expected to occur [31]. Non-linear effects of PPC size and PPC pace were
285 also modelled in both bird and mammal models using second-degree orthogonal polynomials, but
286 were only retained in the model when their inclusion decreased AIC values by > 2 compared with
287 the initial model without the polynomials. In no case where a quadratic model was selected over the
288 linear model did a cubic model outperform the quadratic model, meaning that a second-order
289 polynomial satisfactorily accounted for observed non-linear relationships. Sample size varied across
290 models because some variables (e.g. brain size) had missing values in certain species and rate as
291 well as onset of senescence were only analysed for species in which evidence of reproductive
292 senescence was detected. To test H2 according to which the effect of the degree of sociality acts
293 indirectly through slowing down the pace of life, we reran all the above-mentioned analyses after
294 removing PPC pace from the models.

295 Due to the limited number of bird species, we adopted an AIC-based stepwise forward model
296 selection procedure to avoid over-parametrization of models. As a first step, an intercept model was
297 constructed for each dependent variable. In the second step, each explanatory variable (except
298 metrics of sociality) was added one by one to this model and the model with the smallest AIC value
299 (if $\Delta\text{AIC} < 2$) was further elaborated until adding extra variables did not decrease AIC value by > 2 .
300 This model is referred as the base model. If any of the single-predictor models had $\Delta\text{AIC} < 2$, the
301 intercept model was considered as the base model. In the third step, to test the association between
302 the degree of sociality and reproductive senescence, the sociality traits were added one by one to the
303 base model and the change in AIC was checked (table S3). Given that relative brain size and
304 parental cooperation had missing values for some species, when testing their effect on reproductive
305 senescence metrics, their corresponding base models were refitted for the subset of species with the
306 full set of available data. These models are presented in table S3, while table 2 shows the ANOVA
307 results of the base models presented in table S3.

308 Given the large sample size in mammals, we present the full models with all explanatory variables
309 entered simultaneously (table 3). Consequently, the final sample size is 88 mammalian species (out

310 of 101 species) because brain size data were missing for 13 species. However, repeating the
311 analyses by excluding brain size and keeping only cooperative breeding as sociality trait, which is
312 available for the entire species pool, the results of cooperative breeding remain unchanged (results
313 not shown).

314

315 3. Results

316 (a) Occurrence of senescence in birds and mammals

317 Reproductive senescence was detected in 61% (22 out of the 36 species) of bird species and 68%
318 (69 out of 101 species) of mammal species. The occurrence of reproductive senescence was similar
319 in birds and mammals (Chi-squared test $\chi^2 = 0.34$, df = 1, $p = 0.562$). The probability of detecting
320 reproductive senescence tended to increase with sample size in birds ($\beta \pm \text{s.e.} = 0.43 \pm 0.31$, $p =$
321 0.16), but this effect was not statistically significant (as opposed with mammals, see [31]).

322

323 (b) Allometry, pace of life and the degree of sociality in birds

324 Results of occurrence, rate and onset of reproductive senescence in birds are presented in table 2
325 and table S3.

326 The occurrence of reproductive senescence in birds was unrelated to body size and pace of life, and
327 was independent of the reproductive trait used to assess reproductive senescence. None of the
328 sociality traits was associated with the probability to detect reproductive senescence (table 2a, table
329 S3a).

330 The rate of reproductive senescence decreased non-linearly with increasing body size (linear term: β
331 $\pm \text{s.e.} = -3.23 \pm 0.81$; quadratic term: $\beta \pm \text{s.e.} = -1.41 \pm 0.69$), decreased linearly with an

332 increasingly slower pace of life ($\beta \pm \text{s.e.} = -0.89 \pm 0.23$), and varied among reproductive traits used
333 to assess reproductive senescence. The rate of reproductive senescence was the slowest when using
334 birth rates, intermediate when using the number of hatchlings and fastest when using the number of
335 fledglings. Data standardization did not explain substantial variation in the rate of reproductive
336 senescence either. The rate of reproductive senescence tended to decrease with increasingly later
337 onset of senescence, although this effect was not statistically significant. None of the sociality traits
338 was associated with the rate of reproductive senescence, which does not support H1. Once the
339 marked effect of pace of life was removed from the model, the rate of reproductive senescence was
340 slower in colonial birds than in solitary breeders ($\beta \pm \text{s.e.} = -1.06 \pm 0.35$), in support of H2 (table
341 2b, table S3b).

342 The onset of reproductive senescence increased linearly with both body size ($\beta \pm \text{s.e.} = 0.32 \pm 0.04$)
343 and slower pace of life ($\beta \pm \text{s.e.} = 0.39 \pm 0.14$). None of the sociality traits was related to the age at
344 onset of reproductive senescence, which does not support H1. Once the strong effect of pace of life
345 was removed from the model, the onset of reproductive senescence was later in colonial birds than
346 in solitary species ($\beta \pm \text{s.e.} = 0.41 \pm 0.21$), in support of H2 (table 2c, table S3c).

347 These results do not support H1, but do support H2, which involves an indirect relationship between
348 degree of sociality and both the rate and onset of reproductive senescence via a slowing down of the
349 overall pace of life in species with higher degree of sociality.

350 **Table 2.** Base models of occurrence (a), rate (b) and onset (c) of reproductive senescence in birds
351 (see table S3 for AIC-based stepwise forward model selection in birds). PPC size and PPC pace are
352 the phylogenetic principal components describing size and pace of life, respectively. Models on the
353 left include pace of life, while those on the right do not include pace of life. The statistically
354 significant linear or polynomial effect of pace of life (PPC pace and poly(PPC pace), respectively)
355 is marked in bold in models on the left side. Social traits are italicized and those with statistically

356 significant effect are italicized and marked in bold. α and λ – phylogenetic signal; AIC – Akaike
 357 Information Criterion; n – sample size (number of species).

including pace of life (PPC pace)				excluding pace of life (PPC pace)			
<i>(a)</i> occurrence of reproductive senescence				<i>(a)</i> occurrence of reproductive senescence			
predictors	β (s.e.)	z	p	predictors	β (s.e.)	z	p
intercept	0.57 (0.37)	1.53	0.1254	intercept	0.57 (0.37)	1.53	0.1254
model stats: $\alpha = 0.1860$, AIC = 49.04, $n = 36$							
<i>(b)</i> log rate of reproductive senescence				<i>(b)</i> log rate of reproductive senescence			
predictors	β (s.e.)	t	p	predictors	β (s.e.)	t	p
intercept	-3.37 (0.38)	8.89	< 0.0001	intercept	-3.14 (0.45)	6.98	< 0.0001
poly(PPC size, 2)1	-3.23 (0.81)	4.00	0.001	poly(PPC size, 2)1	-1.10 (0.88)	1.25	0.2291
poly(PPC size, 2)2	-1.41 (0.69)	2.04	0.0584	poly(PPC size, 2)2	-2.25 (0.75)	2.98	0.0088
PPC pace	-0.89 (0.23)	3.79	0.0016	repr. trait (no. hatchlings)	1.40 (0.58)	2.40	0.0288
repr. trait (no. hatchlings)	0.97 (0.54)	1.80	0.091	repr. trait (no. fledglings)	1.08 (0.45)	2.38	0.0299
repr. trait (no. fledglings)	1.12 (0.41)	2.73	0.0149	coloniality	-1.06 (0.35)	3.01	0.0084
model stats: $\lambda = 0.000$, AIC = 53.71, $n = 22$				model stats: $\lambda = 0.000$, AIC = 57.93, $n = 22$			
<i>(c)</i> log onset of reproductive senescence				<i>(c)</i> log onset of reproductive senescence			
predictors	β (s.e.)	t	p	predictors	β (s.e.)	t	p
intercept	2.16 (0.10)	22.65	< 0.0001	intercept	2.05 (0.14)	14.16	< 0.0001
PPC size	0.32 (0.04)	7.37	< 0.0001	PPC size	0.24 (0.05)	4.88	0.0001
PPC pace	0.39 (0.14)	2.88	0.0096	coloniality	0.41 (0.21)	1.96	0.0648
model stats: $\lambda = 0.000$, AIC = 30.19, $n = 22$				model stats: $\lambda = 0.000$, AIC = 34.10, $n = 22$			

358

359 (c) Allometry, pace of life and the degree of sociality in mammals

360 Results of occurrence, rate and onset of reproductive senescence in mammals are presented in table

361 3.

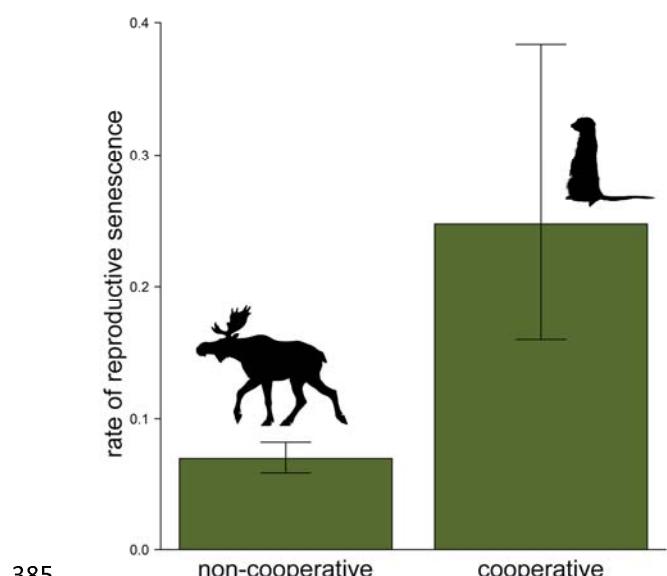
362 Reproductive senescence was more likely to be detected when data originated from longitudinal
 363 rather than transversal studies ($\beta \pm \text{s.e.} = -1.29 \pm 0.52$). Larger-sized mammals were more likely to
 364 experience reproductive senescence than smaller ones ($\beta \pm \text{s.e.} = 0.23 \pm 0.10$). Neither relative brain
 365 size, nor cooperative breeding was related to the probability to detect reproductive senescence in
 366 mammals (table 3a).

367 The rate of reproductive senescence decreased linearly with increasing body size ($\beta \pm \text{s.e.} = -0.43 \pm$
 368 0.06) and non-linearly with increasingly slower pace of life (linear term: $\beta \pm \text{s.e.} = -4.45 \pm 1.35$;

369 quadratic term: $\beta \pm \text{s.e.} = -2.41 \pm 1.08$). Contrary to H1, cooperative breeding mammals had higher
370 rates of reproductive senescence as compared with non-cooperative species ($\beta \pm \text{s.e.} = 1.3 \pm 0.43$;
371 figure 1), while relative brain size was unrelated to the rate of reproductive senescence. When the
372 marked effect of pace of life was removed from the model, species with larger relative brain size
373 had slower rate of reproductive senescence ($\beta \pm \text{s.e.} = -0.64 \pm 0.32$), in support to H2. When the
374 pace of life was not controlled for, however, the relationship between cooperative breeding and the
375 rate of reproductive senescence disappeared, which does not support H1 (table 3b).

376 The age at onset of reproductive senescence increased linearly with both body size and increasingly
377 slower pace of life ($\beta \pm \text{s.e.} = 0.23 \pm 0.05$). Neither relative brain size, nor cooperative breeding was
378 related to the age at onset of reproductive senescence in mammals, which does not support H1.
379 Once the marked effect of pace of life was removed from the models, species with large relative
380 brain size showed a later onset of senescence than species with small relative brain size ($\beta \pm \text{s.e.} =$
381 0.38 ± 0.19 ; table 3c), in support to H2.

382 As in birds, these results do not support H1, but support H2 that involves an indirect relationship
383 between degree of sociality and the rate and onset of reproductive senescence via a slowing down of
384 the overall pace of life in species with higher degree of sociality.



386 **Figure 1.** Difference in the rate of reproductive senescence (\pm s.e.) between cooperative breeding
 387 and non-cooperative breeding mammals. Estimated marginal means are plotted, which were
 388 extracted from the full model of rate of reproductive senescence with pace of life included among
 389 the predictors (see table 3b).

390

391 **Table 3.** Full models of occurrence (a), rate (b) and onset (c) of reproductive senescence in
 392 mammals. PPC size and PPC pace are the phylogenetic principal components describing size and
 393 pace of life, respectively. Models on the left include pace of life, while those on the right do not
 394 include pace of life. The statistically significant linear or polynomial effect of pace of life (PPC
 395 pace and poly(PPC pace), respectively) is marked in bold in models on the left side. Social traits are
 396 italicized and those with statistically significant effect are italicized and marked in bold. α and λ –
 397 phylogenetic signal; AIC – Akaike Information Criterion; n – sample size (number of species).

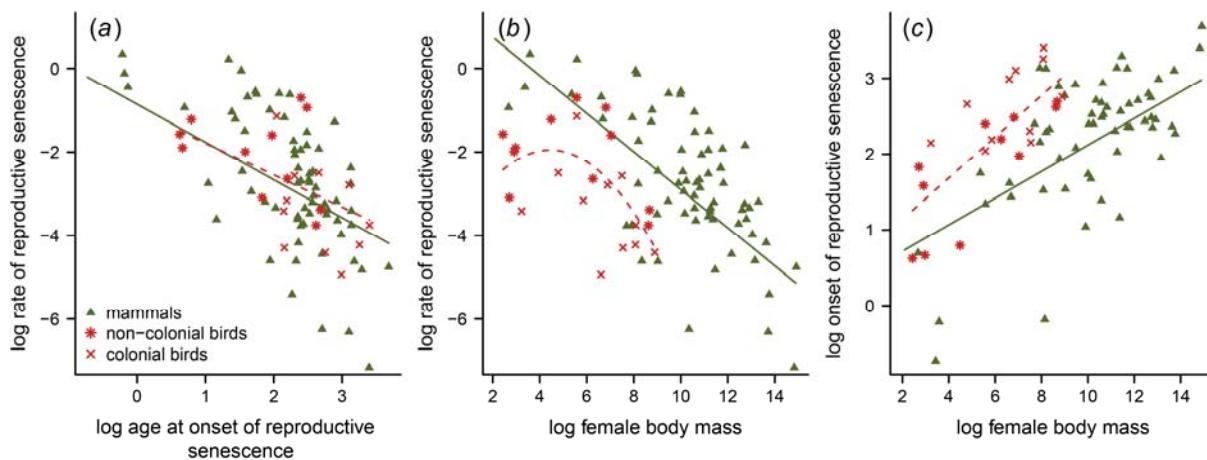
including pace of life (PPC pace)				excluding pace of life (PPC pace)			
(a) occurrence of reproductive senescence				(a) occurrence of reproductive senescence			
predictors	β (s.e.)	z	p	predictors	β (s.e.)	z	p
intercept	1 (0.44)	2.26	0.0236	intercept	1.13 (0.43)	2.62	0.0088
quality (transversal)	-1.29 (0.51)	2.51	0.0119	quality (transversal)	-1.29 (0.52)	2.48	0.0132
hunted (yes)	-0.31 (0.6)	0.51	0.6074	hunted (yes)	-0.4 (0.6)	0.67	0.5058
PPC size	0.23 (0.1)	2.18	0.0294	PPC size	0.23 (0.1)	2.27	0.0233
PPC pace	-0.01 (0.4)	0.03	0.9755				
<i>residual brain size</i>	<i>1.01 (0.64)</i>	<i>1.59</i>	<i>0.1129</i>	<i>residual brain size</i>	<i>0.99 (0.61)</i>	<i>1.62</i>	<i>0.1062</i>
<i>cooperative breeding</i> (yes)	<i>0.1 (0.82)</i>	<i>0.12</i>	<i>0.9077</i>	<i>cooperative breeding</i> (yes)	<i>0.02 (0.83)</i>	<i>0.02</i>	<i>0.9855</i>
model stats: $\alpha = 0.0434$, AIC = 109.46, $n = 88$				model stats: $\alpha = 0.0544$, AIC = 107.28, $n = 88$			
(b) log rate of reproductive senescence				(b) log rate of reproductive senescence			
predictors	β (s.e.)	t	p	predictors	β (s.e.)	t	p
intercept	-2.12 (0.59)	3.58	0.0008	intercept	-1.6 (0.54)	2.97	0.0045
log onset of senescence	-0.03 (0.27)	0.12	0.9083	log onset of senescence	-0.33 (0.24)	1.37	0.1758
quality (transversal)	-0.06 (0.28)	0.21	0.8370	quality (transversal)	-0.07 (0.3)	0.23	0.8170
hunted (yes)	0.54 (0.35)	1.56	0.1260	hunted (yes)	0.56 (0.36)	1.57	0.1220
PPC size	-0.43 (0.06)	6.73	< 0.0001	PPC size	-0.44 (0.08)	5.37	< 0.0001
poly(PPC pace, 2)1	-4.45 (1.35)	3.28	0.0019				
poly(PPC pace, 2)2	-2.41 (1.08)	2.24	0.0295				
<i>residual brain size</i>	<i>-0.14 (0.31)</i>	<i>0.46</i>	<i>0.6483</i>	<i>residual brain size</i>	<i>-0.64 (0.32)</i>	<i>2.03</i>	<i>0.0475</i>
<i>cooperative breeding</i> (yes)	<i>1.3 (0.43)</i>	<i>3.05</i>	<i>0.0037</i>	<i>cooperative breeding</i> (yes)	<i>0.85 (0.49)</i>	<i>1.71</i>	<i>0.0927</i>
model stats: $\lambda = 0.0417$, AIC = 161.09, $n = 58$				model stats: $\lambda = 0.2794$, AIC = 171.72, $n = 58$			

(c) log onset of reproductive senescence				(c) log onset of reproductive senescence			
predictors	β (s.e.)	<i>t</i>	<i>p</i>	predictors	β (s.e.)	<i>t</i>	<i>p</i>
intercept	1.81 (0.18)	10.33	< 0.0001	intercept	1.87 (0.24)	7.63	< 0.0001
quality (transversal)	-0.17 (0.13)	1.3	0.1995	quality (transversal)	-0.17 (0.14)	1.18	0.2444
hunted (yes)	0.15 (0.16)	0.94	0.3494	hunted (yes)	0.04 (0.17)	0.21	0.8311
PPC size	0.18 (0.04)	4.8	< 0.0001	PPC size	0.23 (0.05)	5	< 0.0001
PPC pace	0.54 (0.13)	4.11	0.0001	<i>residual brain size</i>	0.38 (0.19)	2.01	0.0499
<i>residual brain size</i>	0.1 (0.17)	0.56	0.5811	<i>cooperative breeding (yes)</i>	0.12 (0.26)	0.47	0.6375
<i>cooperative breeding (yes)</i>	-0.13 (0.25)	0.55	0.5861	model stats: $\lambda = 0.6053$, AIC = 85.94, $n = 58$	model stats: $\lambda = 0.8102$, AIC = 98.5, $n = 58$		

398

399 (d) Comparing reproductive senescence between birds and mammals

400 In both classes, the rate of reproductive senescence tended to decrease with increasingly later onset
 401 of reproductive senescence, with the same apparent strength (figure 2a). However, the relationship
 402 was statistically significant only in mammals likely because of a lack of power (smaller sample
 403 size) in birds. When looking at the allometric relationships, the rate of reproductive senescence
 404 decreased (figure 2b) and the onset of reproductive senescence occurred later with increasing size in
 405 both birds and mammals (figure 2c). Interestingly, for a given body mass, mammals displayed both
 406 steeper and earlier reproductive senescence than birds did (figure 2b,c), which is in line with the
 407 common view that birds senesce less than similar-sized mammals.



408

409 **Figure 2.** Association between (a) age at onset and rate of reproductive senescence, (b) female
 410 body mass and rate of reproductive senescence, and (c) female body mass and age at onset of

411 reproductive senescence across bird species (* non-colonial, × colonial) and mammal species (▲).
412 Female body mass was used here to measure body size because it captures the differences in size
413 range between birds and mammals unlike PPC size, and it is very strongly correlated with PPC size
414 (table S2). Slopes were obtained from single-predictor phylogenetic regressions between the plotted
415 variables (dashed line for birds, continuous line for mammals). Polynomial effect of size is plotted
416 only for rate of senescence in birds because the quadratic term was only statistically significant in
417 this model (see tables 2 and 3).

418

419 4. Discussion

420 A previously published review revealed an increasing number of case studies reporting reproductive
421 senescence in the wild [2]. Here, we quantified the occurrence of female reproductive senescence
422 on the largest species-level data set so far compiled on birds and mammals. We found that the
423 proportion of species that display detectable reproductive senescence is similar in avian (0.61;
424 present study) and mammalian (0.68; [31]) species. Interestingly, these proportions are similar to
425 those reported in a previous comparative study of 19 species of birds and mammals (0.65; [5]).
426 However, as the current prevalence of reproductive senescence is likely to be under-estimated (see
427 [31] for further discussion), the biological meaning of these values is disputable. Nevertheless, these
428 studies together emphasize that reproductive senescence is the rule rather than the exception, at
429 least in endotherm vertebrates. The positive effect of sample size on the probability of detecting
430 senescence in mammals (see [31]) constitutes a limitation of our analyses, although this limitation is
431 not detectable for birds, likely due to the smaller data set in this class.

432 Our findings highlight that birds display a later onset and a slower rate of reproductive senescence
433 as compared with similar-sized mammals. Note that the strength of senescence in birds increases
434 with offspring developmental phase considered for senescence estimates (i.e. from birth rate to

435 number of hatchlings and number of fledglings), while for mammals, senescence was only
436 computed for birth rates. Therefore, we expect that the differences in onset and rate of reproductive
437 senescence between the two classes would be even stronger if weaning success were also
438 considered in mammals. This notion is supported by a recent review showing that maternal effect
439 senescence (i.e. an increasing offspring mortality with mother age, termed Lansing effect) is very
440 common in mammals, while birds being conspicuous exceptions [59]. The more intense
441 reproductive senescence in mammals than in same-sized birds we report matches the class
442 differences reported in longevity (i.e. birds live c.a. 1.5 times longer than similar-sized mammals
443 [60]). Birds also display a much slower pace of life, and, for a given pace of life, birds and
444 mammals of a given size have similar senescence patterns [5]. This suggests that the *modus*
445 *operandi* of senescence has a deep evolutionary root and is mostly shaped by allometric constraints
446 and pace of life. To test whether the differences between the two classes are explained by flight
447 capacity in birds, and hence their lower environmentally driven mortality, a comparison of
448 reproductive senescence between birds and flying mammals would be promising (see [61] for
449 longevity).

450 In line with previous observations for other biological times (e.g. longevity, gestation length; see
451 [62]), we found strong effects of allometry and pace of life on both the rate and the onset of
452 reproductive senescence in both birds and mammals. The heavier and slower-paced a species is, the
453 more postponed and slower its senescence is. Both senescence metrics correspond to biological
454 times with a dimension of time for the onset of senescence and a dimension of frequency (i.e.
455 inverse of time) (sensu [34]) for the rate of senescence, which explains the negative relationship we
456 found between the rate and the onset of senescence across birds and mammals. Our analyses thus
457 provide a first evidence that these senescence metrics can be interpreted as life-history traits
458 describing the speed of the life cycle of a given species, alike development time [63], age at first
459 reproduction [64] or longevity [65], which have been much more intensively studied. Our results,
460 which are based on the largest number of bird and mammal species compiled to date, bring

461 convincing support that the process of reproductive senescence is embedded in the life-history
462 strategy of a given species [5,20,21] and has a role in the evolution of life histories.

463 The degree of sociality appears to have a very limited direct influence on reproductive senescence
464 when the effects of allometry and pace of life are accounted for, which supports the view expressed
465 above that reproductive senescence in a given species is mostly driven by the species size and
466 position on the slow-fast continuum of life histories. With the exception of cooperative breeding in
467 mammals, none of the sociality traits we analysed (i.e. relative brain size in birds and mammals,
468 colonial breeding and parental cooperation in birds) were associated with either the occurrence or
469 the rate and onset of reproductive senescence. These results support the conclusions reached about
470 the putative role of sociality in the evolution of actuarial senescence and longevity [7].

471 One striking result of this work is that the degree of sociality was associated with a decreased
472 strength of senescence in terms of both rate and onset when species differences in pace of life were
473 not controlled for. As these associations vanished when we controlled for the pace of life, we
474 conclude that the social mode of life *per se* does not influence reproductive senescence. Instead, the
475 social lifestyle seems to shape the entire life-history strategy, which supports H2 and refutes H1.

476 Cooperative breeders often display delayed dispersal and reproductive suppression of subordinates
477 [45], so that the age at first reproduction is also delayed and the number of breeding attempts is thus
478 decreased, which can lead to increased longevity [20]. Moreover, evidence suggests that a slower
479 pace of life is evolutionary linked to colonial breeding in birds [40] and to larger brain size in
480 mammals [66], and species displaying a high degree of sociality also display slower development,
481 delayed age at primiparity, better survival prospects and longer lifespan (reviewed in [7]). Whether
482 a large relative brain size is directly related to a slower pace of life (cognitive buffer hypothesis;
483 [67]) for a given degree of sociality or a large relative brain size is more likely to evolve in social
484 species (social brain hypothesis; [41]), which leads to slow down the pace of life is currently
485 unknown and requires further investigation. However, we cannot rule out the alternative hypothesis
486 (H3) that pace of life has independent effects on both social lifestyle and reproductive senescence,

487 involving the absence of a functional link between reproductive senescence and the degree of
488 sociality. The current view is that sociality shapes the evolution of life histories and senescence [7].
489 However, consistent with the alternative hypothesis, there is evidence in birds showing that species
490 in which a slow pace of life have evolved (i.e. long life) are more prone to evolve a social lifestyle
491 (cooperative breeding) [68]. Therefore, from our findings, we can likely reject a direct association
492 between reproductive senescence and degree of sociality (H1), but whether they are indirectly
493 related through the shaping of senescence by the pace of life (H2) or simply independent responses
494 to the pace of life (H3) cannot be assessed. Future studies using a phylogenetic path analysis or
495 ancestral character reconstruction approach for sociality, life history and senescence traits could
496 differentiate between the latter two alternatives. This analysis will require much improved metrics
497 of the degree of sociality.

498 It might be premature to conclude firmly that the degree of sociality has no direct effect on the
499 magnitude of reproductive senescence. Currently, we lack accurate metrics for measuring the
500 degree of sociality across a wide range of species and the metrics we used in this study have
501 limitations. For instance, cooperative breeding would require a more detailed typology based on
502 four classes (i.e. solitary, social, communal and cooperative; as per [51]) to describe accurately the
503 different levels of social complexity. Moreover, because all colonial species in our data set are
504 seabirds and occupy thus marine (aquatic) habitats, colonial breeding might be confounded by
505 habitat type if aquatic species evolve slower pace of life irrespective of coloniality. However,
506 contrary to this expectation, terrestrial organisms generally have a slower pace of life than aquatic
507 ones [69], which suggests that coloniality might play a role in the evolution of pace of life without
508 being confounded by habitat type. Nevertheless, future studies will be required to assess whether
509 the association between coloniality and reproductive senescence differs (with and without
510 accounting for the pace of life) between terrestrial and marine colonial species. Unfortunately, we
511 failed to identify any data fulfilling our selection criteria on reproductive senescence in terrestrial
512 colonial birds. We also relied on the social brain hypothesis, which proposes that relative brain size

513 is larger in species with a higher degree of social bonds [41], to justify our use of the relative brain
514 size as a measure of the degree of sociality. This hypothesis has received so far mixed support when
515 assessing its plausibility in animal taxa with a wide diversity of social systems [41,70]. However,
516 the social brain hypothesis holds for species displaying complex social interactions, such as
517 cetaceans or primates [41,71]. Our results based on relative brain size should also be treated with
518 caution because brain size is only a rough index of sociality and is related to other life-history traits
519 that might influence senescence (e.g. relationship with longevity [72,73]). Taken together, our
520 conclusion that the degree of sociality has no direct influence on reproductive senescence in birds
521 and mammals will need to be investigated more thoroughly when better measures of the degree of
522 sociality will be available for a substantial set of species. The recent development of social network
523 analysis [74], which allows detailed accounts of individual interactions within populations, should
524 play a key role for doing that.

525 Interestingly, the only detectable direct effect of the degree of sociality on reproductive senescence
526 was opposite to our prediction. We found that cooperatively breeding mammals senesce faster, not
527 slower, than non-cooperative ones for a given size and pace of life. At first sight, this finding
528 contradicts within-population studies that showed almost consistently that helpers buffer the
529 demographic senescence of breeders [7,45]. However, cooperative breeding might have opposite
530 effect on reproductive senescence depending on the level of biological organization we consider.
531 For instance, getting the breeder tenure requires winning aggressive social interactions that increase
532 the level of physiological stress at the long term [75,76], which might exacerbate reproductive
533 senescence [8]. Additionally, the buffered effect of cooperative breeding on reproductive
534 senescence among individuals within a population of a given species can translate into an increased
535 reproductive senescence of cooperative breeding species compared with non-cooperative breeding
536 ones. Within a population of cooperative breeders, reproductively active individuals (i.e.
537 dominants) usually receive alloparental assistance from helpers (i.e. subordinates), which decreases
538 the cost of a given reproductive effort and leads thereby either to a postponed onset or to a

539 decelerated rate of reproductive or actuarial senescence (e.g. load-lightening hypothesis; [24]). For
540 instance, in Alpine marmots (*Marmota marmota*), individuals that have benefited from more
541 helping during their prime-age reproductive stage display a reduced actuarial senescence compared
542 to those that received less help [77], leading to increased individual heterogeneity in the amount of
543 senescence. At the population level, as considered in across-species analyses, the reproductive
544 suppression and associated physiological stress of individuals that help repeatedly before reaching a
545 dominant status and/or the paucity of substantial help when being breeders might lead to more
546 pronounced reproductive senescence. Overall, at the population level, increased costs of helping
547 when subordinate or lack of help when dominant for a large number of individuals might
548 counterbalance the benefits of having many helpers during breeding events that only a reduced
549 number of individuals enjoy. This strong individual heterogeneity in the strength of reproductive
550 senescence within populations of cooperative breeders might lead the average magnitude of
551 reproductive senescence to be higher in these species than in non-cooperatively breeding ones. An
552 alternative explanation is that females of cooperatively breeding mammals have higher reproductive
553 output, which, for a given pace of life, ultimately results in higher rate of reproductive senescence.
554 Indeed, in mammal species in which females receive offspring provisioning help from males,
555 females have higher reproductive output (larger litter size and shorter inter-birth intervals; [78,79]).

556

557 5. Conclusions

558 Our results indicate that degree of sociality is not directly associated with female reproductive
559 senescence. Instead, the positive covariation between the degree of sociality and a slower pace of
560 life has deeper evolutionary roots, which encompass both a later onset and a slower rate of
561 reproductive senescence.

562

563 **Ethics.** This study does not have ethical aspects.

564 **Data accessibility.** The data sets supporting this article have been uploaded as part of the Electronic Supplementary

565 Material (see ESM ‘Data set’).

566 **Authors’ contributions.** C.I.V., J.-F.L. and J.-M.G. designed the study; C.I.V., J.-F.L., O.V., P.L.P., V.R. and J.-M.G.

567 provided data; O.V. and V.R. carried out the statistical analyses; C.I.V., O.V., J.-F.L. and J.-M.G. drafted the

568 manuscript with considerable help from P.L.P. and V.R.; all authors approved the final version of the manuscript.

569 **Competing interests.** We declare we have no competing interests.

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576

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