

1 **Why don't long-finned pilot whales have a widespread post-reproductive**
2 **lifespan? Insights from genetic data.**

3 **Hazel J. Nichols*^{1,2}, Kevin Arbuckle^{1,3}, Karen Fullard⁺⁴, William Amos⁴**

- 4 1. Department of Biosciences, College of Science, Swansea University, Swansea, UK.
5 2. Department of Animal Behaviour, Bielefeld University, Postfach 100131, Bielefeld, Germany.
6 3. Department of Evolution, Ecology and Behaviour, University of Liverpool, Liverpool, UK.
7 4. Department of Zoology, University of Cambridge, Cambridge, UK.

8
9

10 +current address: Nuclear Medicine Department, St Vincent's Hospital, 390 Victoria Road,
11 Darlinghurst, Sydney, NSW 2010, Australia.

12 *Corresponding Author Email: h.j.nichols@swansea.ac.uk

13 **Running Header: kinship dynamics in pilot whales**

14

15 **OrcID**

16 Hazel J Nichols: <https://orcid.org/0000-0002-4455-6065>

17 Kevin Arbukle: <https://orcid.org/0000-0002-9171-5874>

18 William Amos: <https://orcid.org/0000-0002-0971-9914>

19 **Abstract**

20 In a handful of mammals, females show an extended post-reproductive lifespan
21 (PRLS), leading to questions over why they spend a substantial portion of their lifespan non-
22 reproductive. Theoretical and empirical studies suggest that PRLS may evolve when (1)
23 demographic patterns lead to increasing local relatedness as females age, and (2) females
24 come into reproductive competition with their daughters, as these conditions lead to high
25 relative benefits of helping kin versus reproducing in later life. However, evolutionary
26 pathways to PRLS are poorly understood and empirical studies are scarce. Here, we use a
27 dataset of 1522 individuals comprising 22 pods to investigate patterns of reproduction and
28 relatedness in long-finned pilot whales *Globicephala melas*; a toothed whale without
29 species-wide PRLS. We find a similar relatedness structure to whales with PRLS: pods appear
30 composed of related matriline, and relatedness of females to their pod increases with age,
31 suggesting that this species could benefit from late-life help. Furthermore, females with a
32 large number of philopatric adult daughters are less likely to reproduce, implying
33 intergenerational reproductive competition between females. This suggests that individuals
34 may display a plastic cessation of reproduction, switching to investing in existing offspring
35 when they come into competition with their daughters. To the best of our knowledge, this is
36 the first time such a relationship has been described in relation to PRLS, and it raises
37 questions about whether this represents a step towards evolving PRLS or is a stable
38 alternative strategy to widespread post-reproductive periods.

39 **Key words:** post-reproductive lifespan, menopause, cetacean, fecundity, relatedness,
40 demography, plasticity

41

42 Introduction

43 Mammalian reproductive systems mostly age at approximately the same rate as
44 somatic tissue and females continue to reproduce until death (Ellis et al., 2018a). However,
45 in a small number of species, reproductive and somatic ageing are decoupled and females
46 stop reproducing long before they die, creating a widespread and extended period of post-
47 reproductive lifespan (PRLS) representing a distinct life stage (Cohen, 2004; Croft et al.,
48 2015; Ellis et al., 2018a). Why older animals do not increase their direct fitness by continuing
49 to reproduce has been hotly debated and a number of hypotheses have been proposed
50 (Cant and Johnstone, 2008; Cohen, 2004; Ellis et al., 2018a; Huber and Fieder, 2018;
51 Lahdenperä et al., 2004; Levitis et al., 2013; Packer et al., 1998). Humans provide the best-
52 studied example. Women tend to have their last birth at around 38 (Towner et al., 2016),
53 followed by a menopause some 10 years later, precluding further reproduction. Post-
54 reproductive women often have long and healthy lives, even in modern day hunter-gatherer
55 populations (Emery Thompson et al., 2007) and historic populations without access to
56 modern medical care (Levitis et al., 2013). Other examples are rare, but include some
57 toothed whales such as killer whales *Orcinus orca* (Foster et al., 2012), short-finned pilot
58 whales *Globicephala macrorhynchus* (Kasuya and Marsh, 1984), narwhals *Monodon*
59 *monoceros* (Ellis et al., 2018b), beluga whales *Delphinapterus leucas* (Ellis et al., 2018b)
60 Asian elephants *Elephas maximus* (Chapman et al., 2019) and possibly also false killer
61 whales *Pseudorca crassidens* (Photopoulou et al., 2017) (but see Ellis et al. (2018b)).

62 Explanations for PRLS fall into two main classes; non-adaptive and adaptive. Non-
63 adaptive decoupling of reproductive and somatic ageing may occur if traits that are strongly
64 selected early in life have negative consequences on reproduction in late life, and/or if traits
65 associated with aging are less visible to natural selection because few individuals live to
66 express them (Hamilton, 1966; Packer et al., 1998; Williams et al., 2006). Similarly, PRLS may
67 evolve due to links with other aspects of life-history even without impacts on fitness. For
68 example, in guppies, *Poecilia reticulata*, selection on reproductive lifespan appears to co-
69 select for post-reproductive lifespan (Reznick et al., 2005). Furthermore, disease and other
70 stochastic processes are likely to explain why, in many mammalian species, a small
71 proportion of females have been observed to have post-reproductive periods (Cohen,

72 2004). As this is unlikely to represent a distinct life-stage, this phenomenon is termed post
73 reproductive viability (Levitis et al., 2013) to distinguish it from PRLS affecting all females.

74 While short periods of postreproductive viability may arise non-adaptively, the
75 extended periods of PRLS are likely to be the result of adaptive processes (Nichols et al.,
76 2016). Adaptive explanations for PRLS focus on the fitness benefits that older females may
77 continue to accrue through behaviors that increase the fitness of their descendants (Croft et
78 al., 2015). Such explanations have received empirical support in humans, where the
79 presence of grandmothers increases the production of grand-offspring (Lahdenperä et al.,
80 2004; Levitis et al., 2013; Sear and Mace, 2008) and in killer whales, where post-
81 reproductive females substantially enhance the survival of their own offspring (Foster et al.,
82 2012), for example by providing valuable ecological knowledge (Brent et al., 2015). The
83 relative benefits of helping rather than reproducing may be enhanced by rising costs of
84 gestation and birth with age (Grimes, 1994) and by extended periods of offspring
85 dependency during which offspring lose fitness if the mother dies (Shanley and Kirkwood,
86 2001).

87 Where adaptive PRLS evolves through kin selection, the social system likely plays a
88 critical role. Specifically, older females need access to close relatives to help, which will only
89 occur in species that live in family groups (Nichols et al., 2016); a situation that usually arises
90 through offspring remaining with their mothers beyond weaning. Indeed, philopatry has
91 been proposed to be particularly important for the evolution of PRLS because it can lead to
92 an increase in average relatedness to other group members throughout the lifetime of a
93 female (Johnstone and Cant, 2010). For example, ancestral human females probably
94 dispersed to new family groups before reproducing, leading to an initial low relatedness to
95 their new families which increases over time as a result of her subsequent descendants
96 (Johnstone and Cant, 2010). In cetaceans such as killer whales, both sexes are philopatric,
97 but mating occurs outside of the group (Croft et al., 2017; Pilot et al., 2010). Here, average
98 relatedness between a young female and her social group is relatively low because she was
99 the product of an extra-group mating. However, her offspring remain within the social
100 group, and hence average relatedness between the female and other group members
101 increases over the female's lifespan (Croft et al., 2017). This change in relatedness over time
102 may lead to a predisposition towards the evolution of an adaptive period of post-

103 reproductive helping (Johnstone and Cant, 2010). Such a link between philopatry and
104 prolonged PRLS is supported by a comparative study of mammals (Nichols et al., 2016).

105 Although philopatry generates a relatedness structure within which kin selection can
106 favor late-life helping, the evolution of PRLS also depends on a balance between its relative
107 costs and benefits (Cant and Johnstone, 2008; Cant et al., 2009; Johnstone and Cant, 2010).
108 First, there is unlikely to be a fitness benefit to older females from ceasing reproduction if
109 there is no fitness cost to their relatives when they do breed. PRLS should therefore only
110 evolve where inter-generational reproductive competition occurs (Cant and Johnstone,
111 2008). Evidence for this from humans is mixed (Croft et al., 2015), but support has been
112 found in killer whales, where local group relatedness increases with age and the costs of co-
113 breeding with kin are higher for older than for younger females (Croft et al., 2017). Second,
114 post-reproductive females must be able to contribute towards increasing the fitness of their
115 relatives. For example, post-reproductive resident killer whales have been shown to act as a
116 repository for ecological information, leading their groups to find salmon in times of food
117 shortage (Brent et al., 2015). Maternal death consequently has a strong impact on offspring
118 survival, especially on sons, even when the offspring are adult (Foster et al., 2012). Similarly,
119 PRLS has been proposed to be associated with foraging niches that require the build-up of
120 neural capital, and hence result in older individuals being able to acquire an excess of
121 resources, which they may redistribute to their relatives (Aimé et al., 2017). Thus, where
122 there is no reproductive competition, the benefits of ecological knowledge are limited
123 and/or there are few opportunities for alloparental care, adaptive PRLS should not evolve.

124 One interesting puzzle regarding PRLS is why it pays to evolve irreversible
125 reproductive cessation, as appears to occur in all species currently identified as having
126 significant PRLS (Ellis et al., 2018b). If females maintained plasticity in PRLS, they may be
127 able to adaptively switch resources between producing further offspring and helping
128 existing offspring, dependent on their current circumstances. For example, females with few
129 or no offspring within their group (those whose previous offspring have died or emigrated)
130 would likely benefit from further reproduction, regardless of their age. Here, the sex of a
131 female's philopatric offspring may be important. For example, where both sexes remain
132 philopatric but mating occurs between groups (as occurs in some toothed whales), older
133 females come into conflict with their adult daughters as they both produce offspring in the

134 natal group (Croft et al., 2017). However, they are unlikely to come into conflict with
135 reproductive sons, who's offspring are in other groups. Under these circumstances, older
136 females may benefit from ceasing reproduction when they have daughters of reproductive
137 age in their group but would not benefit if they have only philopatric sons.

138 It is currently unclear why PRLS is not a reversible trait, but it is possible that the
139 physiological mechanisms that govern reductions in fertility may constrain against
140 reversibility (Huber and Fieder, 2018). However, young females of many cooperatively
141 breeding species (species with non-reproductive alloparents) experience reversible declines
142 in fertility when in competition with older relatives (Russell, 2004), suggesting that
143 reversibility may be possible. A further prospect is that some species may display substantial
144 plasticity in the timing of reproductive cessation or may have reversible pauses in
145 reproduction, but these possibilities could be difficult to detect on a population level due to
146 the presence of older reproductive females and because plasticity in fertility in older age
147 may be difficult to distinguish from reproductive senescence (a decline over age in fertility).

148 Toothed whales (Odontoceti) provide an interesting opportunity to investigate
149 patterns of reproduction and their relationship to social organization for several reasons.
150 Firstly, maternal investment tends to be high, either due to high energetic costs of lactation
151 or long periods of offspring dependency (Oftedal, 1997). Secondly, in several species,
152 offspring of one or both sexes remain with their mothers well beyond weaning and may
153 continue to receive maternal care (Brent et al., 2015; Pilot et al., 2010). Third, reproductive
154 senescence is common, with 10 of the 16 species investigated by Ellis et al. (2018b)
155 experiencing reproductive senescence, and at least four (possibly five) of these species
156 exhibiting extended PRLS comparable in duration to humans (Cohen, 2004; Croft et al.,
157 2015; Ellis et al., 2018a; Ellis et al., 2018b). Curiously, although many toothed whales appear
158 to have similar social systems, PRLS varies greatly in presence, length, and timing. For
159 example, short-finned and long-finned pilot whales *Globicephala melas* are very closely
160 related (~1-2mya divergence (Hedges et al., 2006)) sister species that both appear to live in
161 stable, multigenerational, matrilineal groups where both sexes remain philopatric and
162 mating is non-local (Foote, 2008). Both have been studied in drive fisheries and show
163 similar maximum longevity of around 55-60 years, although life-expectancy is generally
164 shorter in long-finned pilot whales (Ellis et al., 2018b). Despite this, the oldest pregnant

165 females found so far for the two species differ greatly in age: 35 years in short-finned
166 (Kasuya and Marsh, 1984) and 55 years in long-finned pilot whales (Martin and Rothery,
167 1993). Accordingly, periods of PRLS differ greatly between the species: PrR (a population-
168 level measure of the proportion of female years spent post-reproductive (Levitis and Lackey,
169 2011)) is 0.26 in the short-finned pilot whale and 0.002 in the long-finned pilot whale (Ellis
170 et al., 2018a). This raises the question of why these two species differ so greatly in PRLS
171 despite having similar social systems and lifestyles.

172 Here, we use data collected in the late 1980s from a long-finned pilot whale drive
173 fishery to help understand why this species does not show PRLS. Specifically, we use
174 microsatellite genotypes of individuals from 22 social groups to test the hypothesis that
175 long-finned pilot whales lack widespread PRLS because older females lack suitable relatives
176 to direct late-life help towards. To do this, we test three predictions: if the relatedness
177 structure of long-finned pilot whales acted as a barrier to the evolution of PRLS, we would
178 expect (1) a lack of relatives within pods, (2) in particular an absence of philopatric adult
179 offspring, and/or (3) no increase in relatedness between females and other group members
180 as females age. Finally, we investigate the hypothesis that individual females could exhibit
181 plasticity in the timing of PRLS by testing the prediction that females are more likely to be
182 pregnant if they have few philopatric offspring in their social group, after accounting for
183 age-related changes in fecundity. Furthermore, as females are likely to experience
184 competition from reproductive daughters but not sons, we also test the prediction that the
185 probability of pregnancy depends on the number of philopatric daughters present in the
186 social group, but is independent of the number of philopatric sons.

187 **Methods**

188 *Physiological and genetic data collection*

189 Data were obtained from 1522 long-finned pilot whales *Globicephala melas*
190 comprising 95% of individuals from 22 pods harvested between 1986 and 1989 as part of a
191 legal traditional subsistence hunt in the Faroe Islands (Zachariassen, 1993). Scientific
192 observers of the harvest were certain that there was no splitting or merging of the pods
193 during the hunt, hence these pods comprised of entire naturally occurring social groups
194 (Bloch et al., 1993a). Pods ranged in size from 16 to 175 individuals (median 57) and

195 contained adults and juveniles of both sexes. Pilot whale social behavior is currently poorly
196 understood, but observational studies suggest that pods may sometimes temporarily split
197 into smaller subunits of ~7 individuals (Augusto et al., 2017b; De Stephanis et al., 2008;
198 Ottensmeyer and Whitehead, 2003). As our data are not longitudinal, we cannot comment
199 on the long-term stability of the pods captured in the hunt, but we have no reason to
200 believe that the pods we sampled are not representative of those found in the wild
201 population (and therefore representative of the social structure within which females find
202 themselves). Nevertheless, as relatedness is likely to be diluted in larger pods, we took pod
203 size into account in our analyses where appropriate.

204 Upon capture, the total body length and sex of whales were recorded, and age was
205 determined by counting the growth layer groups visible in a tooth section (Lockyer, 1993).
206 Skin samples were taken for genetic analysis and females were dissected to confirm
207 whether they were pregnant at the time of capture. Due to time-constraints when sampling
208 a large number of whales, it was not possible to take every measurement for each
209 individual, hence gaps in the data occurred. For individuals without tooth sections (9.7% of
210 whales), age was estimated from length data where possible, following Nichols et al. (2014).
211 Females over 400 cm and males over 500 cm long were likely fully grown so age could not
212 be estimated using length. These individuals were therefore considered as adults but were
213 excluded from analyses where accurate age data was required.

214 Genotyping was carried out as described in Fullard et al. (2000) using a panel of nine
215 highly polymorphic microsatellite loci: 199/200, 417/418, 468/469, 409/470, 415/416, and
216 464/465 (Amos et al., 1993); EV37, EV94, EV1 (Valsecchi and Amos, 1996). A subset of pods
217 for which sampling and morphometric data collection was particularly comprehensive
218 ($N=737$ individuals comprising 11 pods) were genotyped at an additional seven loci: D14 and
219 D22 (Shinohara et al., 1997); FCB6/17, FCB3 and FCB1 (Buchanan et al., 1996); SW10
220 (Richard et al., 1996); Gm8 (Fullard et al., 2000). Although this meant that pods differed in
221 the number of microsatellites used in maternity assignments, previous analyses revealed no
222 effect on patterns of maternity (Nichols et al., 2014). Consequently, we did not include this
223 as a separate factor in our models. Individuals genotyped at fewer than seven markers or
224 that lacked sufficient age and sex information were excluded from downstream analyses.

225 Our analyses always used the maximum number of individuals for which data were
226 available.

227 *Relatedness calculations*

228 Pairwise relatedness was calculated using the program Kingroup (Konovalov et al.,
229 2004). We selected Lynch and Ritland's (1999) measure of relatedness following
230 recommendations by Csilléry et al. (Csilléry et al., 2006), who compared the performance of
231 various measures of relatedness. As relatives are likely to be present within groups, we
232 applied a bias correction that excludes other group-members when calculating relatedness
233 for that pair, as recommended by Konovalov et al. (2004).

234 *Parentage analysis*

235 Maternity analysis was conducted following Nichols et al. (2014) using the program
236 Cervus (Marshall et al., 1998). In brief, females were considered as potential mothers if they
237 were in the same pod and at least 6 years older than the candidate offspring. A threshold of
238 6 years was chosen as females as young as 5 and 6 were very occasionally found to be
239 pregnant. As pods include relatives, simulations to generate the critical value of delta
240 allowed for 10% of candidate mothers being related to the true mother by 0.25. Although
241 almost-complete pods were sampled, it is likely that some mothers had died or emigrated
242 since the offspring was born. Hence, we included the conservative estimate of 50% mothers
243 having been sampled. Re-genotyping 45 samples revealed an average per-allele error rate of
244 0.012, which was incorporated into simulations to generate critical delta.

245 Our downstream analyses incorporated 472 offspring assigned to 280 mothers at a
246 minimum of 90% confidence. A further 250 potential mothers in our dataset had no
247 offspring genetically assigned, bringing the total number of females analyzed to 530.
248 Dissections revealed that 104 of the 530 females (19.6%) were pregnant at the time of
249 capture. The 104 unborn fetuses were assigned to the mother they were dissected from
250 without the need for genetic analyses.

251 *Statistical analyses*

252 Statistical analyses were conducted in R version 3.5.3 using the lme4 package (Bates
253 et al., 2013). Data included multiple individuals from each pod, so generalized linear mixed
254 models (GLMMs) were used to control for pseudoreplication, with pod fitted as a random
255 factor in all models. We tested for a quadratic effect of age in our models, and retained this
256 where significant ($P > 0.05$), tested using analysis of deviance. P values presented are those
257 associated with removing the term from the model.

258 In order to investigate patterns of relatedness between different sex and age groups
259 of individuals, we first calculated the relatedness between all intra-pod comparisons. We
260 then extracted 3 sets of data: 1) relatedness between all females and adult males, 2)
261 relatedness between all females and adult females, and 3) relatedness between all females
262 and all juveniles. Individuals were considered Juvenile if under 10 years of age (Bloch et al.,
263 1993b): although females occasionally give birth younger, parentage analysis assigned just
264 1.6% of offspring to females below 10. We then fit normally-distributed GLMMs to each of
265 these datasets with relatedness as the response variable and pod size, female age and age^2
266 plus the interaction between age and pod size as explanatory variables. Since the data were
267 pairwise relatedness values, individuals were present in the data several times.
268 Consequently, we included individual identity as a random effect in these models in addition
269 to pod identity.

270 To investigate whether the number of offspring assigned to a female changes
271 throughout her lifespan, we constructed a Poisson-distributed GLMM with the number of
272 offspring assigned to each female as the response term and female age and age^2 included as
273 explanatory terms. To investigate the influence of existing offspring on fecundity, we
274 constructed a binomial-distributed GLMM with whether or not a female was pregnant at
275 the time of capture as the response term and age, age^2 and the number of existing
276 philopatric offspring as the explanatory terms. To investigate whether reproductive
277 competition may influence fecundity, we refitted this model including the number of male
278 and female philopatric adult offspring as separate explanatory variables, instead of the total
279 number of offspring.

280 *Ethical note*

281 Data were collected from long-finned pilot whales harvested in the late 1980s as part
282 of a legal traditional subsistence hunt in the Faroe Islands. Whales have been hunted there
283 for at least 700 years (probably considerably longer) and hunts are non-commercial, with
284 the resultant meat being processed and consumed by local communities. No animals were
285 killed for the purposes of scientific data collection; instead, researchers collected data from
286 dead whales with permission from the Faroese government. No payment was made for
287 access to harvested whales or genetic samples. Data collection therefore did not fuel the
288 trade or consumption of whale meat. The authors do not condone whaling. This research
289 was approved by Swansea University College of Science Ethics Committee: SU-Ethics-Staff-
290 290119/111.

291 **Results**

292 *Are pods composed of relatives?*

293 Average levels of relatedness within pods (derived from genetic markers rather than
294 pedigrees) were low but highly variable (mean relatedness within 22 pods = 0.06, range 0.01
295 – 0.23). Low average relatedness is perhaps not surprising given the large sizes of many
296 pods (median 57 individuals, range 16 to 175). While the majority of pod-members had low
297 relatedness, there is also evidence of close relatives being present within pods,
298 demonstrated by the left skew in Figure 1.

299 Furthermore, the vast majority of individuals had multiple close relatives present in
300 their pods, here defined as relatedness over 0.25; the average expected level of relatedness
301 between half siblings (Figure 2a). Some pods appear to comprise several family units,
302 possibly representing separate matrilineal lines (for a clear example, see pod 131 in Figure 2a).
303 These family units are also related to each other, with several ties linking lesser relatives
304 (here defined as relatedness being above 0.125; the average expected level of relatedness
305 between first cousins) between units (e.g. see pod 131, Figure 2b). Similar patterns are
306 shown in other pods (Figures 2a and b). This supports the idea that pods represent extended
307 family groups composed of multiple related matrilineal lines.

308 A small proportion of individuals (43 individuals representing 3.1% of the
309 population) had no close relatives ($r > 0.25$) present in their pod (median 1.5 individuals per
310 pod, range 0-7). There was a greater proportion of males than females with no close

311 relatives (4.6% males, 2.1% females, two-proportions z-test; $\chi^2 = 6.51$, $df=1$, $p=0.0107$),
312 possibly indicating that some males are temporarily associating with a non-natal group in
313 search of mating opportunities. It is also possible that individuals with no close relatives
314 could be present in their natal pod but their closest relatives have died, migrated or may be
315 present in the pod but are not included in our analysis due to PCR failures during genotyping
316 or missing tissue samples (95% of individuals were sampled). Almost all individuals had
317 lesser relatives ($r>0.125$) present within the pod; just 4 individuals, representing 0.29% of
318 the population had no within-pod relatives at $r>0.125$.

319 *Are philopatric adult offspring present with their mothers?*

320 Of the 530 genotyped potential mothers of known age, at least one offspring was
321 genetically assigned to 280 females (mean offspring per female = 0.89, range 0-4). The
322 number of offspring assigned to females increased with age in a quadratic fashion (GLMM:
323 $\chi^2 = 34.52$, $df = 1$, $p = 4.23 \times 10^{-9}$, Figure 3, Table 1). Each female can expect to have one
324 offspring present in their pod by the age of 25, rising to almost two by age 40 (Figure 3). The
325 number of assigned offspring declined in females over 40, possibly due to the death or
326 dispersal of mature offspring, but few data are available for older females so this decline
327 should be interpreted with caution.

328 Both males and females were present in the same pod as their mothers, even up to
329 the ages of 31 (males) and 38 (females) (Figure 4). A total of 69 adult (aged 10+) males
330 (34.6% male offspring) and 116 adult females (43.9% female offspring) were found to be
331 present in the same pod as their mother. This confirms previous analyses of a smaller
332 dataset and demonstrates that both sexes show philopatry well beyond sexual maturity
333 (Amos et al., 1991; Amos et al., 1993).

334 *Does relatedness between females and other group members increase as females age?*

335 Relatedness of females to adult male and female pod-members increased
336 significantly throughout the lifespan, with relatedness of females to males increasing at a
337 faster rate than relatedness between females (Figure 5a; Table 1). The relatedness of
338 females to juveniles also changed significantly throughout the lifespan, although in a
339 quadratic fashion, first increasing and then decreasing (Figure 5a, Table 1). These

340 relationships were influenced by pod size, indicated by the significant interaction between
341 pod size and female age (Table 1, Figure 5b-d), with relatedness being generally lower in
342 larger pods.

343 Females in an average sized pod (median pod size = 57) can expect their relatedness
344 to male pod members to increase from 0.06 when they are born to 0.15 by the time they
345 are 50 years old (Figure 5b). In contrast, their relatedness to adult female pod members
346 remains relatively stable, increasing from 0.11 to 0.14 over the same time period (Figure 5c),
347 while their relatedness to juveniles remains relatively low, not exceeding 0.10 (Figure 5d).
348 These results are similar to the patterns predicted to predispose species to evolving
349 adaptive PRLS by Johnstone and Cant (2010), and the levels of relatedness are only
350 marginally lower than empirical data from toothed whales with prolonged PRLS (Croft et al.
351 (2017) and Table S1).

352 *Are females more likely to be pregnant if they have fewer philopatric offspring?*

353 Dissections found that 104 females of known age were pregnant at the time of
354 capture. We found a quadratic relationship between female pregnancy state and female
355 age, with females of intermediate age being most likely to be pregnant (GLMM: $X^2 = 7.47$, df
356 $= 1$, $p = 0.00626$, Figure 6a, Table 1). This is consistent with reproductive senescence
357 occurring in older females, as has been found previously in long-finned pilot whales and
358 across several other species of toothed whale (Ellis et al., 2018b). After accounting for age-
359 related changes in fecundity, we found that the probability of females being pregnant
360 decreased as the number of existing philopatric offspring belonging to that female increased
361 (GLMM: $X^2 = 10.1$, $df = 1$, $p = 0.00148$, Figure 6b, Table 1). None of the 23 females with 4
362 philopatric offspring were pregnant, 3 of 29 females (10.3%) with 3 philopatric offspring
363 were pregnant, while 21.1% of the 478 females with fewer than 3 philopatric offspring were
364 found to be pregnant at the time of capture.

365 We considered two potential drivers for the relationship between the number of
366 philopatric offspring and current pregnancy. First, older females may be ceasing
367 reproduction when they come into conflict with their reproductive daughters. Second
368 females with a large number of offspring may be more likely to have a current dependent
369 calf, and females with dependent calves are less likely to become pregnant again:

370 dependent calves were found to affect pregnancy status in a previous study (Nichols et al.,
371 2014). To investigate whether the relationship could be explained by reproductive
372 competition, we re-fitted the model of pregnancy status, this time including only adult (aged
373 10+) philopatric offspring. We found that the probability of females being pregnant
374 significantly decreased as the number of existing philopatric daughters increased (GLMM: χ^2
375 = 4.68, df = 1, p = 0.0305, Table 1), but this relationship was not found with the number of
376 philopatric sons (GLMM: χ^2 = 1.39, df = 1, p = 0.238, Table 1).

377 **Discussion**

378 *Is the relatedness structure of long-finned pilot whales likely to act as a barrier to the*
379 *evolution of widespread PRLS?*

380 We used genetic data to show that social groups (pods) of long-finned pilot whales
381 are composed of networks of relatives, often containing several clusters of close relatives
382 ($r > 0.25$) linked together by a mixture of close and lesser relatives ($r > 0.125$). Consistent with
383 this, we confirmed earlier reports of lifelong philopatry of both sexes (Amos et al., 1991;
384 Amos et al., 1993), with sons and daughters being present in the same pod as their mothers
385 well into adulthood and mothers being accompanied by up to four philopatric offspring. The
386 social system of the long-finned pilot whale appears to sit within the bounds of other whale
387 species that have PRLS (Table S1). Resident killer whales, the best studied example, show
388 lifelong philopatry of both sexes (Barrett-Lennard, 2000; Pilot et al., 2010) and bisexual
389 philopatry is possible in the remaining species, although data are extremely limited and
390 some dispersal of one or both sexes is likely (Table S1). These dispersal patterns are
391 supported by evidence from mitochondrial DNA, which shows a single mtDNA haplotype in
392 killer whale pods, indicating a single extended matriline (Barrett-Lennard and Ellis (2001),
393 Table S1), while long-finned pilot whales (Oremus, 2008), false killer whales (Chivers et al.,
394 2010) and a larger aggregation of narwhal (Palsbøll et al., 1997) all comprise multiple
395 haplotypes that represent multiple, potentially related, matriline.

396 Although long-finned pilot whales live in groups of relatives, average within-pod
397 relatedness is generally lower than in short-finned pilot whales and resident killer whales
398 (Table S1); we found that mean relatedness within pods was 0.06 (range 0.01 – 0.23) in
399 comparison to 0.097 (range -0.1 to 0.38) from incomplete sampling of short finned pilot

400 whale pods (Alves et al., 2013), and average pedigree relatedness values of 0.22-0.33
401 between female resident killer whales and the rest of their pod (Croft et al., 2017). These
402 differences in relatedness are likely due to differences in pod size; long-finned pilot whale
403 pods are marginally larger than those of short-finned pilot whales and are considerably
404 larger than those of resident killer whales (Table S1). However, note that studies have used
405 different measures of relatedness, have collected data from different populations and have
406 used different methods to define group-membership (see Table S1 and references therein)
407 so comparisons should be interpreted with appropriate caution.

408 Relatively low relatedness within long-finned pilot whale pods may reduce the
409 benefits of helping (Hamilton, 1964), and hence reduce the probability of late-life help
410 evolving. This might be particularly important if help is directed towards pod-members at
411 random, and if help carries high costs. However, if help is preferentially directed towards
412 related group-members (such as philopatric offspring), relatively low average relatedness
413 may not preclude the evolution of altruistic behavior. Indeed, observational studies of
414 other populations suggest that larger long-finned pilot whale pods may be composed of
415 small, stable sub-units in which average relatedness could be much higher (Augusto et al.,
416 2017b; De Stephanis et al., 2008; Ottensmeyer and Whitehead, 2003). Similar social
417 systems have been observed or hypothesized for all six species of whales with PRLS, with
418 long-term associations between small groups of close relatives that in turn form larger
419 aggregations (although data is severely limited for some species; see Table S1 and
420 references therein). Despite lower average relatedness within groups than some other
421 species with PRLS, it therefore seems unlikely that the social structure of long-finned pilot
422 whale pods constrains against the evolution of a post-reproductive period by preventing
423 females from directing late life help towards relatives, specifically philopatric young.

424 A particularly strong piece of evidence suggesting that long-finned pilot whales have
425 demographic patterns that could predispose them to evolving PRLS comes from age-related
426 changes in relatedness. Johnstone and Cant (2010) predict PRLS will be favored by
427 philopatry when this causes females to become more related to their social group, and
428 particularly to males, as they age. This is what we find for long-finned pilot whales: a
429 female's relatedness to adult males in a median sized pod can be expected to increase from
430 0.06 to 0.15 over her lifespan, while her relatedness to other females increases from 0.11 to

431 0.14. A similar pattern is found in resident killer whales, with pedigree relatedness to other
432 females remaining stable at around 0.33, while relatedness to males increases from 0.16 to
433 0.33, but then decreases again when females enter their post-reproductive period,
434 presumably as they do not continue to produce philopatric offspring beyond this point to
435 compensate for the mortality of existing offspring (Croft et al., 2017). Such patterns are also
436 found in some human populations. For example, matrilineal Mosuo of southwest China
437 display an unusual dispersal system whereby both sexes are philopatric to their natal
438 homestead (Wu Jia-Jia et al., 2013). Men do not live with their wives or children, instead
439 visiting them at night, resulting in a relatedness structure that closely matches Johnstone
440 and Cant's (2010) model predictions (Johnstone and Cant, 2019).

441 *Why don't long-finned pilot whales have PRLS?*

442 Despite displaying a relatedness structure that may predispose them to evolving
443 PRLS, long-finned pilot whales do not show widespread PRLS; only ~4% of adult female long-
444 finned pilot whales had ceased ovulating compared with 25% in short-finned pilot whales
445 (Foote, 2008; Martin and Rothery, 1993), a species that does show PRLS. We also found a
446 pregnant female aged 45, close to the maximum life expectancy. However, we did find
447 evidence of reproductive senescence; there was a peak of pregnancy in females aged in
448 their 20s but relatively few pregnant females over 40 years old. Such patterns are consistent
449 with previous work on a larger dataset of long-finned pilot whales (Martin and Rothery,
450 1993) and are common across many species of mammal in the wild (Nussey et al., 2013).

451 There are several reasons why long-finned pilot whales may not show PRLS. First,
452 there may be few opportunities for helping. In resident killer whales, food can be
453 unpredictable and the ecological knowledge of older females appears to aid its location and
454 results in increased survival of philopatric adult offspring (Brent et al., 2015). Long-finned
455 pilot whales feed mainly on squid, particularly *Loligo pealei* (Desportes and Mouritsen,
456 1988), supplemented with Atlantic mackerel *Scomber scombrus* (Abend and Smith, 1997).
457 Their prey move seasonally with changes in water temperature and with time of day
458 (Serchuk FM and WF, 1974). While it is possible that ecological knowledge could be
459 important in locating mobile prey, local knowledge may be considerably less important if
460 prey are continually followed over long distances, which may happen to a greater degree in

461 long-finned pilot whales than resident killer whales and short-finned pilot whales. However,
462 helping is not necessarily limited to finding food, and older females might offer other forms
463 of help. Augusto et al (Augusto et al., 2017a) found that long-finned pilot whale calves were
464 often 'escorted' by individuals unlikely to be parents. This might provide protection,
465 allowing mothers to spend more time foraging, particularly during deeper dives. Similar
466 behavior is observed in sperm whales (which do not appear to have PRLS) (Konrad et al.,
467 2018). However, little is known about the costs and benefits of escorting and in long-finned
468 pilot whales it does not seem to be primarily conducted by older females (Augusto et al.,
469 2017a), although data are extremely limited, so its relevance to PRLS evolution is unclear.
470 Allonursing, whereby non-mothers suckle young, has also been observed in toothed whales,
471 including wild sperm whales where closer relatives are more likely to allonurse calves
472 (Konrad et al., 2018) and also in captive beluga whales (Leung et al., 2010). Long-finned pilot
473 whales are not known to allonurse, but data on this behavior is extremely difficult to collect
474 due to the difficulties of sexing and ageing individuals and identifying mothers from
475 observational data (Augusto et al., 2017a). Future work on the costs and benefits and
476 distribution of helping behavior in toothed whales with and without PRLS will help to reveal
477 the degree to which patterns of PRLS are explained by helping behavior, however collecting
478 behavioral data on these species is a challenging and time-consuming process.

479 A second potential reason for the absence of PRLS in long-finned pilot whales relates
480 to the possibility that older females in species with PRLS cease reproduction to reduce
481 competition with their own descendants (Cant and Johnstone, 2008; Cant et al., 2009). If
482 competition between generations is low, for example because food is generally not limiting,
483 female long-finned pilot whales may be able to continue to reproduce without reducing the
484 reproductive output of their philopatric offspring. A similar situation appears to exist in the
485 African elephant *Loxodonta africana*, where matriarchs act as a repository for knowledge,
486 and groups led by older, still reproductive, matriarchs have higher reproductive success than
487 groups led by younger females (McComb et al., 2001). Unfortunately, the longitudinal data
488 required to fully understand intergenerational competition in long-finned pilot whales is
489 currently lacking. However, our finding that the probability of being pregnant declines with
490 the number of philopatric daughters suggests that females may refrain from breeding to
491 avoid reproductive competition with existing daughters, and can do so plastically (rather

492 than via an fixed and irreversible PRLS). Reproductive competition between females and
493 their philopatric daughters may therefore be substantial in long-finned pilot whales.

494 Third, it is possible that long-finned pilot whales lack sufficient variation in post-
495 reproductive viability to evolve PRLS. Post-reproductive viability (short post-reproductive
496 periods that don't represent a distinct life stage (Levitis et al., 2013; Levitis and Lackey,
497 2011)) appears to arise by chance in some mammals and may evolve into longer periods of
498 PRLS under appropriate demographic conditions (Nichols et al., 2016). Long-finned pilot
499 whales have higher late-life mortality rates than species with PRLS (Foote, 2008), which
500 could result in too few females reaching a sufficient age to for selection pressure to extend
501 the post-reproductive period (Foote, 2008). However, since post-reproductive viability is
502 found in closely related species (Ellis et al., 2018b), it is unclear why this trait appears to be
503 particularly reduced in long-finned pilot whales. Additionally, our study finds that
504 pregnancy likelihood is influenced by existing offspring, suggesting that there is individual
505 variation in the amount of time spent post-reproductive in long-finned pilot whales. Even if
506 small, this existing variation could present sufficient material for selection on extended
507 PRLS.

508 A final possibility is that PRLS in toothed whales and humans is a result of non-
509 adaptive processes. For example, it may result due to oocytes having a limited 'shelf life'
510 and hence resulting in longer-lived species undergoing early reproductive senescence in
511 comparison to shorter-lived species, unless there is strong selection to the contrary (Huber
512 and Fieder, 2018). However, this seems unlikely to explain why toothed whales with PRLS
513 stop reproducing considerably earlier than species without PRLS (Ellis et al., 2018b). It is also
514 possible that PRLS can result from selection on other traits, such as an extended lifespan in
515 males (Tuljapurkar et al., 2007). However, males of post-reproductive species tend to have
516 shorter lifespans than females, making this possibility unlikely.

517 *Is there any evidence of plasticity in the timing of reproductive cessation?*

518 We found that females were less likely to be pregnant if they had a larger number of
519 genetically assigned offspring present in the pod (while controlling for age dependent
520 changes in fecundity), indicating that female fertility depends on previous reproduction. We
521 note that this relationship persisted after dependent calves were removed from the dataset,

522 suggests that females may refrain from breeding when they have adult offspring present in
523 their pod, rather than simply when they have dependent offspring. This suggests that
524 females with several existing offspring may invest in enhancing the quality of these
525 offspring, rather than in producing further offspring. Such trade-offs appear to occur in
526 other long-lived species with extended periods of maternal care. In humans, for example, a
527 study of 163,827 births to 101,195 mothers across sub-Saharan Africa found that the
528 probability of a child surviving to age 5 decreases by 14% for each subsequent child born to
529 the mother, likely due to increased competition for maternal resources between siblings
530 (Lawson et al., 2012). However, we note that in humans there is currently no evidence that
531 women refrain from reproducing once they have a certain number of children (Towner et
532 al., 2016).

533 A particularly interesting finding is that the fecundity of female long-finned pilot
534 whales was significantly reduced by the presence of philopatric daughters but not sons. This
535 relationship suggests that females may refrain from reproducing (or possibly are actively
536 suppressed) when this brings them into conflict with their reproductive daughters. This
537 could be viewed as a plastic adaptive post-reproductive period, only occurring in females
538 with high potential for reproductive conflict. We suggest that long-term studies of wild long-
539 finned pilot whales investigate this possibility further. Inter-generational reproductive
540 conflict has been shown to occur in killer whales, whereby the mother's offspring are less
541 likely to survive than the daughter's offspring if they are born at the same time (Croft et al.,
542 2017). This conflict has been proposed to be an important factor in the evolution of PRLS in
543 killer whales (Croft et al., 2017), however it is not known whether plasticity in the timing of
544 the onset of PRLS occurs in the species, and if so whether plasticity serves to reduce conflict.

545 It is currently unclear whether patterns of pregnancy in long-finned pilot whales
546 represent flexibility in the timing of reproductive cessation, or represent a reversible pause
547 in reproduction such that a female may begin to reproduce again should her existing
548 offspring disperse or die. If reversibility is important for this species, there may be
549 disadvantages to losing the ability to reproduce and undergoing a physiological menopause.
550 Future studies investigating the mechanisms determining fecundity in this species would
551 shed light on these possibilities. Although the underlying mechanisms are not yet
552 understood, our study suggests that in long-finned pilot whales a post-reproductive period

553 may occur in individuals that benefit from it, but be rare on a population-wide level, and
554 thus be difficult to distinguish from reproductive senescence. This plastic cessation of
555 reproduction may represent a first step towards the evolution of irreversible species-wide
556 PRLS, or alternatively could represent a stable alternative strategy to widespread post-
557 reproductive periods. The possibility of adaptive plasticity in reproductive cessation
558 warrants further attention in this species, and in other species that may benefit from late-
559 life helping, both in cases where population-wide post-reproductive life stages occur, and
560 where they do not. Given that we find that long-finned pilot whales meet the demographic
561 conditions which should promote the evolution of PRLS (which occurs in the very closely
562 related short-finned pilot whales), but they seem to have evolved a plastic cessation of
563 reproduction, our results raise the question of why some species evolve irreversible PRLS if
564 adaptive plasticity is possible?

565

566 **Author Contributions** HN designed the study, conducted statistical analyses and wrote the
567 manuscript; KF carried out the molecular lab work; WA collected field data, coordinated molecular
568 data collection and helped draft the manuscript; KA conducted statistical analyses and helped draft
569 the manuscript. All authors commented on the manuscript and gave final approval for publication.

570 **Funding** This work was supported by a Leverhulme Trust International Academic Fellowship (IAF-
571 2018-006) and by an Alexander von Humboldt Foundation Research Fellowship awarded to HN and a
572 scholarship from the Bradlow Foundation to KF.

573 **Acknowledgements** We thank Dorete Bloch and all members of the 'Grind Team' for sample
574 collection and Katya Ognyanova for a useful R tutorial (Ognyanova, 2018). Many thanks also go to
575 Michael Cant and Rufus Johnstone for valuable discussions on PRLS and comments on the
576 manuscript.

577 **Data Accessibility** Analyses reported in this article can be reproduced using the data provided by
578 Nichols HJ (2019): <https://doi.org/10.5061/dryad.cjsxksn29>

579

580 **References**

- 581 Abend AG, Smith TD, 1997. Differences in stable isotope ratios of carbon and nitrogen between long-
582 finned pilot whales (*Globicephala melas*) and their primary prey in the western north
583 Atlantic. *ICES Journal of Marine Science* 54:500-503. doi: 10.1006/jmsc.1996.0192.
- 584 Aimé C, André J-B, Raymond M, 2017. Grandmothering and cognitive resources are required for the
585 emergence of menopause and extensive post-reproductive lifespan. *PLoS computational*
586 *biology* 13:e1005631.
- 587 Alves F, Quérroul S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C, 2013. Population
588 structure of short - finned pilot whales in the oceanic archipelago of Madeira based on
589 photo - identification and genetic analyses: implications for conservation. *Aquatic*
590 *Conservation: Marine and freshwater ecosystems* 23:758-776.
- 591 Amos B, Barrett J, Dover GA, 1991. Breeding behaviour of pilot whales revealed by DNA
592 fingerprinting. *Heredity* 67:49-55.
- 593 Amos B, Schlötterer C, Tautz D, 1993. Social structure of pilot whales revealed by analytical DNA
594 profiling. *Science* 260:670-672.
- 595 Augusto J, Frasier T, Whitehead H, 2017a. Characterizing alloparental care in the pilot whale
596 (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada *Marine*
597 *Mammal Science* 33:440-456.
- 598 Augusto J, Frasier T, Whitehead H, 2017b. Social structure of long-finned pilot whales (*Globicephala*
599 *melas*) off northern Cape Breton Island, Nova Scotia. *Behaviour* 154:509-540.
- 600 Barrett-Lennard LG, Ellis G, 2001. Population structure and genetic variability in northeastern Pacific
601 killer whales: towards an assessment of population viability: Canadian Science Advisory
602 Secretariat.
- 603 Bates D, Maechler MB, B., Walker S, 2013. lme4: Linear mixed-effects models using Eigen and S4. R
604 package version 1.0-5. <http://CRANR-project.org/package=lme4>.
- 605 Bloch D, Desportes G, Mouritsen R, Skaaning S, Stefansson E, 1993a. An introduction to studies of
606 the ecology and status of the long-finned pilot whale (*Globicephala melas*) off the Faroe
607 Islands, 1986-1988. Report of the International Whaling Commission (Special Issue 14):1-32.
- 608 Bloch D, Lockyer CH, Zachariassen M, 1993b. Age and growth parameters of the long-finned pilot
609 whale off the Faroe Islands. In: Donovan GP, Lockyer CH, Martin AR, editors. *Biology of*
610 *northern hemisphere pilot whales* Cambridge, UK: International Whaling Commission. p.
611 163-207.
- 612 Brent LJ, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP, 2015. Ecological knowledge,
613 leadership, and the evolution of menopause in killer whales. *Current Biology* 25:746-750.

614 Buchanan FC, Friesen MK, Littlejohn RP, Clayton JW, 1996. Microsatellites from the beluga whale
615 *Delphinapterus leucas*. *Molecular Ecology* 5:571-575.

616 Cant MA, Johnstone RA, 2008. Reproductive conflict and the separation of reproductive generations
617 in humans. *Proceedings of the National Academy of Sciences* 105:5332-5336.

618 Cant MA, Johnstone RA, Russell AF, 2009. Reproductive conflict and the evolution of menopause. In:
619 Hager R, Jones C, editors. *Reproductive skew in vertebrates: Proximate and ultimate causes*
620 Cambridge, UK: Cambridge University Press. p. 24-50.

621 Chapman SN, Jackson J, Htut W, Lummaa V, Lahdenperä M, 2019. Asian elephants exhibit post-
622 reproductive lifespans. *BMC evolutionary biology* 19:193.

623 Chivers SJ, Baird RW, Martien KM, Taylor BL, Archer E, Gorgone AM, Hancock BL, Hedrick NM,
624 Matilla D, McSweeney DJ, 2010. Evidence of genetic differentiation for Hawaii insular false
625 killer whales (*Pseudorca crassidens*). CASCADIA RESEARCH COLLECTIVE OLYMPIA WA.

626 Cohen AA, 2004. Female post-reproductive lifespan: a general mammalian trait. *Biological Reviews*
627 79:733-750.

628 Croft DP, Brent LJ, Franks DW, Cant MA, 2015. The evolution of prolonged life after reproduction.
629 *Trends in ecology & evolution* 30:407-416.

630 Croft DP, Johnstone RA, Ellis S, Natrass S, Franks DW, Brent LJ, Mazzi S, Balcomb KC, Ford JK, Cant
631 MA, 2017. Reproductive conflict and the evolution of menopause in killer whales. *Current*
632 *Biology* 27:298-304.

633 Csilléry K, Johnson T, Beraldi D, Clutton-Brock T, Coltman D, Hansson B, Spong G, Pemberton JM,
634 2006. Performance of Marker-Based Relatedness Estimators in Natural Populations of
635 Outbred Vertebrates. *Genetics* 173:2091-2101. doi: 10.1534/genetics.106.057331.

636 De Stephanis R, Verborgh P, Pérez S, Esteban R, Minvielle-Sebastia L, Guinet C, 2008. Long-term
637 social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar.
638 *Acta Ethologica* 11:81.

639 Desportes G, Mouritsen R, 1988. Diet of the pilot whale, *Globicephala melas*, around the Faroe
640 Islands. ICES CM.

641 Ellis S, Franks DW, Natrass S, Cant MA, Bradley DL, Giles D, Balcomb KC, Croft DP, 2018a.
642 Postreproductive lifespans are rare in mammals. *Ecology and evolution* 8:2482-2494.

643 Ellis S, Franks DW, Natrass S, Currie TE, Cant MA, Giles D, Balcomb KC, Croft DP, 2018b. Analyses of
644 ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales.
645 *Scientific reports* 8:12833.

646 Emery Thompson M, Jones JH, Pusey AE, Brewer-Marsden S, Goodall J, Marsden D, Matsuzawa T,
647 Nishida T, Reynolds V, Sugiyama Y, Wrangham RW, 2007. Aging and Fertility Patterns in Wild

648 Chimpanzees Provide Insights into the Evolution of Menopause. *Current Biology* 17:2150-
649 2156. doi: <http://dx.doi.org/10.1016/j.cub.2007.11.033>.

650 Foote AD, 2008. Mortality rate acceleration and post-reproductive lifespan in matrilineal whale
651 species. *Biology Letters* 4:189-191. doi: 10.1098/rsbl.2008.0006.

652 Foster EA, Franks DW, Mazzi S, Darden SK, K.C. B, Ford JKB, Croft DP, 2012. Adaptive prolonged
653 postreproductive life span in killer whales. *Science* 337:1313. doi: doi:
654 10.1126/science.1224198.

655 Fullard KJ, Early G, Heide-Jørgensen MP, Bloch D, Rosing-Asvid A, Amos W, 2000. Population
656 structure of long-finned pilot whales in the North Atlantic: a correlation with sea surface
657 temperature? *Molecular Ecology* 9:949-958.

658 Grimes DA, 1994. The morbidity and mortality of pregnancy Still risky business. *American Journal of*
659 *Obstetrics and Gynecology* 170:1489-1494. doi: [http://dx.doi.org/10.1016/S0002-](http://dx.doi.org/10.1016/S0002-9378(94)05009-X)
660 [9378\(94\)05009-X](http://dx.doi.org/10.1016/S0002-9378(94)05009-X).

661 Hamilton WD, 1964. The genetical theory of social behaviour I, II. *Journal of Theoretical Biology* 7:1-
662 52.

663 Hamilton WD, 1966. The moulding of senescence by natural selection. *Journal of theoretical biology*
664 12:12-45.

665 Hedges SB, Dudley J, Kumar S, 2006. TimeTree: a public knowledge-base of divergence times among
666 organisms. *Bioinformatics* 22:2971-2972.

667 Huber S, Fieder M, 2018. Evidence for a maximum "shelf-life" of oocytes in mammals suggests that
668 human menopause may be an implication of meiotic arrest. *Scientific reports* 8:14099-
669 14099. doi: 10.1038/s41598-018-32502-2.

670 Johnstone RA, Cant MA, 2010. The evolution of menopause in cetaceans and humans: the role of
671 demography. *Proceedings of the Royal Society of London Series B, Biological Sciences*
672 277:3765-3771.

673 Johnstone RA, Cant MA, 2019. Evolution of menopause. *Current Biology* 29:R112-R115. doi:
674 10.1016/j.cub.2018.12.048.

675 Kasuya T, Marsh H, 1984. Life history and reproductive biology of the short-finned pilot whale,
676 *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Reports of the International*
677 *Whaling Commission* 6:259310.

678 Konovalov DA, Manning C, Henshaw MT, 2004. kingroup: a program for pedigree relationship
679 reconstruction and kin group assignments using genetic markers. *Molecular Ecology Notes*
680 4:779-782. doi: 10.1111/j.1471-8286.2004.00796.x.

681 Konrad CM, Frasier TR, Whitehead H, Gero S, 2018. Kin selection and allocare in sperm whales.
682 Behavioral Ecology 30:194-201.

683 Lahdenperä M, Lummaa V, Helle S, Tremblay M, Russell AF, 2004. Fitness benefits of prolonged post-
684 reproductive lifespan in women. Nature 428:178.

685 Lawson DW, Alvergne A, Gibson MA, 2012. The life-history trade-off between fertility and child
686 survival. Proceedings of the Royal Society of London B: Biological Sciences 279:4755-4764.
687 doi: 10.1098/rspb.2012.1635.

688 Leung ES, Vergara V, Barrett-Lennard LG, 2010. Allonursing in captive belugas (*Delphinapterus*
689 *leucas*). Zoo biology 29:633-637.

690 Levitis DA, Burger O, Lackey LB, 2013. The human post-fertile lifespan in comparative evolutionary
691 context. Evolutionary Anthropology: Issues, News, and Reviews 22:66-79.

692 Levitis DA, Lackey LB, 2011. A measure for describing and comparing postreproductive life span as a
693 population trait. Methods in Ecology and Evolution 2:446-453.

694 Lockyer CH, 1993. A report on patterns of deposition of dentine and cement in teeth of pilot whales,
695 genus *Globicephala*. In: Donovan GP, Lockyer CH, Martin AR, editors. Biology of northern
696 hemisphere pilot whales Cambridge, UK: International Whaling Commission. p. 137-161.

697 Lynch M, Ritland K, 1999. Estimation of pairwise relatedness with molecular markers. Genetics
698 152:1753-1766.

699 Marshall TC, Slate JBKE, Kruuk LEB, Pemberton JM, 1998. Statistical confidence for likelihood-based
700 paternity inference in natural populations. Molecular Ecology 7:639-655.

701 Martin AR, Rothery P, 1993. Reproductive parameters of female long-finned pilot whales
702 (*Globicephala melas*) around the Faroe Islands. In: Donovan GP, Lockyer CH, Martin AR,
703 editors. Biology of northern hemisphere pilot whales Cambridge, UK: International Whaling
704 Commission. p. 263-304.

705 McComb K, Moss C, Durant SM, Baker L, Sayialel S, 2001. Matriarchs As Repositories of Social
706 Knowledge in African Elephants. Science 292:491-494. doi: 10.1126/science.1057895.

707 Nichols, HJ (2019), Data from: Why don't long-finned pilot whales have widespread post-
708 reproductive lifespan? Insights from genetic data. Behavioral Ecology.
709 <https://doi.org/10.5061/dryad.cjsxksn29>

710 Nichols HJ, Fullard KJ, Amos W, 2014. Costly sons do not lead to adaptive sex ratio adjustment in
711 pilot whales, *Globicephala melas*. Animal Behaviour 88:203-209. doi:
712 10.1016/j.anbehav.2013.12.015.

713 Nichols HJ, Zecherle L, Arbuckle K, 2016. Patterns of philopatry and longevity contribute to the
714 evolution of post-reproductive lifespan in mammals. Biology letters 12:20150992.

715 Nussey DH, Froy H, Lemaitre J, Gaillard J, Austad SN, 2013. Senescence in natural populations of
716 animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research*
717 *Reviews* 12:214-225. doi: <http://dx.doi.org/10.1016/j.arr.2012.07.004>.

718 Oftedal OT, 1997. Lactation in Whales and Dolphins: Evidence of Divergence Between Baleen- and
719 Toothed-Species. *Journal of Mammary Gland Biology and Neoplasia* 2:205-230. doi:
720 10.1023/a:1026328203526.

721 Oremus M, 2008. Genetic and demographic investigation of population structure and social system
722 in four delphinid species: ResearchSpace@ Auckland.

723 Ottensmeyer CA, Whitehead H, 2003. Behavioural evidence for social units in long-finned pilot
724 whales. *Canadian Journal of Zoology* 81:1327-1338.

725 Packer C, Tatar M, Collins A, 1998. Reproductive cessation in female mammals. *Nature* 392:807.

726 Palsbøll PJ, Heide-Jørgensen MP, Dietz R, 1997. Population structure and seasonal movements of
727 narwhals, *Monodon monoceros*, determined from mtDNA analysis. *Heredity* 78:284.

728 Photopoulou T, Ferreira IM, Best PB, Kasuya T, Marsh H, 2017. Evidence for a postreproductive
729 phase in female false killer whales *Pseudorca crassidens*. *Frontiers in zoology* 14:30.

730 Pilot M, Dahlheim ME, Hoelzel AR, 2010. Social cohesion among kin, gene flow without dispersal and
731 the evolution of population genetic structure in the killer whale (*Orcinus orca*). *Journal of*
732 *Evolutionary Biology* 23:20-31. doi: 10.1111/j.1420-9101.2009.01887.x.

733 Reznick D, Bryant M, Holmes D, 2005. The evolution of senescence and post-reproductive lifespan in
734 guppies (*Poecilia reticulata*). *PLoS biology* 4:e7.

735 Richard KR, Whitehead H, Wright JM, 1996. Polymorphic microsatellites from sperm whales and
736 their use in the genetic identification of individuals from naturally sloughed pieces of skin.
737 *Molecular Ecology* 5:313-315.

738 Russell AF, 2004. Mammals: comparisons and contrasts. In: Koenig W, Dickinson J, editors. *Ecology*
739 *and Evolution of Cooperative Breeding in Birds* Cambridge, UK: Cambridge University Press.

740 Sear R, Mace R, 2008. Who keeps children alive? A review of the effects of kin on child survival.
741 *Evolution and human behavior* 29:1-18.

742 Serchuk FM, WF R, 1974. Aspects of the distribution and abundance of the long-finned squid, *Loligo*
743 *pealei*, between Cape Hatteras and Georges Bank. US Department of Commerce.

744 Shanley DP, Kirkwood TBL, 2001. Evolution of the human menopause. *BioEssays* 23:282-287. doi:
745 10.1002/1521-1878(200103)23:3<282::AID-BIES1038>3.0.CO;2-9.

746 Shinohara M, Domingo-Roura X, Takenaka O, 1997. Microsatellites in the bottlenose dolphin,
747 *Tursiops truncatus*. *Molecular Ecology* 6:695-696.

748 Towner MC, Nenko I, Walton SE, 2016. Why do women stop reproducing before menopause? A life-
749 history approach to age at last birth. *Philosophical Transactions of the Royal Society of*
750 *London B: Biological Sciences* 371. doi: 10.1098/rstb.2015.0147.

751 Tuljapurkar SD, Puleston CO, Gurven MD, 2007. Why Men Matter: Mating Patterns Drive Evolution
752 of Human Lifespan. *PLOS ONE* 2:e785. doi: 10.1371/journal.pone.0000785.

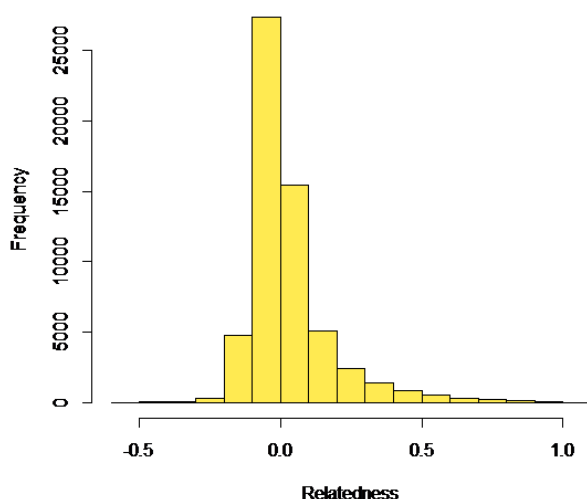
753 Valsecchi E, Amos W, 1996. Microsatellite markers for the study of cetacean populations. *Molecular*
754 *Ecology* 5:151-156.

755 Williams PD, Day T, Fletcher Q, Rowe L, 2006. The shaping of senescence in the wild. *Trends in*
756 *Ecology & Evolution* 21:458-463. doi: <http://dx.doi.org/10.1016/j.tree.2006.05.008>.

757 Wu Jia-Jia, He Qiao-Qiao, Deng Ling-Ling, Wang Shi-Chang, Mace Ruth, Ji Ting, Yi T, 2013. Communal
758 breeding promotes a matrilineal social system where husband and wife live apart.
759 *Proceedings of the Royal Society B: Biological Sciences* 280:0130010. doi:
760 <http://dx.doi.org/10.1098/rspb.2013.0010>.

761 Zachariassen P, 1993. Pilot whale catches in the Faroe Islands, 1709-1992 In: Donovan GP, Lockyer
762 CH, Martin AR, editors. *Biology of northern hemisphere pilot whales* Cambridge, UK:
763 International Whaling Commission. p. 69-88.

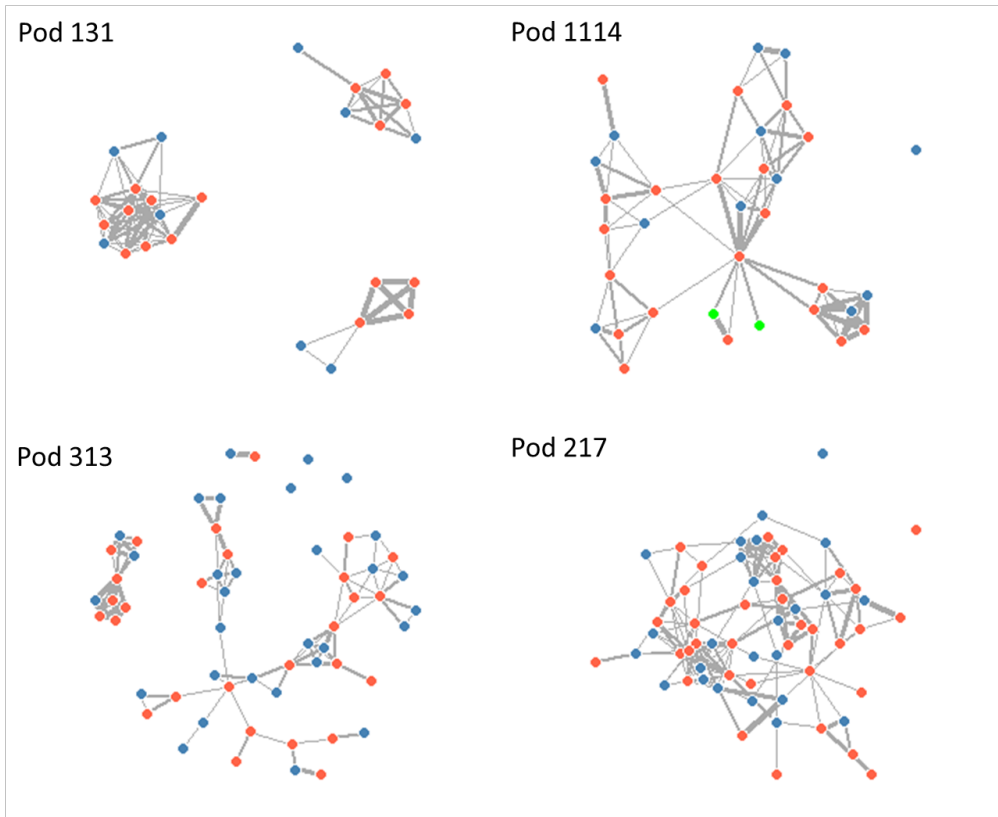
764 **Figures and Legends**



765

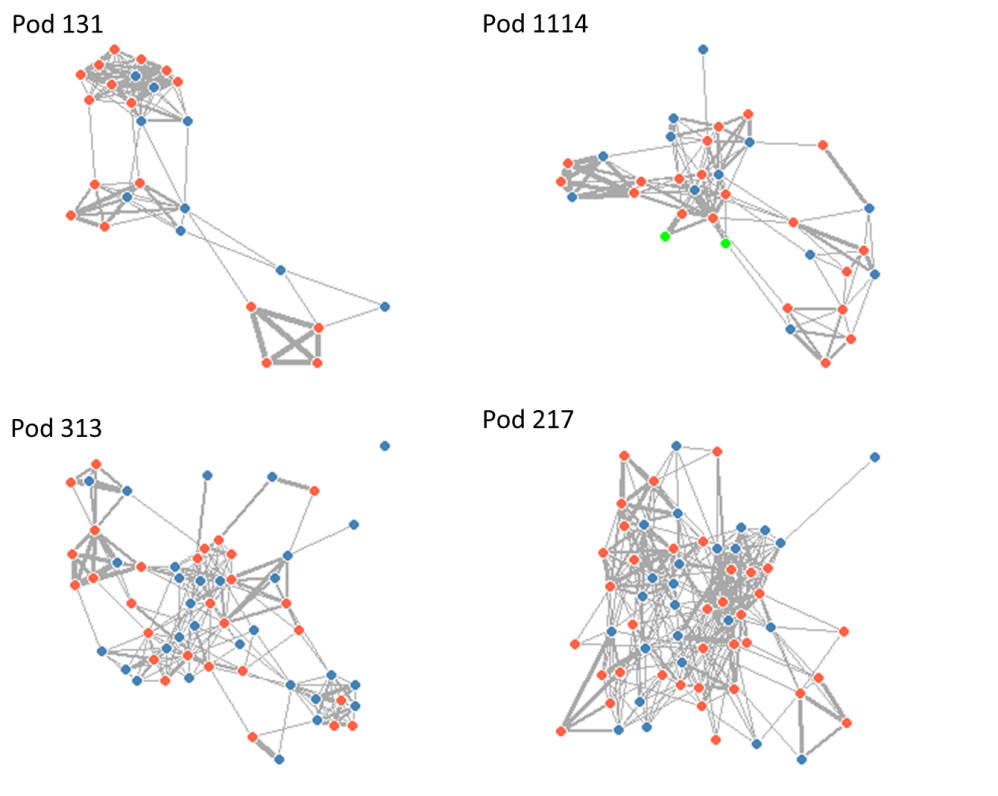
766 Figure 1. The distribution of within-pod relatedness values is left-skewed; most individuals
767 have multiple close relatives within their pod but have low relatedness to the remainder of
768 their pod. Data comprises 58792 pairwise relatedness values between individuals from the
769 same pod. Note that relatedness values below zero represent individuals that are less
770 genetically related to each other than the population average.

a)



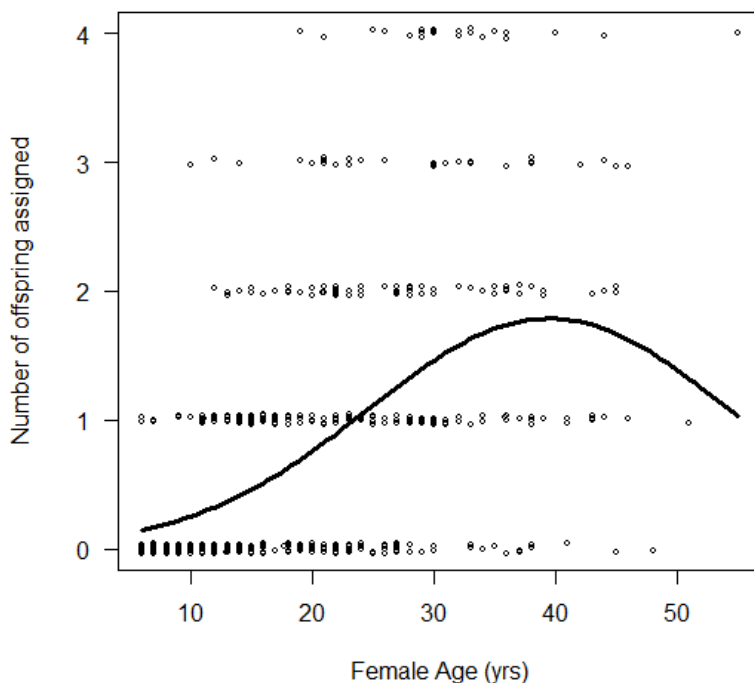
771

b)



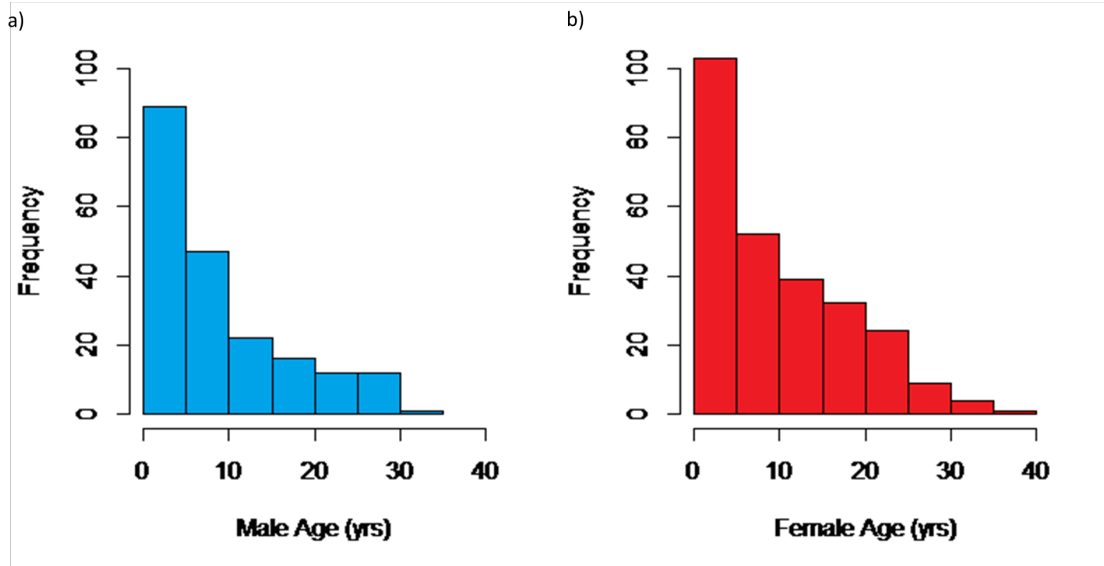
772

773 Figure 2. Relatedness networks within four pods: 131 (total pod size is 26 individuals, all
774 genotyped), 1114 (total pod size is 32 individuals plus 3 fetuses, 34 genotyped whales are
775 included), 313 (total pod size is 57 individuals plus 6 fetuses, 58 genotyped whales are
776 included), 217 (total pod size is 59 individuals plus 5 fetuses, 61 genotyped whales are
777 included). Blue dots represent males, red dots represent females, and green dots represent
778 unsexed fetuses. Grey lines show cases where relatedness between two individuals is above
779 (a) 0.25, the expected average value between half siblings, and (b) 0.125, the expected
780 average value between cousins. Thicker grey lines indicate higher relatedness values.



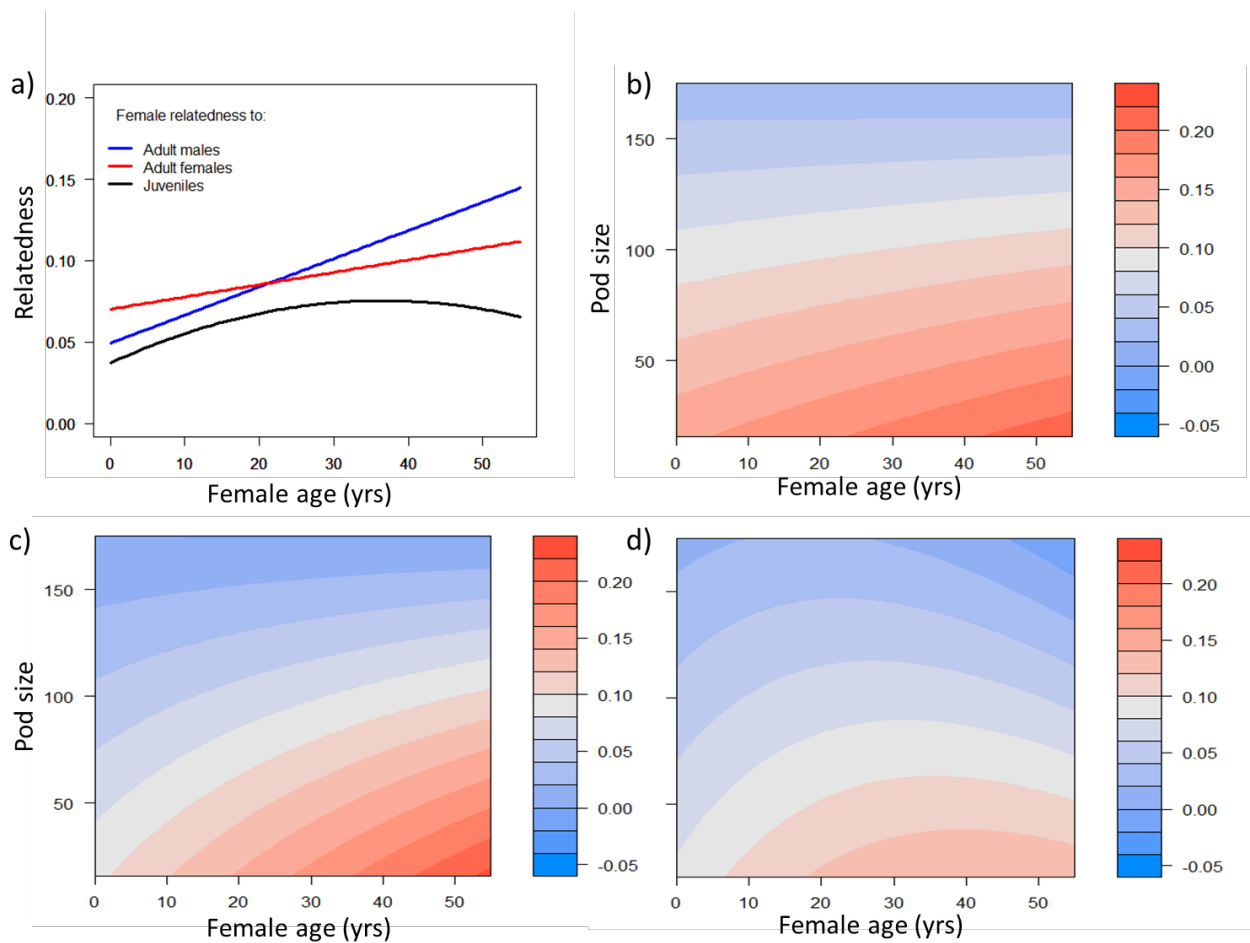
781

782 Figure 3. The number of genetically assigned offspring present in the pod for females of
783 different ages. Open circles represent the data but note that we have jittered their positions
784 slightly for clarity since data can only take integer values.



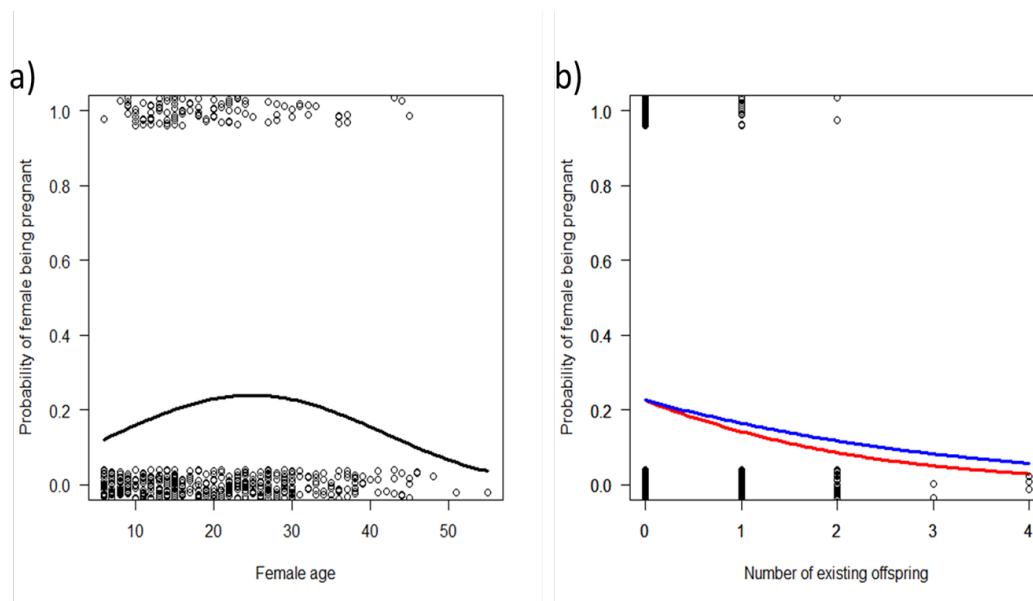
785

786 Figure 4. The number of (a) males and (b) females of different ages, present in the same pod
 787 as their genetically assigned mother. Data comprises 463 assigned offspring with known sex
 788 and age.



789

790 Figure 5. Relatedness between females and other members of her pod, predicted from
 791 GLMMs containing pod and individual ID as random effects. (a) Shows average relatedness
 792 between females and adult males (blue), adult females (red) and juveniles (black) over the
 793 female lifespan in a median sized pod (57 individuals). Note that this plot does not include
 794 the interaction between age and group size so does not fully represent the GLMM, but it is
 795 included for comparison with other studies and theoretical models that do not take group
 796 size into account. Contour plots show changes in female relatedness to (b) adult males (c)
 797 adult females and (d) juveniles, dependent on female age and pod size.



798

799 Figure 6. The probability of being pregnant (a) for females of different ages and (b) for
 800 females with different numbers of adult sons (blue – upper line) and daughters (red – lower
 801 line) present in the pod. Lines are predictions from GLMMs containing pod ID as a random
 802 effect. Open circles represent the data but note that we have jittered their positions slightly
 803 for clarity since data can only take values of 0 and 1.

804

805 Tables and Table Legends

806 Table 1. Summary of all GLMMs conducted. Models of relatedness over the lifespan used
 807 relatedness values from 809 genotyped females (for which the age and sex was also known)

808 in 25 pods. Models of pregnancy status used 530 females from 22 pods. P values presented
 809 are associated with removing the term from the model.

Model	Term	Effect size	SE	t or z value	p-value
Relatedness between females and adult male pod-members	Intercept	0.0842	0.0255	3.30	NA
	Female age	0.00260	0.000406	6.42	NA
	Pod size	-0.000602	0.000305	-1.97	NA
	Age: pod size	-1.50×10^{-5}	3.46×10^{-6}	-4.34	1.52×10^{-5}
Relatedness between females and adult female pod-members	Intercept	0.0117	0.0239	4.89	NA
	Female age	0.00118	0.000361	3.28	NA
	Pod size	-0.000808	0.000288	-2.81	NA
	Age: pod size	-7.34×10^{-6}	3.19×10^{-6}	-2.31	0.0213
Relatedness between females and juvenile pod-members	Intercept	0.0634	0.0139	4.56	NA
	Female age	0.00263	0.000351	7.50	NA
	Female age ²	-2.88×10^{-5}	6.88×10^{-6}	-4.18	2.92×10^{-5}
	Pod size	-0.000455	0.000165	-2.76	NA
Number of genetically assigned offspring present in pod	Age: pod size	-9.07×10^{-6}	1.95×10^{-6}	-4.65	3.47×10^{-6}
	Intercept	-2.94	0.282	-10.4	NA
	Female age	0.178	0.0203	8.77	NA
	Female age ²	-0.00226	0.000373	-6.07	4.23×10^{-9}
Probability of a female currently being pregnant	Intercept	-2.82	0.577	4.90	NA
	Female age	0.154	0.0532	2.90	NA
	Female age ²	-0.00308	0.00116	-2.65	0.00626
	N existing offspring	-0.448	0.148	-3.04	0.00148
Probability of a female currently being pregnant	Intercept	-2.59	0.561	-4.62	NA
	Female age	0.116	0.0508	2.28	NA
	Female age ²	-0.00234	0.00113	-2.07	0.0366
	N daughters	-0.566	0.280	-2.02	0.0305
	N sons	-0.392	0.349	-1.13	0.238

810

811