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

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Running Header: kinship dynamics in pilot whales

Lay summary: Long-finned pilot whales don't go through a species-wide menopause despite having a social structure that predicts they may benefit from one. Humans and a few whales have a menopause, where females stop breeding part way through their lifespan, possibly to focus on helping their existing children and grandchildren. Despite being surrounded by relatives, long-finned pilot whales don't have widespread menopause. Instead, individual females with many offspring are less likely to breed, regardless of their age.

Abstract

In a handful of mammals, females show an extended post-reproductive lifespan (PRLS), leading to questions over why they spend a substantial portion of their lifespan non-reproductive. Theoretical and empirical studies suggest that PRLS may evolve when (1) demographic patterns lead to increasing local relatedness as females age, and (2) females come into reproductive competition with their daughters, as these conditions lead to high relative benefits of helping kin versus reproducing in later life. However, evolutionary pathways to PRLS are poorly understood and empirical studies are scarce. Here, we use a dataset of 1522 individuals comprising 22 pods to investigate patterns of reproduction and relatedness in long-finned pilot whales *Globicephala melas*; a toothed whale without species-wide PRLS. We find a similar relatedness structure to whales with PRLS: pods appear composed of related matrilines, and relatedness of females to their pod increases with age, suggesting that this species could benefit from late-life help. Furthermore, females with a large number of philopatric adult daughters (but not sons) are less likely to reproduce, implying intergenerational reproductive competition between females. This suggests that individuals may display a plastic cessation of reproduction, switching to investing in existing offspring when they come into competition with their daughters. To the best of our knowledge, this is the first time such a relationship has been described in relation to PRLS, and it raises questions about whether this represents a step towards evolving PRLS or is a stable alternative strategy to widespread post-reproductive periods.

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

Introduction

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

Explanations for PRLS fall into two main classes; non-adaptive and adaptive. Non-adaptive decoupling of reproductive and somatic ageing may occur if traits that are strongly selected early in life have negative consequences on reproduction in late life, and/or if traits associated with aging are less visible to natural selection because few individuals live to express them (Hamilton, 1966; Packer et al., 1998; Williams et al., 2006). Similarly, PRLS may evolve due to links with other aspects of life-history even without impacts on fitness. For example, in guppies, *Poecilia reticulate,* selection on reproductive lifespan appears to co-select for post-reproductive lifespan (Reznick et al., 2005). Furthermore, disease and other stochastic processes are likely to explain why, in many mammalian species, a small proportion of females have been observed to have post-reproductive periods (Cohen, 2004). As this is unlikely to represent a distinct life-stage, this phenomenon is termed post reproductive viability (Levitis et al., 2013) to distinguish it from PRLS affecting all females.

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

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

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

One interesting puzzle regarding PRLS is why it pays to evolve irreversible reproductive cessation, as appears to occur in all species currently identified as having significant PRLS (Ellis et al., 2018b). If females maintained plasticity in PRLS, they may be able to adaptively switch resources between producing further offspring and helping existing offspring, dependent on their current circumstances. For example, females with few or no offspring within their group (those whose previous offspring have died or emigrated) would likely benefit from further reproduction, regardless of their age. Here, the sex of a female's philopatric offspring may be important. For example, where both sexes remain philopatric but mating occurs between groups (as occurs in some toothed whales), older females come into conflict with their adult daughters, as they both produce offspring in the natal group (Croft et al., 2017). However, they are unlikely to come into conflict with reproductive sons, who's offspring are in other groups. Under these circumstances, older females may benefit from ceasing reproduction when they have daughters of reproductive age in their group but would not benefit if they have only philopatric sons.

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

Toothed whales (Odontoceti) provide an interesting opportunity to investigate patterns of reproduction and their relationship to social organization for several reasons. Firstly, maternal investment tends to be high, either due to high energetic costs of lactation or long periods of offspring dependency (Oftedal, 1997). Secondly, in several species, offspring of one or both sexes remain with their mothers well beyond weaning and may continue to receive maternal care (Brent et al., 2015; Pilot et al., 2010). Third, reproductive senescence is common, with 10 of the 16 species investigated by Ellis et al. (2018b) experiencing reproductive senescence, and at least four (possibly five) of these species exhibiting extended PRLS comparable in duration to humans (Cohen, 2004; Croft et al., 2015; Ellis et al., 2018a; Ellis et al., 2018b). Curiously, although many toothed whales appear to have similar social systems, PRLS varies greatly in presence, length, and timing. For example, short-finned and long-finned pilot whales *Globicephala melas* are very closely related (~1-2mya divergence (Hedges et al., 2006)) sister species that both appear to live in stable, multigenerational, matrilineal groups where both sexes remain philopatric and mating is non-local (Foote, 2008). Both have been studied in drive fisheries and show similar maximum longevities of around 55-60 years, although life-expectancy is generally shorter in long-finned pilot whales (Ellis et al., 2018b). Despite this, the oldest pregnant females found so far for the two species differ greatly in age: 35 years in short-finned (Kasuya and Marsh, 1984) and 55 years in long-finned pilot whales (Martin and Rothery, 1993). Accordingly, periods of PRLS differ greatly between the species: PrR (a population-level measure of the proportion of female years spent post-reproductive (Levitis and Lackey, 2011)) is 0.26 in the short-finned pilot whale and 0.002 in the long-finned pilot whale (Ellis et al., 2018a). This raises the question of why these two species differ so greatly in PRLS despite having similar social systems and lifestyles.

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

Methods

Physiological and genetic data collection

Data were obtained from 1522 long-finned pilot whales *Globicephala melas* comprising 95% of individuals from 22 pods harvested between 1986 and 1989 as part of a legal traditional subsistence hunt in the Faroe Islands (Zachariassen, 1993). Scientific observers of the harvest were certain that there was no splitting or merging of the pods during the hunt, hence these pods comprised of entire naturally occurring social groups (Bloch et al., 1993a). Pods ranged in size from 16 to 175 individuals (median 57) and contained adults and juveniles of both sexes. Pilot whale social behavior is currently poorly understood, but observational studies suggest that pods may sometimes temporarily split into smaller subunits of ~7 individuals (Augusto et al., 2017b; De Stephanis et al., 2008; Ottensmeyer and Whitehead, 2003). As our data are not longitudinal, we cannot comment on the long-term stability of the pods captured in the hunt, but we have no reason to believe that the pods we sampled are not representative of those found in the wild population (and therefore representative of the social structure within which females find themselves). Nevertheless, as relatedness is likely to be diluted in larger pods, we took pod size into account in our analyses where appropriate.

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

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

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

Relatedness calculations

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

Parentage analysis

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

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

Statistical analyses

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

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

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

Ethical note

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

Results

Are pods composed of relatives?

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

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

A small proportion of individuals (43 individuals representing 3.1% of the population) had few or no close relatives ($r>0.25$) present in their pod (median 1.5 individuals per pod, range 0-7). There was a greater proportion of males than females with no close relatives (4.6% males, 2.1% females, two-proportions z-test; $X^2 = 6.51$, df=1, p=0.0107), possibly indicating that some males are temporarily associating with a non-natal group in search of mating opportunities. It is also possible that individuals with no close relatives could be present in their natal pod but their closest relatives have died, migrated or may be present in the pod but are not included in our analysis due to PCR failures during genotyping or missing tissue samples (95% of individuals were sampled). Almost all individuals had lesser relatives (r>0.125) present within the pod; just 4 individuals, representing 0.29% of the population had no within-pod relatives at r>0.125.

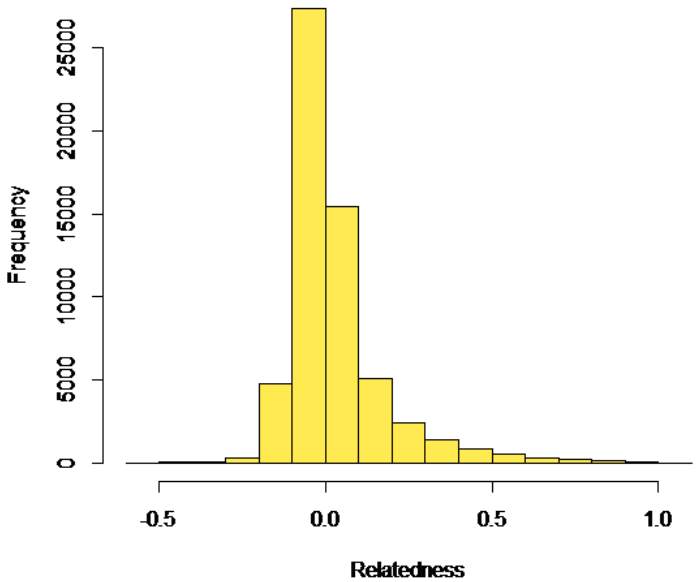
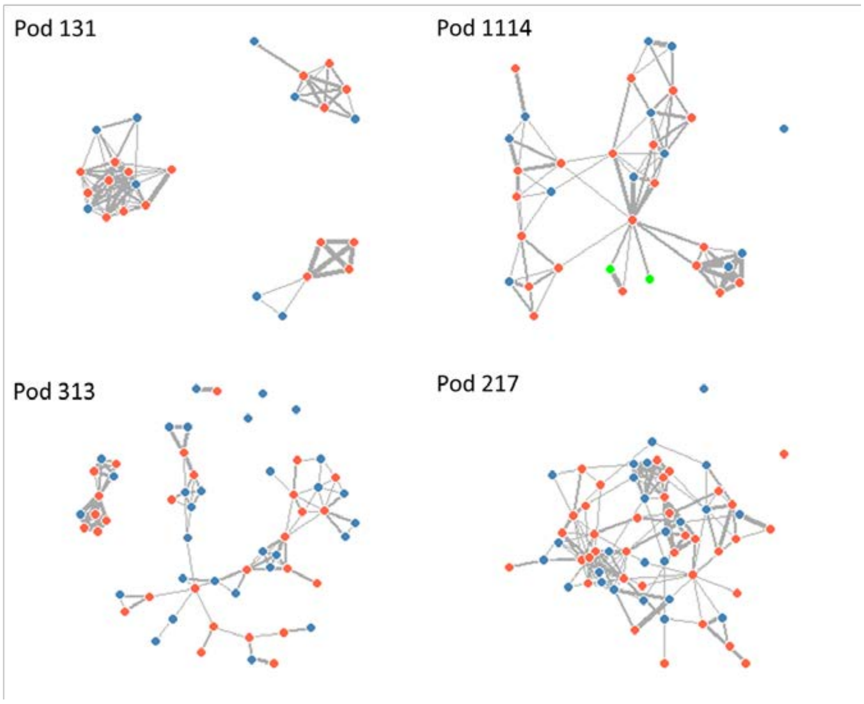


Figure 1. The distribution of within-pod relatedness values is left-skewed; most individuals have multiple close relatives within their pod but have low relatedness to the remainder of their pod. Data comprises 58792 pairwise relatedness values between individuals from the same pod. Note that relatedness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

a)



b)

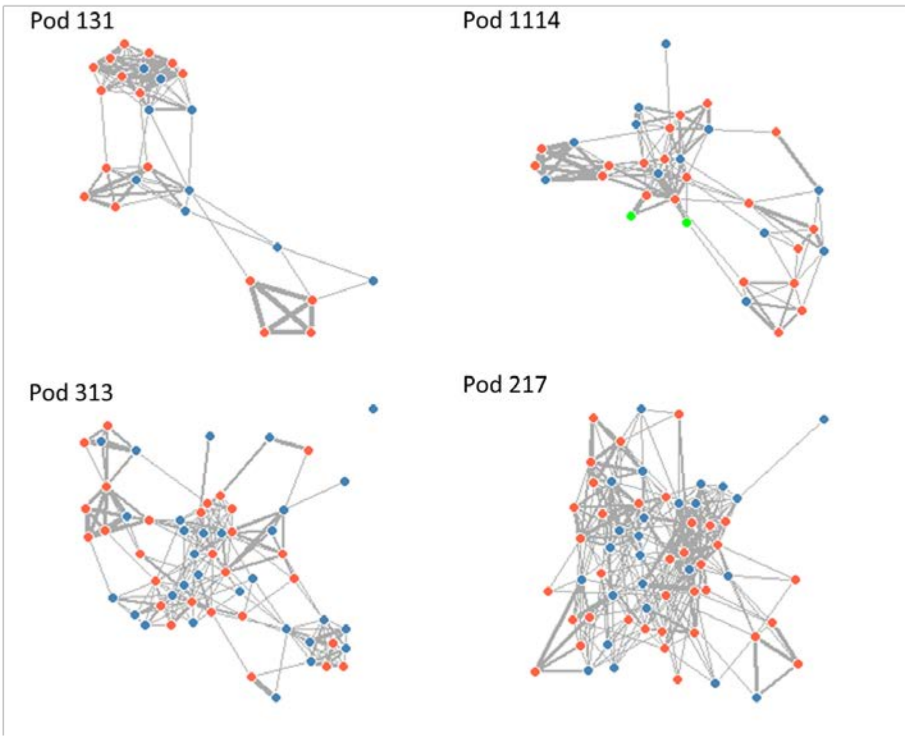


Figure 2. Relatedness networks within four pods: 131 (total pod size is 26 individuals, all genotyped), 1114 (total pod size is 32 individuals plus 3 fetuses, 34 genotyped whales are included), 313 (total pod size is 57 individuals plus 6 fetuses, 58 genotyped whales are included), 217 (total pod size is 59 individuals plus 5 fetuses, 61 genotyped whales are

included). Blue dots represent males, red dots represent females, and green dots represent unsexed fetuses. Grey lines show cases where genetic marker-based relatedness between two individuals is above (a) 0.25, the expected average value between half siblings, and (b) 0.125, the expected average value between cousins. Thicker grey lines indicate higher relatedness values.

Are philopatric adult offspring present with their mothers?

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

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

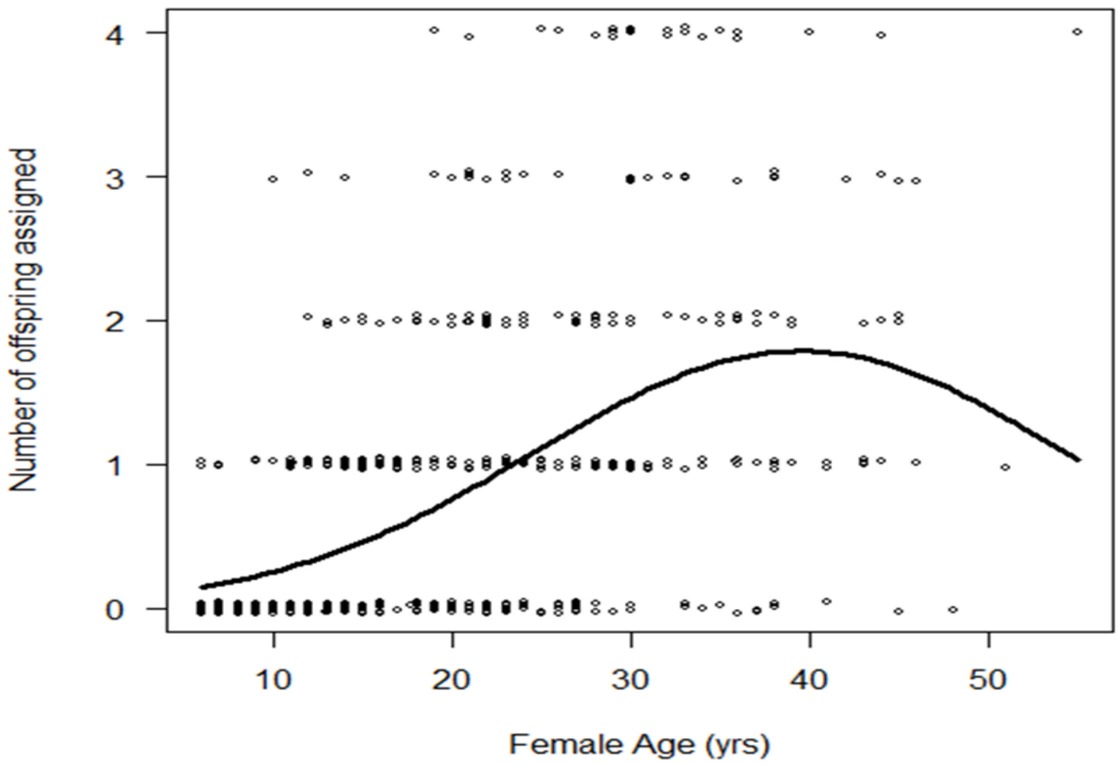


Figure 3. The number of genetically assigned offspring present in the pod for females of different ages. Open circles represent the data but note that we have jittered their positions slightly for clarity since data can only take integer values.

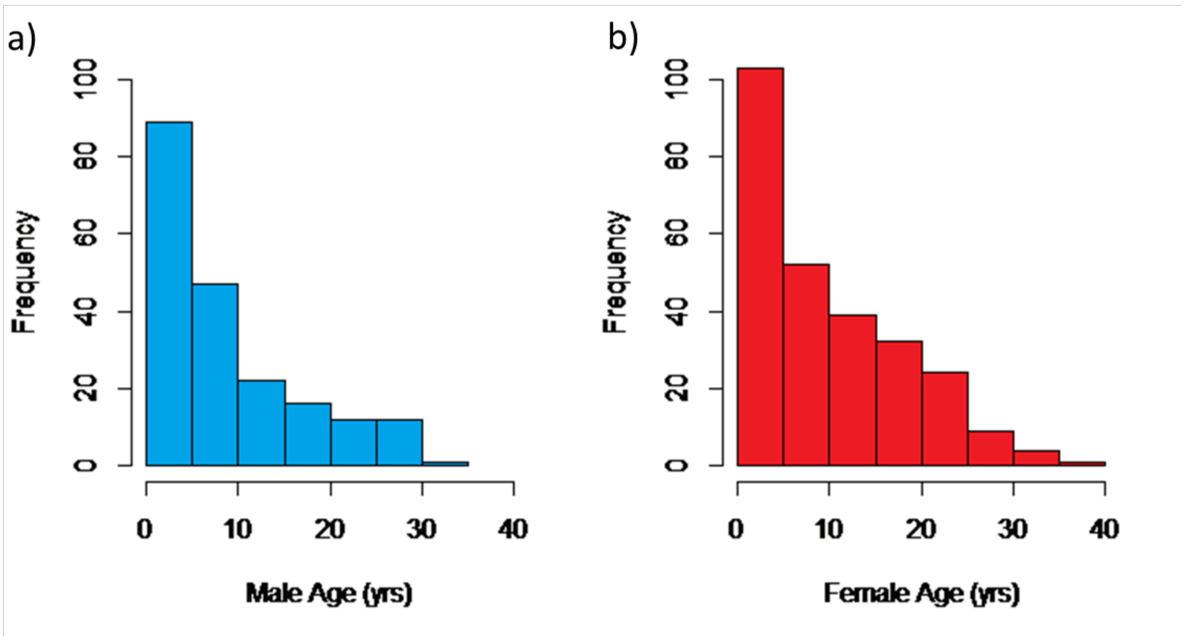


Figure 4. The number of (a) males and (b) females of different ages, present in the same pod as their genetically assigned mother. Data comprises 463 assigned offspring with known sex and age.

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

Relatedness of females to adult male and female pod-members increased significantly throughout the lifespan, with relatedness of females to males increasing at a faster rate than relatedness between females (Figure 5a; Table 1). The relatedness of females to juveniles also changed significantly throughout the lifespan, although in a quadratic fashion, first increasing and then decreasing (Figure 5a, Table 1). These relationships were influenced by pod size, indicated by the significant interaction between pod size and female age (Table 1, Figure 5b-d), with relatedness being generally lower in larger pods.

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

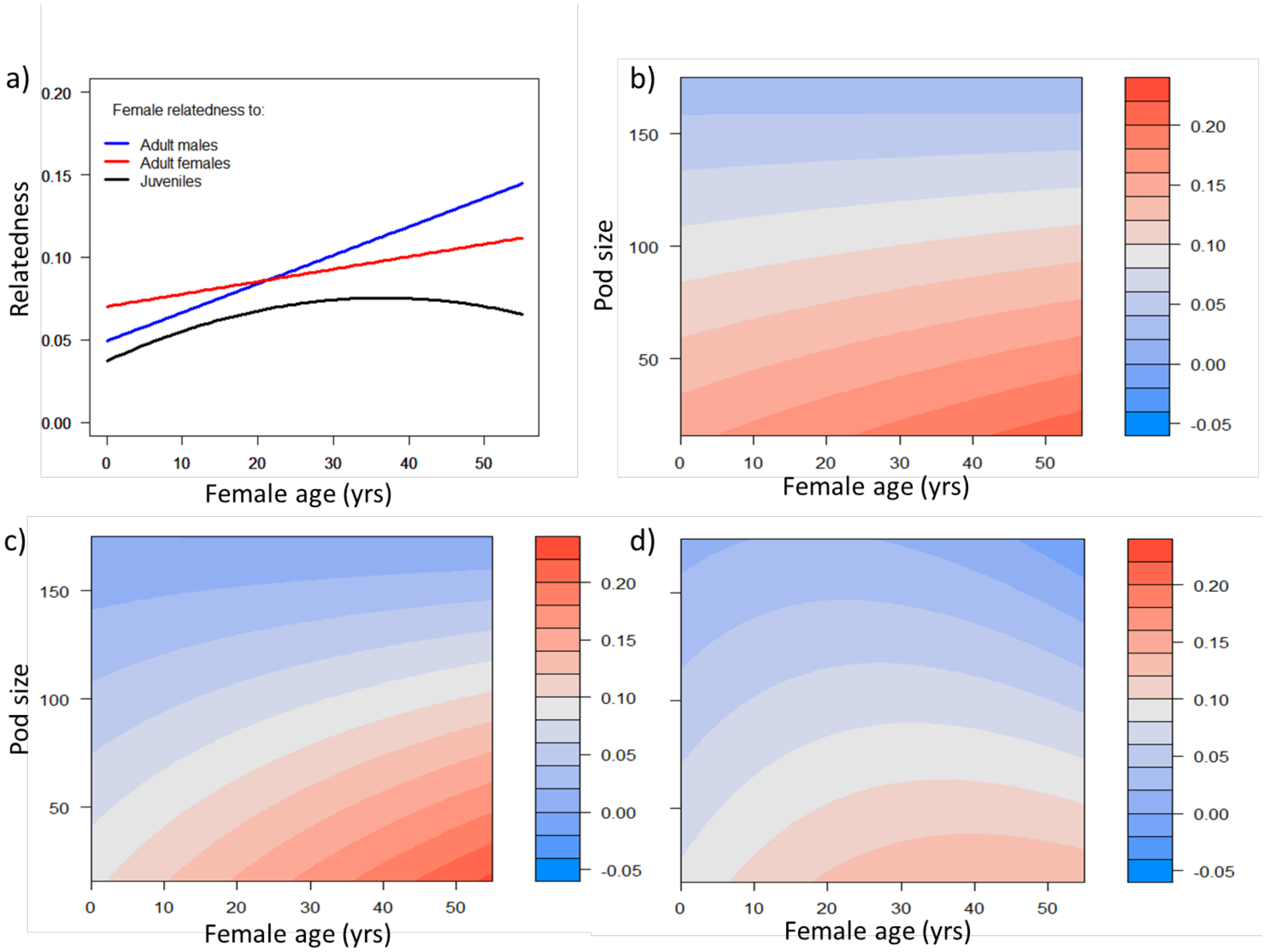


Figure 5. Relatedness between females and other members of her pod, predicted from GLMMs containing pod and individual ID as random effects. (a) Shows average relatedness between females and adult males (blue), adult females (red) and juveniles (black) over the female lifespan in a median sized pod (57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

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

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

We considered two potential drivers for the relationship between the number of philopatric offspring and current pregnancy. First, older females may be ceasing reproduction when they come into conflict with their reproductive daughters. Second females with a large number of offspring may be more likely to have a current dependent calf, and females with dependent calves are less likely to become pregnant again: dependent calves were found to affect pregnancy status in a previous study (Nichols et al., 2014). To investigate whether the relationship could be explained by reproductive competition, we re-fitted the model of pregnancy status, this time including only adult (aged 10+) philopatric offspring. We found that the probability of females being pregnant significantly decreased as the number of existing philopatric daughters increased (GLMM: X^2 = 4.68, df = 1, p = 0.0305, Table 1), but this relationship was not found with the number of philopatric sons (GLMM: X^2 = 1.39, df = 1, p = 0.238, Table 1).

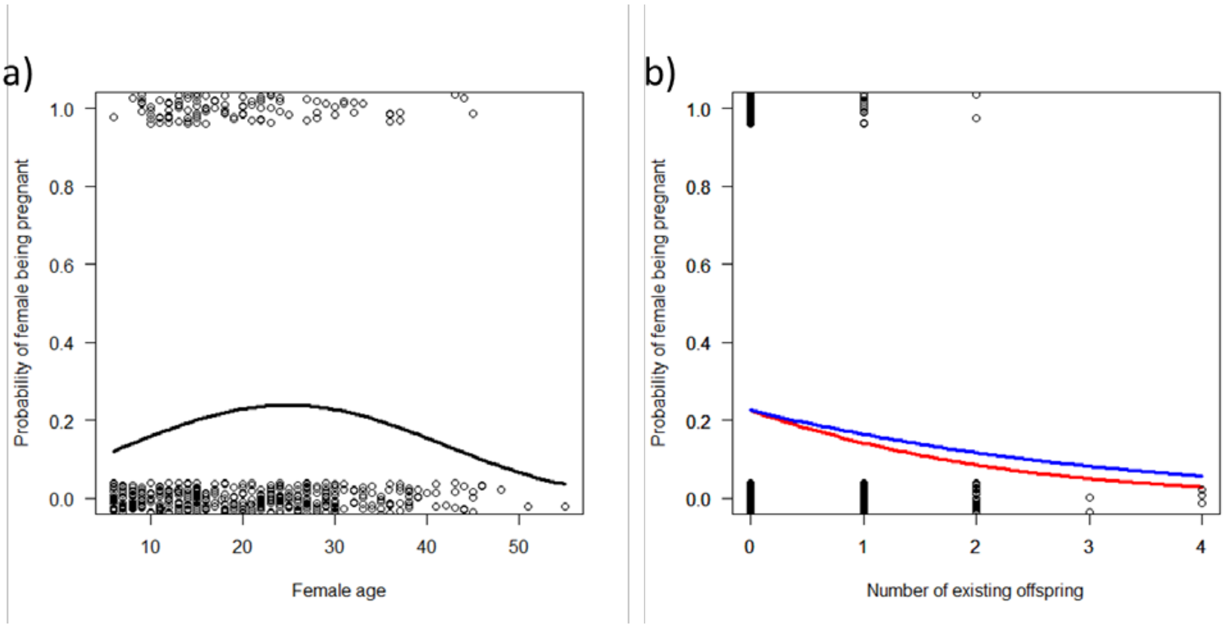


Figure 6. The probability of being pregnant (a) for females of different ages and (b) for females with different numbers of adult sons (blue) and daughters (red) present in the pod. Lines are predictions from GLMMs containing pod ID as a random effect. Open circles represent the data but note that we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

Table 1. Summary of all GLMMs conducted. Models of relatedness over the lifespan used relatedness values from 809 genotyped females (for which the age and sex was also known) in 25 pods. Models of pregnancy status used 530 females from 22 pods. P values presented are associated with removing the term from the model.

Model	**Term**	**Effect size**	**SE**	**t or z value**	**p-value**
Relatedness	Intercept	0.0842	0.0255	3.30	NA
between females	Female age	0.00260	0.000406	6.42	NA
and adult male	Pod size	-0.000602	0.000305	-1.97	NA
pod-members	Age: pod size	-1.50×10^{-5}	3.46×10^{-6}	-4.34	1.52×10^{-5}
Relatedness	Intercept	0.0117	0.0239	4.89	NA
between females	Female age	0.00118	0.000361	3.28	NA
and adult female	Pod size	-0.000808	0.000288	-2.81	NA
pod-members	Age: pod size	-7.34×10^{-6}	3.19×10^{-6}	-2.31	0.0213
Relatedness	Intercept	0.0634	0.0139	4.56	NA
between females	Female age	0.00263	0.000351	7.50	NA
and juvenile pod-	Female age^2	-2.88×10^{-5}	6.88×10^{-6}	-4.18	2.92×10^{-5}
members	Pod size	-0.000455	0.000165	-2.76	NA
	Age: pod size	-9.07×10^{-6}	1.95×10^{-6}	-4.65	3.47×10^{-6}
Number of	Intercept	-2.94	0.282	-10.4	NA
genetically	Female age	0.178	0.0203	8.77	NA
assigned	Female age^2	-0.00226	0.000373	-6.07	4.23×10^{-9}
offspring present					
in pod					
Probability of a	Intercept	-2.82	0.577	4.90	NA
female currently	Female age	0.154	0.0532	2.90	NA

being pregnant	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

Discussion

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

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

Although long-finned pilot whales live in groups of relatives, average within-pod relatedness is generally lower than in short-finned pilot whales and resident killer whales

(Table S1); we found that mean relatedness within pods was 0.06 (range 0.01 – 0.23) in comparison to 0.097 (range -0.1 to 0.38) from incomplete sampling of short finned pilot whale pods (Alves et al., 2013), and average pedigree relatedness values of 0.22-0.33 between female resident killer whales and the rest of their pod (Croft et al., 2017). These differences in relatedness are likely due to differences in pod size; long-finned pilot whale pods are marginally larger than those of short-finned pilot whales and are considerably larger than those of resident killer whales (Table S1). However, note that studies have used different measures of relatedness, have collected data from different populations and have used different methods to define group-membership (see Table S1 and references therein) so comparisons should be interpreted with appropriate caution.

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

A particularly strong piece of evidence suggesting that long-finned pilot whales have demographic patterns that could predispose them to evolving PRLS comes from age-related changes in relatedness. Johnstone and Cant (2010) predict PRLS will be favored by philopatry when this causes females to become more related to their social group, and particularly to males, as they age. This is what we find for long-finned pilot whales: a female's relatedness to adult males in a median sized pod can be expected to increase from 0.06 to 0.15 over her lifespan, while her relatedness to other females increases from 0.11 to 0.14. A similar pattern is found in resident killer whales, with pedigree relatedness to other females remaining stable at around 0.33, while relatedness to males increases from 0.16 to 0.33, but then decreases again when females enter their post-reproductive period, presumably as they do not continue to produce philopatric offspring beyond this point to compensate for the mortality of existing offspring (Croft et al., 2017). Such patterns are also found in some human populations. For example, matrilineal Mosuo of southwest China display an unusual dispersal system whereby both sexes are philopatric to their natal homestead (Wu Jia-Jia et al., 2013). Men do not live with their wives or children, instead visiting them at night, resulting in a relatedness structure that closely matches Johnstone and Cant's (2010) model predictions (Johnstone and Cant, 2019).

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

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

There are several reasons why long-finned pilot whales may not show PRLS. First, there may be few opportunities for helping. In resident killer whales, food can be unpredictable and the ecological knowledge of older females appears to aid its location and results in increased survival of philopatric adult offspring (Brent et al., 2015). Long-finned pilot whales feed mainly on squid, particularly *Loligo pealei* (Desportes and Mouritsen, 1988), supplemented with Atlantic mackerel *Scomber scombrus* (Abend and Smith, 1997). Their prey move seasonally with changes in water temperature and with time of day (Serchuk FM and WF, 1974). While it is possible that ecological knowledge could be important in locating mobile prey, local knowledge may be considerably less important if prey are continually followed over long distances, which may happen to a greater degree in long-finned pilot whales than resident killer whales and short-finned pilot whales. However, helping is not necessarily limited to finding food, and older females might offer other forms of help. Augusto et al (Augusto et al., 2017a) found that long-finned pilot whale calves were often 'escorted' by individuals unlikely to be parents. This might provide protection, allowing mothers to spend more time foraging, particularly during deeper dives. Similar behavior is observed in sperm whales (which do not appear to have PRLS) (Konrad et al., 2018). However, little is known about the costs and benefits of escorting and in long-finned pilot whales it does not seem to be primarily conducted by older females (Augusto et al., 2017a), although data are extremely limited, so its relevance to PRLS evolution is unclear. Allonursing, whereby non-mothers suckle young, has also been observed in toothed whales, including wild sperm whales where closer relatives are more likely to allonurse calves (Konrad et al., 2018) and also in captive beluga whales (Leung et al., 2010). Long-finned pilot whales are not known to allonurse, but data on this behavior is extremely difficult to collect due to the difficulties of sexing and ageing individuals and identifying mothers from observational data (Augusto et al., 2017a). Future work on the costs and benefits and distribution of helping behavior in toothed whales with and without PRLS will help to reveal the degree to which patterns of PRLS are explained by helping behavior, however collecting behavioral data on these species is a challenging and time-consuming process.

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

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

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

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

We found that females were less likely to be pregnant if they had a larger number of genetically assigned offspring present in the pod (while controlling for age dependent changes in fecundity), indicating that female fertility depends on previous reproduction. We note that this relationship persisted after dependent calves were removed from the dataset, suggests that females may refrain from breeding when they have adult offspring present in their pod, rather than simply when they have dependent offspring. This suggests that females with several existing offspring may invest in enhancing the quality of these offspring, rather than in producing further offspring. Such trade-offs appear to occur in other long-lived species with extended periods of maternal care. In humans, for example, a study of 163,827 births to 101,195 mothers across sub-Saharan Africa found that the probability of a child surviving to age 5 decreases by 14% for each subsequent child born to the mother, likely due to increased competition for maternal resources between siblings (Lawson et al., 2012). However, we note that in humans there is currently no evidence that women refrain from reproducing once they have a certain number of children (Towner et al., 2016).

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

It is currently unclear whether patterns of pregnancy in long-finned pilot whales represent flexibility in the timing of reproductive cessation, or represent a reversible pause in reproduction such that a female may begin to reproduce again should her existing offspring disperse or die. If reversibility is important for this species, there may be disadvantages to losing the ability to reproduce and undergoing a physiological menopause. Future studies investigating the mechanisms determining fecundity in this species would shed light on these possibilities. Although the underlying mechanisms are not yet understood, our study suggests that in long-finned pilot whales a post-reproductive period may therefore occur in individuals that benefit from it, but be rare on a population-wide level, and thus be difficult to distinguish from reproductive senescence. This plastic cessation of reproduction may represent a first step towards the evolution of irreversible species-wide PRLS, or alternatively could represent a stable alternative strategy to widespread post-reproductive periods. The possibility of adaptive plasticity in reproductive cessation warrants further attention in this species, and in other species that may benefit from late-life helping, both in cases where population-wide post-reproductive life stages occur, and where they do not. Given that we find that long-finned pilot whales meet the demographic conditions which should promote the evolution of PRLS (which occurs in the very closely related short-finned pilot whales), but they seem to have evolved a plastic cessation of reproduction, our results raise the question of why some species evolve irreversible PRLS if adaptive plasticity is possible?

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

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

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

Data Accessibility Data is available in Dryad. https://doi.org/10.5061/dryad.cjsxksn29

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Figure Legends

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

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

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

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

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

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

Tables and Table Legends

Table 1. Summary of all GLMMs conducted. Models of relatedness over the lifespan used relatedness values from 809 genotyped females (for which the age and sex was also known) in 25 pods. Models of pregnancy status used 530 females from 22 pods. P values presented are associated with removing the term from the model.

Model	**Term**	**Effect size**	**SE**	**t or z value**	**p-value**
Relatedness	Intercept	0.0842	0.0255	3.30	NA
between females	Female age	0.00260	0.000406	6.42	NA

and adult male	Pod size	-0.000602	0.000305	-1.97	NA
pod-members	Age: pod size	-1.50×10^{-5}	3.46×10^{-6}	-4.34	1.52×10^{-5}
Relatedness	Intercept	0.0117	0.0239	4.89	NA
between females	Female age	0.00118	0.000361	3.28	NA
and adult female	Pod size	-0.000808	0.000288	-2.81	NA
pod-members	Age: pod size	-7.34×10^{-6}	3.19×10^{-6}	-2.31	0.0213
Relatedness	Intercept	0.0634	0.0139	4.56	NA
between females	Female age	0.00263	0.000351	7.50	NA
and juvenile pod-	Female age^2	-2.88×10^{-5}	6.88×10^{-6}	-4.18	2.92×10^{-5}
members	Pod size	-0.000455	0.000165	-2.76	NA
	Age: pod size	-9.07×10^{-6}	1.95×10^{-6}	-4.65	3.47×10^{-6}
Number of	Intercept	-2.94	0.282	-10.4	NA
genetically	Female age	0.178	0.0203	8.77	NA
assigned	Female age^2	-0.00226	0.000373	-6.07	4.23×10^{-9}
offspring present					
in pod					
Probability of a	Intercept	-2.82	0.577	4.90	NA
female currently	Female age	0.154	0.0532	2.90	NA
being pregnant	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	Intercept	-2.59	0.561	-4.62	NA
female currently	Female age	0.116	0.0508	2.28	NA
being pregnant	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