

A long post-reproductive lifespan is a shared trait among genetically distinct killer whale populations

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Abstract

The extended female post-reproductive lifespan found in humans and some toothed whales remains an evolutionary puzzle. Theory predicts demographic patterns resulting in increased female relatedness with age (kinship dynamics) can select for a prolonged post-reproductive lifespan due to the combined costs of inter-generational reproductive conflict and benefits of late-life helping. Here we test this prediction using >40 years of longitudinal demographic data from the sympatric yet genetically distinct killer whale ecotypes: resident and Bigg's killer whales. The female relatedness with age is predicted to increase in both ecotypes, but with a less steep increase in Bigg's due to their different social structure. Here, we show that there is a significant post-reproductive lifespan in both ecotypes with >30% of adult female years being lived as post-reproductive, supporting the general prediction that an increase in local relatedness with age predisposes the evolution of a post-reproductive lifespan. Differences in the magnitude of kinship dynamics however, did not influence the timing or duration of the post-reproductive lifespan with females in both ecotypes terminating reproduction before their mid-40s followed by an expected post-reproductive period of ~20 years. Our results highlight the important role of kinship dynamics in the evolution of a long post-reproductive lifespan in long-lived mammals, while further implying that the timing of menopause may be a robust trait that is persistent despite substantial variation in demographic patterns among population.

Introduction

The evolution of an extended female post-reproductive lifespan is extremely rare in nature and is at present only known in five species of wild mammals¹⁻³. Outside of the prolonged post-reproductive lifespan seen in humans the only other species of mammals in which females have evolved early cessation of reproduction are toothed whales: short-finned pilot whales (*Globicephala macrorhynchus*), narwhals (*Monodon monoceros*), belugas (*Delphinapterus leucas*) and resident-ecotype killer whales (*Orcinus orca*)^{1,4}. Some evidence suggests that also the false killer whales (*Pseudorca crassidens*) have a substantial post-reproductive period⁵. In resident-ecotype killer whales, for example, adult females typically give birth to their last calf in their mid 30's to early 40's followed by a post-reproductive lifespan that may span many decades¹. In the classical view of evolutionary theory, early termination of reproduction is not a beneficial trait^{6,7} and understanding

why and how the post-reproductive lifespan has evolved remains a considerable challenge for evolutionary biology.

Adaptive explanations for the evolution of a long post-reproductive lifespan have tended to focus on the inclusive fitness benefits of helping kin in late life^{8–10}. Females can gain inclusive fitness benefits in late life by ceasing reproduction and instead invest their energy in helping existing offspring survive and reproduce (‘the mother hypothesis’)⁶. Further, through behaviours that help increase the survival of grandchildren, such as providing ecological knowledge¹¹ or provisioning¹², post-reproductive females can increase their inclusive fitness (‘the grandmother hypothesis’)¹³. In humans, grandmother benefits appear to be key for the evolution of a long post-reproductive lifespan^{13,14} and recent work in resident killer whales provides support for both the mother and grandmother hypothesis with the presence of both mothers and post-reproductive grandmothers having a positive impact on the survival of their adult offspring and grandoffspring^{8,15}. However, the inclusive fitness benefits from helping are likely not on its own sufficient to explain the timing of menopause in both killer whales and humans¹⁶ leading to the search for additional mechanisms that can contribute to the early termination of reproduction^{17,18}. Recent work has shown that kin-selected costs, as well as benefits, are important for the evolution of extended post-reproductive lifespans^{4,19}.

Demographic patterns with either female-biased dispersal and local mating or natal philopatry of both sexes and non-local mating, give rise to age-specific changes in the relatedness of an individual to its group (kinship dynamics), in particular an increase in average female relatedness to other group members with age¹⁹. In the case of resident killer whales, females are born into social unit (‘matriline’) consisting of their mother, siblings and other more distant relatives²⁰. As they age, their own sons replace more distantly related males in the matriline, increasing their average local relatedness to the group over time²¹. This ultimately leads to an asymmetry in selection for helping and harming with age, which means that older females that are more related on average to the group are under stronger selection to help, while younger females are under stronger selection to harm⁴. Thus, in competition for reproduction older females experience a larger inclusive fitness cost compared with younger females²¹. The combination of such inclusive costs of inter-generational reproductive conflict and inclusive fitness benefits of helping kin are hypothesised to be key predictors for the evolution of a long post-reproductive lifespan in mammals^{1,4,19}.

Investigating kinship dynamics and age-specific life history changes requires long-term social and demographic data that captures most of the lifespan of animals. These data are therefore rare in long-lived mammals. The long term data collected on different populations of killer whales in the coastal waters of the USA and Canada now extends over more than four decades, providing an unique opportunity to examine the link between kinship dynamics and life history evolution in a long-lived marine mammal. In addition to the support for the mother and grandmother hypotheses in resident killer whales^{8,15}, there is strong support for the reproductive conflict hypothesis with offspring of older females that are born into conflict with offspring of a younger female having a 1.7 times higher mortality risk²¹. However, it is still unknown whether these traits are shared between different populations of killer whales. Killer whales are among the most widely dispersed mammals on the planet and are found in all oceans^{22,23}. Lineages that differ morphologically²⁴ and behaviourally²⁵ and are genetically isolated²⁶, are referred to as ecotypes. Three killer whale ecotypes are sympatric in the northeast Pacific and among them are several populations of both resident and Bigg’s killer whales^{27,28}. In the waters off the west coast of North America are the Northern and Southern populations of resident killer whales and the West Coast Transient populations of Bigg’s killer whales (Table 1; a third offshore ecotype is also encountered, but only very rarely is not considered here)^{26,27,29}. Both populations of residents are specialist fish-eaters with salmon making up the almost all of their prey^{20,30}, whereas Bigg’s killer whales are specialised in hunting marine mammals³¹. This differentiation in diet is reflected in the social behaviour of the ecotypes with resident killer whales typically being observed travelling in larger social groups consisting of several maternal groups, compared to Bigg’s killer whales. The mean group size of cohesive maternal groups however are similar for the two ecotypes (Table 1)³². In resident killer whales there is almost no dispersal of males and limited dispersal of females from the maternal group. In contrast, there is dispersal of both sexes from the maternal group of Bigg’s killer whales^{31,33}, which may be related to maintaining optimal group foraging size for predating on marine mammals^{34,35}.

Ecotype ²⁶	Genetic population ²⁷	Prey specialisation	Maternal group size Mean (range)	Social structure
Resident	Southern residents	Fish (mainly salmon) ³⁶	4.33 (1-16) ³⁷	Natal philopatry of males and females, non-local mating ³⁸ (but see 39).
	Northern residents	Fish (mainly salmon) ³⁶	6.5 (1-19) ³²	Natal philopatry of males and some females, non-local mating ^{28,38}
Bigg's	West Coast Transients (WCT) ⁴⁰	Marine mammals (mainly pinnipeds and small cetaceans) ³¹	3.9 (1-8) ⁴¹	Some dispersal of males and females from natal group, non-local mating inferred ^{31,33}

The difference in demography observed between the resident and Bigg's ecotypes are predicted to generate different patterns of kinship dynamics (age-specific changes in relatedness) which can be illustrated using the theoretical model presented by Johnstone & Cant (2010)⁴. Previous theoretical work on kinship dynamics in resident killer whales predicted an increase in local relatedness with female age⁴ which has been confirmed using individual-based demographic and social data from resident killer whales²¹. Here, we use this established modelling framework to predict the patterns of age-related changes in kinship for female Bigg's killer whales allowing us to directly compare the predicted kinship dynamics between the resident and Bigg's ecotype. Using this approach it is predicted that female local relatedness will increase with age for both killer whale ecotypes, albeit with a weaker relationship under the demographic conditions of Bigg's killer whales (Fig. 1)⁴. This increase in female local relatedness is opposite to the pattern observed in most mammals (male dispersal and local mating), and it predicts that there will be selection for a post-reproductive female lifespan in both killer whale ecotypes. We hypothesise however, that the difference in the strength of the kinship dynamics will lead to a lower potential for inclusive fitness benefits from helping kin in late life and inclusive fitness costs of reproductive conflict with younger females for Bigg's females²¹. Given the predicted differences in kinship dynamics, and assuming the costs and benefits of reproduction with age are equal and that these don't change with changing dispersal, we predict that selection for a post-reproductive lifespan will be weaker in Bigg's killer whales compared to resident killer whales⁴ and we further hypothesise that this will be reflected by an older age at last reproduction, and a shorter post-reproductive lifespan in female Bigg's killer whales.

Here we test for the presence of a post-reproductive period in Bigg's killer whales and compare female post-reproductive lifespan between the sympatric resident and Bigg's killer whale ecotypes. Using over 40 years of individual-based demographic data, we model survival trajectories using a Bayesian hierarchical framework⁴² and calculate the post-reproductive representation (PrR)⁴³ to compare the presence of a long post-reproductive lifespan in both resident and Bigg's killer whale ecotypes, as well as the timing of a potential post-reproductive lifespan. We show that females in both ecotypes have a prolonged post-reproductive lifespan. However, in contrast to our predictions, the timing and duration of the female post-reproductive lifespan did not appear to differ between ecotypes.

Methods

Here we use post-reproductive representation (PrR) as a measure for post-reproductive lifespan, which is measured as the proportion of adult female years being lived by post-reproductive females⁴³. While a

decline in fertility with age is a general trait among animals⁴⁴, the long post-reproductive periods, often spanning more than a decade, observed in humans and some toothed whales is a rare trait. Reports of post-reproductive lifespan in other species often reflect individual variation in senescence, rather than a general trait at the population level or are calculated for populations living under artificial conditions often with reduced mortality risk^{3,45–47}. A significant advantage of the PrR measure is that it is a population-level measure that is directly comparable between species or populations with different lengths of lifespan as it is the number of female years lived post-reproductively out of all years lived by females in a given population, while PrR also allows for a test of whether the post reproductive lifespan is significantly larger than what is expected by chance⁴³.

Data type and collection

Long-term photo-identification data have been collected on three killer whale populations with overlapping geographical ranges in the waters off Washington State, the state of Alaska, USA and British Columbia, Canada: Northern resident, Southern resident and Bigg's killer whales⁴¹ (Table 2). Photo-identification studies began in 1972 for Bigg's, 1973 for Northern residents and 1976 for Southern residents. Data collection were boat-based and during each encounter identification photos of dorsal fins and saddle were obtained from the left side of each whale^{38,48}. Sex was determined based on the pigmentation of the ventral side of genital or mammary slits, the presence of neonates or the size and shape of the dorsal fin of adults⁴¹.

	Southern residents	Northern residents	Bigg's
Study start	1976	1973	1972
Collected by	Center for Whale Research	Fisheries and Oceans Canada	Fisheries and Oceans Canada
Individuals in datasets	207	564	506
Females (adult*)	94 (67)	193 (159)	180 (145)
Males (adult*)	86 (45)	170 (124)	121 (82)
Unknown sex	27	201	205
Known year of birth	128	433	351
Known year of death	124	238	126
Known year of birth and death	59	131	70
Adult sex ratio⁺	0.40	0.44	0.36

The Center for Whale Research (www.whaleresearch.com) collected the long-term dataset for Southern residents. With all alive members of this population being observed each year of the study, this provides a near-complete life history for the population including information on survival for males and females and reproduction for females. Fisheries and Oceans Canada collected the long-term data on both Bigg's and Northern residents, which includes the survival for most individuals and reproduction for females. However, a multi-year lack of encounters with some matrilineal groups generated uncertainty for year of death of some individuals (Table 2). We used the photo-identification data as capture-mark-recapture data in the format of a sighting matrix, i.e. absence/presence for each individual during each year.

In all three datasets, year of birth was only included for animals that were born after the start of the given study, otherwise year of birth was zero, indicating birth year as unknown (Table 2). In Southern residents, newborn individuals were observed within their first year of life. In Northern residents and Bigg's, if an individual was not observed within the first year of life, year of birth was estimated based on body length of the individual when it was first observed⁴¹. For all populations, year of death of an individual was determined either directly from strandings or based on an individual missing from its matrilineal group on a single (individual less than 3 years old) or on several (individual more than 3 years old) occasions⁴¹. If year of birth and/or death were unknown for a given individual, these values were assigned a zero and would be estimated by the model (see Table 2 for number of individuals with known birth and death year).

Estimating age-specific survival

As killer whales are a long-lived species, a common feature of the observation data from all three populations is that some individuals were born before the studies started (i.e. left truncated) and some were still alive at the end of the study (i.e. right-censored). This gives rise to uncertainties regarding some birth and death years in the datasets. Further, some individuals have gaps in their sighting history of more than 1 year likely due to their preference for waters beyond the core study areas. This introduces uncertainty in the recapture probability and year of death of these individuals. To account for the uncertainties and missing observations in the data we used a Bayesian hierarchical framework to estimate the age-specific survival and mortality for all three populations⁴². This framework estimates the unknowns and uncertainties as latent variables (i.e. variables to be estimated) and combines this with flexible parametric mortality functions to predict the age-specific survival of the three killer whale populations⁴⁹. Although the data on Southern residents is near-complete, we have used the same approach on all datasets to ensure the results are directly comparable. Given that males and females likely have different mortality trajectories³⁰ the sex of individuals was included as a covariate in the analyses.

We fitted ten different mortality and survival models to each of the three datasets using the BaSTA package⁴⁹ in R version 3.6.2⁵⁰. The different functions tested either describes a constant mortality that is independent of age (Exponential), an exponential increase in mortality with age (Gompertz)⁵¹, an increase or decrease in mortality as a power function of age (Weibull)⁵² or an initial exponential increase in mortality that plateaus after a given age (Logistic)⁵³. Adding a shape term to the mortality function allows the mortality to have an initial decline from birth (bathtub shape)⁵⁴ or an added constant mortality rate that is independent of age (Makeham)⁵⁵. We ran the models for four Markov chain Monte Carlo chains (MCMC) to evaluate convergence of the model. The final model specifications, where convergence for all model types had been reached, were: four MCMC chains, 1,000,000 iterations, 200,001 burn-in, and 10,001 thinning⁵⁶. We visually inspected convergence in the parameter traces for the four chains, to ensure that all chains had mixed properly. Further, convergence was assessed formally for each model on the basis of the scale reduction (\hat{R}), where $\hat{R} < 1.1$ indicates convergence^{49,57}.

Testing the fit of the model

We used the deviance information criterion (DIC) to evaluate the model fit and predictive power of the different models, a measure analogous to Akaike's information criterion (AIC)⁵⁸ (but see Spiegelhalter et al (2014)⁵⁹). The importance of including the categorical covariate of sex was investigated using the Kullback-Leibler discrepancy, which is informed by the overlap of the posterior distribution of parameter estimates^{60–62}. For data including only individuals of known sex, the Gompertz model with a bathtub shape described the mortality and survival trajectory well for all three populations, as the second best fit for Southern and Northern residents and the best fit for Bigg's (Table 3). Mathematically, the Gompertz bathtub model consists of three elements

$$\mu(x) = e^{a_0 - a_1 x} + c + \exp(b_0 + b_1 x)$$

where a_0 and a_1 defines the initial decline in mortality from birth, c defines the mortality through the adult stage and b_0 and b_1 defines the exponential increase in mortality at the senescent stage. This model therefore offers great flexibility in the age of onset of aging as well as changes in the rate of aging throughout life^{42,49,54} and we use this model for quantifying the post-reproductive lifespan for all three populations to best ensure direct comparison between the three populations. Given the lack of data on older whales and the related uncertainty around ages at death, we included weakly informative prior distributions that allowed the models to explore the parameter space while reflecting a plausible range of resulting values for survival. These prior distributions were informed using known life history traits for the populations²⁹. For the final model (Gompertz with bathtub shape) we ran the model with the following prior means (and standard deviations): $a_0 = -3$ ($\sigma = 1$), $a_1 = 0.2$ ($\sigma = 0.05$), $c = 0.001$ ($\sigma = 0.001$), $b_0 = -4$ ($\sigma = 1$), $b_1 = 0.05$ ($\sigma = 0.01$). All prior distributions were normally distributed and truncated at 0, except for a_0 and b_0 . Further, recapture probabilities for all three populations were assumed to be time-dependent as there are variations in observation efforts across the study periods. This time-dependency of recapture probabilities was therefore

included in the model, as it allows for variation of the parameter estimates for each time period (10-year period).

Permutations of individuals with unknown sex

The sex of a substantial portion of individuals were not determined in the Northern resident and Bigg’s populations (Table 2). These individuals were all under 15 years old. In mammals, mortality is often higher in early life, and by excluding juvenile individuals from the analyses, we are likely underestimating such early-life mortality. Instead of including them as a third category of “unknown sex”, which would – in essence – calculate the mortality trajectory of an artificial short-lived sex, we used a permutation approach to assign a sex to these individuals randomly. This way we are able to include the early life mortality into the full age-specific mortality trajectory. We implemented the same Bayesian hierarchical model that was the best overall fit for individuals of known sex, the Gompertz bathtub model, which was confirmed by a trial run on a random dataset as the best fit for the full data. Although only 21 individuals were of unknown sex in the Southern residents, we also ran the same number of permutations on this population for comparability. We ran 1000 permutations, where sex was randomly assigned to individuals of unknown sex for each permutation. Both populations have a female-biased adult sex ratio (Table 2), and we assumed a sex ratio of 1:1 at birth. We used the permuted output to calculate the variation in post-reproductive representation in all three populations.

Southern residents	Southern residents	Southern residents	Northern residents	Northern residents	Northern residents
Model	Shape	DIC	Model	Shape	DIC
Gompertz	Makeham	3464	Gompertz	Simple	68
Gompertz	Bathtub	3506	Gompertz	Bathtub	68
Weibull	Makeham	3543	Logistic	Simple	69

Calculating post-reproductive representation

To calculate PrR two data series were obtained, the l_x and m_x series. The first series, l_x , is the probability of survival to a given age x , obtained from the survival model output (Fig. 2). The second, m_x , is calculated as the proportion of offspring born to females of age x out of all females that were alive at that age. To get m_x we used the age of females, where known or estimated year of birth was available, and the age at which females gave birth. If a female was not observed in a given year it was recorded as “no birth”.

Mathematically, PrR is based on l_x and e_x , where e_x is the life expectancy at age x . A multiplication of these terms gives T_x (the total individual years lived after age x). PrR is then calculated from T_x at age B and M , which are the ages, where 5% and 95% of female fecundity has been realised (inferred from m_x). Thus, the formula for calculating PrR is:

$$PrR = \frac{T_M}{T_B} = \frac{l_M}{l_B} * \frac{e_M}{e_B}$$

The input was a lifetable consisting of l_x (from the basta model output) and m_x (calculated from the observational data). To test the statistical significance of the PrR value it was tested against the null hypothesis that survivorship and fecundity declines with the same rate, which would lead to $PrR = 0$. We simulated 9999 populations of 1000 individuals, where this null hypothesis was true and compared each of these null populations to each permutation of the observed population. The simulated null populations were generated based on the demographic parameters of the given killer whale population. The p-value was obtained by evaluating how many of these simulated populations had a PrR greater than or equal to the PrR values obtained from the observed populations, with the number of samples included in both the numerator and denominator^{1,63}.

Results

Overall, 198 Southern resident, 568 Northern resident and 510 Bigg’s killer whales were observed in these populations over the >40 year period of observations (Table 1) and included in the analysis. The adult sex ratio for all datasets was female-biased (Table 2). There was a substantial number of individuals, where the sex had not been determined with 202 in Northern residents and 209 in Bigg’s killer whales (Table 2).

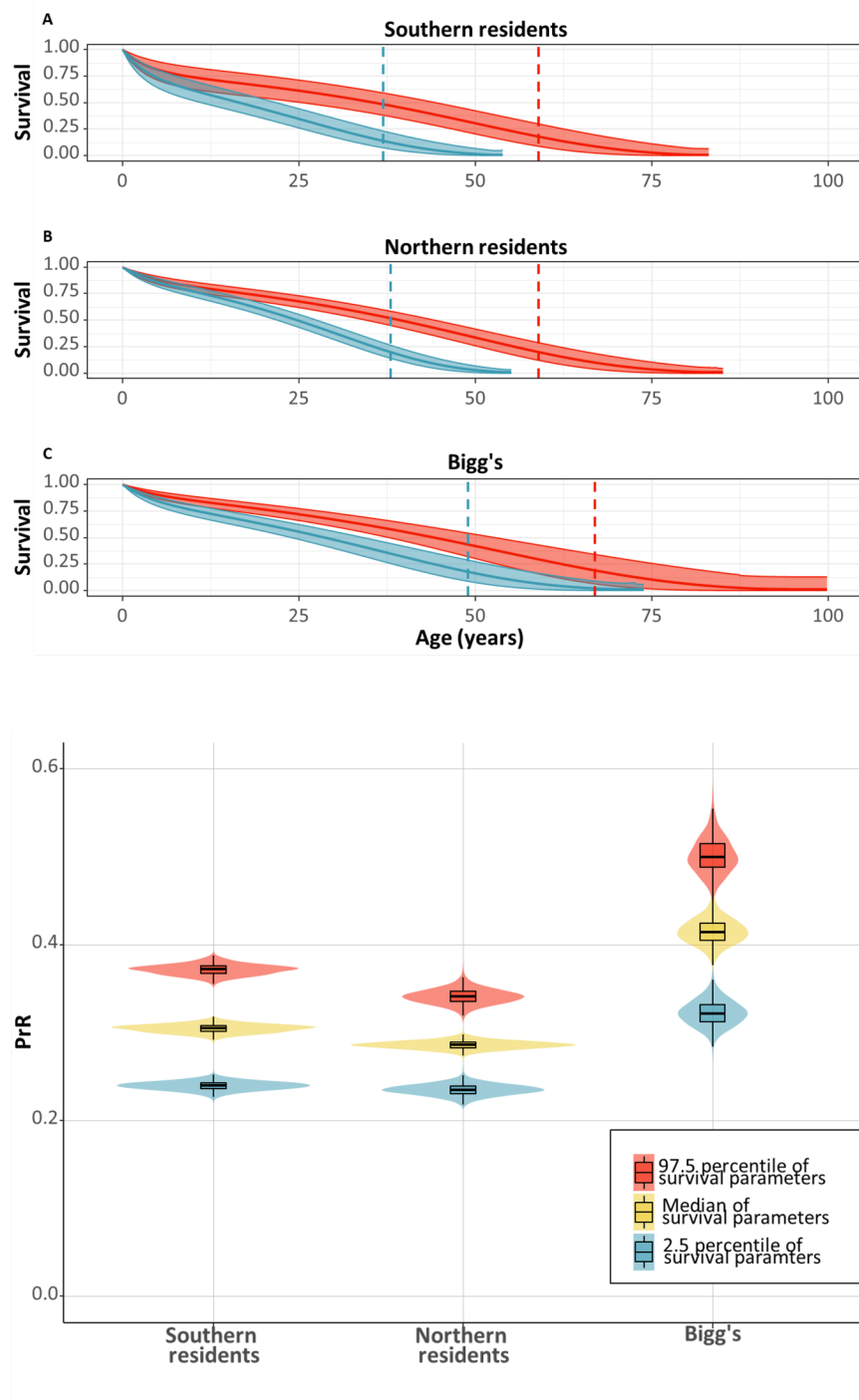
Age-specific survival

The model (Gompertz with bathtub shape) reveals a clear age- and sex-specific pattern of survival for all three populations (Fig. 2). We assessed the fit of the model by plotting the estimated survival probability together with the observed survival probability of individuals of known age (Supplementary Fig. S1). The models predict that 95% of the female lifespan on average has occurred (age where $l_x = 0.05$) after a median±standard deviation of 59±0.5 years (credible interval: 52±0.5 - 65±0.7 years) for Southern residents, 59±0.6 years (credible interval: 54±0.6 - 65±1 years) for Northern residents and 66±2 years (credible interval: 56±1 - 77±3 years) for Bigg’s. For males, the model predicts that 95% of the male lifespan has occurred after a median of 37±0.1 years (credible interval: 33±0.2 - 41±0.5 years) for Southern residents, 38±0.3 (credible interval: 36±0.4 - 41±0.5) for Northern residents and 49±1 (credible intervals: 43±1 - 56±1) for Bigg’s killer whales. The variation arises from the permutations.

Post-reproductive representation

All three populations had a post-reproductive representation that was significantly greater than zero ($p < 0.05$), with estimated PrR values above 0.3 for all three populations (Fig. 3). For all three populations, median expected female lifespan as post-reproductive was >20 years (Table 4) and the probability of surviving until age M (the age when 95% of female fecundity has occurred) was median >40%.

	Age B (5% fecundity)	Additional years of life expected at age B	Age M (95% fecundity)
Southern residents	13 ^a	39±0.5 ^b	41 ^a
Northern residents	11 ^a	39±1 ^b	41 ^a
Bigg’s	12 ^a	46±2 ^b	37 ^a



Discussion

We show that three sympatric killer whale populations, have comparably long post-reproductive female lifespans. With a median of more than 30% of all adult female years in all three populations being lived by post-reproductive females, it is a substantial life history stage (Fig. 3). This is the first evidence showing a

long post-reproductive period as a shared trait among genetically distinct killer whale populations, suggesting that it could have evolved in a common ancestor to current killer whales and that it might be present in other discrete populations. Indeed, phylogenomic analysis suggests that the divergence between the lineages leading to resident and Bigg's ecotypes is the earliest divergence of extant killer whale lineages occurring over 350,000 years ago⁶⁴. If the shared presence of a post-reproductive lifespan in both residents and Bigg's is due to a shared ancestral trait, this suggests that a post-reproductive lifespan is an ancestral state of all extant killer whale ecotypes.

From the survival model output, the survival patterns is similar in all three killer whale populations, with females expected to live substantially longer than males and females being able to live >50 years (Fig. 2). Interestingly, the model predicts that male Bigg's killer whales may have a longer expected lifespan compared to resident males (Fig. 2.), a pattern that may be influenced by the difference in their environments, both social^{65,66} and ecological (such as the recent prey abundance of the favourable prey of Bigg's⁶⁷). However, this could also be an effect of male dispersal in Bigg's, resulting in more uncertainty for the model around the ages at death of males. In females the survival trajectory of this study is generally supported by previous estimates of lifespan in killer whales^{29,30}. We used a Bayesian hierarchical approach to estimate the age-specific survival, with the benefit of being able to include individuals with unknown age of birth and death. Further, through permutations we were able to include individuals of unknown sex which likely produces random variation in the model output. Rather than considering maximum longevity, comparing the ages when 95% of years have been lived in each population is a more reliable measure (Fig. 2). This metric indicates that Bigg's females are expected to live longer than females from both resident populations with a difference of ~10 years (Fig. 2). However, despite the differences in the estimated maximum lifespan, the results clearly show that all three populations have significant post-reproductive periods with similar ages of onset of the post-reproductive life stage in females (Table 4).

The cessation of female reproduction well before the end of life in a limited number of wild mammals largely remains an evolutionary puzzle. Yet, there is growing evidence that it has evolved based on the combined inclusive fitness benefits of helping and the costs of reproductive conflict for older females³. The opportunity for females to help kin is integral to the adaptiveness of ceasing reproduction well before the end of life^{9,15}. Previous research in both humans and resident killer whales, has shown that older females are able to provide help that positively affects the survival and reproduction of their kin^{15,68,69}. Especially in humans, offspring can have a long period, where they rely on older individuals for help providing food⁴. Our study demonstrates that females of both resident and Bigg's killer whales can expect to live more than 20 years after they cease reproduction, allowing for a substantial period with the potential for helping kin. In resident killer whales, mothers impact the survival of their offspring well into their adult years¹⁵, and grandmothers are important repositories for ecological knowledge for relatives¹¹ increasing the survival of their grandoffspring⁸. Although dispersal of both males and females is more pronounced within the Bigg's ecotype, the post-reproductive females are never observed on their own, but always with either their son(s) or daughter(s)⁴¹. Further, the smaller matriline may consist of up to three generations of maternally related kin and are regularly observed associating with individuals outside of the maternal group^{31,41}. These patterns of association provide opportunities for social interactions that can lead to inclusive fitness benefits for older females^{11,70}. While the earlier dispersal of females from Bigg's groups likely reduces the occurrence of reproductive conflict between mothers and daughters (Fig. 1)⁴, Bigg's groups can also consist of reproductively active females from different generations, similar to the resident killer whales. The similarity in the timing of the cessation of reproduction at around 40 years in both the resident and Bigg's ecotypes, indicate that Bigg's females may also experience inter-generational reproductive conflict and that this plays an important role in shaping fertility patterns across the different ecotypes. Testing this hypothesis requires more work on quantifying the kin structure and mortality patterns of Bigg's killer whales.

Here we found that the differences in dispersal patterns between resident and Bigg's killer whales did not predict the timing of the cessation of reproduction and the length of the post-reproductive lifespan. Similarly in humans, Snopkowski et al. (2014) compared age at menopause across ethnic groups with different patterns of post-marital residence to explore whether differences in dispersal pattern had an effect on the timing of

menopause⁷¹. They showed that female-biased dispersal, expected to lead to an increase in female local relatedness with age, did not result in an earlier age at menopause compared to groups with male-biased dispersal patterns⁷¹. It is possible that modern societies in both humans and killer whales are different from the ancestral societies in which the evolutionary effects of reproductive conflict and the timing of menopause occurred. The lack of variation in the timing of reproductive cessation despite differences in dispersal patterns has important implications for our understanding of the evolution of a long post-reproductive period in mammals, including humans. Although patterns of kinship dynamics may predispose females to evolve a prolonged post-reproductive lifespan, the costs and benefits of reproductive conflict and helping are going to be shaped by the ecology of the population. For example, despite the close resemblance of demographic patterns between short- and long-finned (*Globicephalas melas*) pilot whales^{72,73}, indicating similar kinship patterns, a long post-reproductive lifespan has only been observed in the short-finned pilot whales¹, which could be a result of difference in ecology of the two species. Moreover, there are several examples of primate species with female-biased dispersal and local mating (e.g. chimpanzee, bonobos and gorillas^{74–76}), and thus an increase in female local relatedness with age similar to humans, where a prolonged post-reproductive lifespan has not evolved¹. It is likely that we may find similarly prolonged post-reproductive lifespans in other killer whale populations or other mammal species as we gather more individual-based data on long-lived social mammals. Some evidence already suggests that false killer whales (*Pseudorca crassidens*)⁵ and Asian elephants (*Elephas maximus*) have a long period as post-reproductive, although for Asian elephants it is likely a social rather than physiological trait⁷⁷.

The similarity in the timing of menopause among killer whales and humans is curious and could hint at there being a similar driver of the evolution of onset of menopause. Current models investigating the role of kinship dynamics for driving the evolution of menopause make specific predictions regarding how patterns of helping and harming will change with age^{4,19} yet they do not predict how these patterns will drive the timing of menopause or the length of the post-reproductive lifespan. Hence our prediction that differences in dispersal patterns would lead to different selection pressures for a post-reproductive period in the two different killer whale ecotypes are currently based on the reasoning that kinship dynamics are an indicator for the strength of selection for helping vs harming across the lifespan. It is possible that menopause can not easily be reversed once evolved which may help explain the universality in the timing of menopause in humans, and likely also killer whales, despite the evident differences among societies, such as patterns of dispersal⁷¹.

In conclusion, when taken together with previous work, our findings support the hypothesis that kinship dynamics play a key role in the evolution of a prolonged post-reproductive lifespan. However, contrary to our predictions, the timing and expected duration of the post-reproductive lifespan did not vary with the dispersal pattern from the natal group, which likely represents different costs and benefits of helping and harming in the two ecotypes. These were, however, not taken into account in our predictions, but would be valuable to disentangle in future research to better understand the drivers for the timing of long post-reproductive lifespans in mammals. Nevertheless, the clear similarity of the post-reproductive period in some of the most genetically distinct killer whale populations echoes what has been observed across different human societies. This indicates a long post-reproductive period being an ancestral trait in killer whales, and likely present in other killer whale populations and ecotypes.

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Author contributions

M.L.K.N., D.P.C., S.E., M.C. and D.W.F. developed the research; D.K.E., K.C.B., J.R.T. and T.D-V. collected the data; M.L.K.N. analysed the data in discussion with T.D-V., S.E., D.W.F., M.W. and D.P.C.; M.L.K.N. wrote the first draft and constructed figures with input from S.E., D.W.F. and D.P.C.; all authors provided feedback on subsequent drafts.

The authors declare that there are no competing interests.

Data availability

Data to replicate the analyses are available from the online repository: <https://doi.org/10.5061/dryad.6t1g1jwxx>. Requests for access to raw data can be directed to the authors, the Center for Whale Research (www.whaleresearch.com) or Fisheries and Oceans Canada (www.dfo-mpo.gc.ca)

References

1. Ellis, S. *et al.* Postreproductive lifespans are rare in mammals. *Ecol. Evol.* **8** , 2482–2494 (2017).
2. Ellis, S. *et al.* Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. *Sci. Rep.* **8** , 12833 (2018).
3. Croft, D. P., Brent, L. J. N., Franks, D. W. & Cant, M. A. The evolution of prolonged life after reproduction. *Trends Ecol. Evol.* **30** , 407–416 (2015).
4. Johnstone, R. A. & Cant, M. A. The evolution of menopause in cetaceans and humans: the role of demography. *Proc. R. Soc. B Biol. Sci.* **277** , 3765–3771 (2010).
5. Photopoulou, T., Ferreira, I. M., Best, P. B., Kasuya, T. & Marsh, H. Evidence for a postreproductive phase in female false killer whales *Pseudorca crassidens*. *Front. Zool.* **14** , 30 (2017).
6. Williams, G. C. Pleiotropy, Natural Selection, and the Evolution of Senescence. *Evolution* **11** , 398–411 (1957).
7. Hamilton, W. D. The moulding of senescence by natural selection. *J. Theor. Biol.* **12** , 12–45 (1966).
8. Nattrass, S. *et al.* Postreproductive killer whale grandmothers improve the survival of their grandoffspring. *Proc. Natl. Acad. Sci.* 201903844 (2019) doi:10.1073/pnas.1903844116.
9. Sear, R. & Mace, R. Who keeps children alive? A review of the effects of kin on child survival. *Evol. Hum. Behav.* **29** , 1–18 (2008).
10. Kim, P. S., Coxworth, J. E. & Hawkes, K. Increased longevity evolves from grandmothering. *Proc. R. Soc. B Biol. Sci.* **279** , 4880–4884 (2012).
11. Brent, L. J. N. *et al.* Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr. Biol.* **25** , 746–750 (2015).

12. Hawkes, K., O'Connell, J. F. & Blurton Jones, N. G. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Curr. Anthropol.* **38** , 551–577 (1997).
13. Hawkes, K. The grandmother effect. *Nature* **428** , 128–129 (2004).
14. Hawkes, K. & Coxworth, J. E. Grandmothers and the evolution of human longevity: A review of findings and future directions. *Evol. Anthropol. Issues News Rev.* **22** , 294–302 (2013).
15. Foster, E. A. *et al.* Adaptive Prolonged Postreproductive Life Span in Killer Whales. *Science* **337** , 1313–1313 (2012).
16. Hill, K. & Hurtado, A. M. The evolution of premature reproductive senescence and menopause in human females. *Hum. Nat.* **2** , 313–350 (1991).
17. McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. Matriarchs As Repositories of Social Knowledge in African Elephants. *Science* **292** , 491–494 (2001).
18. Moss, C. J. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *J. Zool.* **255** , 145–156 (2001).
19. Cant, M. A. & Johnstone, R. A. Reproductive conflict and the separation of reproductive generations in humans. *Proc. Natl. Acad. Sci.* **105** , 5332–5336 (2008).
20. Bigg, M. A., Olesiuk, P. F., Ellis, G., Ford, J. K. B. & Balcomb III, K. C. *Social organization and genealogy of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State* . 383–405 (1990).
21. Croft, D. P. *et al.* Reproductive conflict and the evolution of menopause in killer whales. *Curr. Biol.* **27** , 298–304 (2017).
22. Baird, R. W. The killer whale: foraging specializations and group hunting. in *Cetaceans Societies* (eds. Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H.) (1999).
23. Ford, J. K. B. *The Encyclopedia of Marine Mammals* . (Elsevier, 2009).
24. Baird, R. & Stacey, P. Variation in saddle patch pigmentation in populations of killer whales (*Orcinus orca*) from British Columbia, Alaska, and Washington State. *Can. J. Zool.* **66** , 2582–2585 (2011).
25. Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B. & Deecke, V. B. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? *Biol. J. Linn. Soc.* **106** , 1–17 (2012).
26. Morin, P. A. *et al.* Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Res.* **20** , 908–916 (2010).
27. Parsons, K. M. *et al.* Geographic patterns of genetic differentiation among killer whales in the northern North Pacific. *J. Hered.* **104** , 737–754 (2013).
28. Barrett-Lennard, L. G. & Ellis, G. M. *Population Structure and Genetic Variability in Northeastern Pacific Killer Whales: Towards an Assessment of Population Viability* . 35 (2001).
29. Olesiuk, P., Ellis, G. & Ford, J. *Life History and Population Dynamics of Northern Resident Killer Whales (Orcinus orca) in British Columbia* . (2005).
30. Olesiuk, P. F., Bigg, M. A. & Ellis, G. M. *Life history and population dynamics of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State* . (1990).
31. Ford, J. K. B. & Ellis, G. M. *Transients: mammal-hunting killer whales of British Columbia, Washington, and Southeastern Alaska* . (UBC Press, 1999).

32. Towers, J. *et al.* *Photo-identification Catalogue and Status of the Northern Resident Killer Whale Population in 2019* . (2020).
33. Baird, R. W. & Whitehead, H. Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* **78** , 2096–2105 (2000).
34. Krause, J., Krause, P. of F. B. and E. J., Ruxton, G. D., Ruxton, G. & Ruxton, I. G. *Living in Groups* . (OUP Oxford, 2002).
35. Baird, R. W. & Dill, L. M. Ecological and social determinants of group size in *transient* killer whales. *Behav. Ecol.* **7** , 408–416 (1996).
36. Ford, J. & Ellis, G. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Mar. Ecol. Prog. Ser.* **316** , 185–199 (2006).
37. Center for Whale Research. <https://www.whaleresearch.com/>.
38. Bigg, M. A., Ellis, G., Ford, J. K. B. & Balcomb III, K. C. *Killer Whales: A Study of Their Identification, Genealogy and Natural History in British Columbia and Washington State* . (Phantom Press and Publishers, 1987).
39. Ford, M. J. *et al.* Inbreeding in an endangered killer whale population. *Anim. Conserv.* **21** , 423–432 (2018).
40. Sharpe, D. L., Castellote, M., Wade, P. R. & Cornick, L. A. Call types of Bigg’s killer whales (*Orcinus orca*) in western Alaska: using vocal dialects to assess population structure. *Bioacoustics* **28** , 74–99 (2019).
41. Towers, J. R. *et al.* *Photo-identification catalogue, population status, and distribution of Bigg’s killer whales known from coastal waters of British Columbia, Canada* . (2019).
42. Colchero, F. & Clark, J. S. Bayesian inference on age-specific survival for censored and truncated data: age-specific survival analysis when age is unknown. *J. Anim. Ecol.* **81** , 139–149 (2012).
43. Levitis, D. A. & Lackey, L. B. A measure for describing and comparing postreproductive life span as a population trait: measuring postreproductive life span. *Methods Ecol. Evol.* **2** , 446–453 (2011).
44. Packer, C., Tatar, M. & Collins, A. Reproductive cessation in female mammals. *Nature* **392** , 807–811 (1998).
45. Packer, C., Lewis, S. & Pusey, A. Comparative analysis of non-offspring nursing. *Anim. Behav.* **43** , 265–281 (1992).
46. Cohen, A. A. Female post-reproductive lifespan: a general mammalian trait. *Biol. Rev.* **79** , 733–750 (2004).
47. Levitis, D. A., Burger, O. & Lackey, L. B. The human post-fertile lifespan in comparative evolutionary context. *Evol. Anthropol. Issues News Rev.* **22** , 66–79 (2013).
48. Bigg, M. A., MacAskie, I. B. & Ellis, G. *Abundance and movements of killer whales off eastern and southern Vancouver Island with comments on management* . (1976).
49. Colchero, F., Jones, O. R. & Rebke, M. BaSTA: an R package for Bayesian estimation of age-specific survival from incomplete mark-recapture/recovery data with covariates. *Methods Ecol. Evol.* **3** , 466–470 (2012).
50. R Core Team. *R: A language and environment for statistical computing* . (R Foundation for Statistical Computing, 2019).
51. Gompertz, B. On the nature of the function expressive of the law of human mortality, and on a new. *Phil. Trans. R. Soc. Lond.* **115** , 513–583 (1825).

52. Pinder, J. E., Wiener, J. G. & Smith, M. H. The Weibull distribution: a new method of summarizing survivorship data. *Ecology* **59** , 175–179 (1978).
53. Vaupel, J. W., Manton, K. G. & Stallard, E. The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* **16** , 439–454 (1979).
54. Siler, W. A competing-risk model for animal mortality. *Ecology* **60** , 750–757 (1979).
55. Makeham, W. M. On the Law of Mortality. *J. Inst. Actuar.* 1866-1867 **13** , 325–358 (1867).
56. Gelman, A. *et al.* *Bayesian Data Analysis* . (CRC Press, 2014).
57. Kruschke, J. *Doing Bayesian Data Analysis: A Tutorial with R, JAGS, and Stan* . (Academic Press, 2014).
58. Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & van der Linde, A. Bayesian measures of model complexity and fit. *J. R. Stat. Soc. Ser. B Stat. Methodol.* **64** , 583–639 (2002).
59. Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & van der Linde, A. The deviance information criterion: 12 years on. *J. R. Stat. Soc. Ser. B Stat. Methodol.* **76** , 485–493 (2014).
60. McCulloch, R. E. Local modal influence. *J. Am. Stat. Assoc.* **84** , 473–478 (1989).
61. Larson, S. M., Colchero, F., Jones, O. R., Williams, L. & Fernandez-Duque, E. Age and sex-specific mortality of wild and captive populations of a monogamous pair-bonded primate (*Aotus azarae*). *Am. J. Primatol.* **78** , 315–325 (2016).
62. Kullback, S. & Leibler, R. A. On information and sufficiency. *Ann. Math.* **22** , 79–86 (1951).
63. Ruxton, G. D. & Neuhäuser, M. Improving the reporting of P-values generated by randomization methods. *Methods Ecol. Evol.* **4** , 1033–1036 (2013).
64. Morin, P. A. *et al.* Geographic and temporal dynamics of a global radiation and diversification in the killer whale. *Mol. Ecol.* **24** , 3964–3979 (2015).
65. Lemaître, J.-F. *et al.* Sex differences in adult lifespan and aging rates of mortality across wild mammals. *Proc. Natl. Acad. Sci.* (2020) doi:10.1073/pnas.1911999117.
66. Ellis, S. *et al.* Mortality risk and social network position in resident killer whales: Sex differences and the importance of resource abundance. *Proc. R. Soc. B Biol. Sci.* **284** , (2017).
67. Shields, M. W., Hysong-Shimazu, S., Shields, J. C. & Woodruff, J. Increased presence of mammal-eating killer whales in the Salish Sea with implications for predator-prey dynamics. *PeerJ* **6** , e6062 (2018).
68. Hawkes, K., O’Connell, J. F., Jones, N. G. B., Alvarez, H. & Charnov, E. L. Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci.* **95** , 1336–1339 (1998).
69. Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russell, A. F. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* **428** , 178–181 (2004).
70. Towers, J. R. *et al.* Infanticide in a mammal-eating killer whale population. *Sci. Rep.* **8** , 4366 (2018).
71. Snopkowski, K., Moya, C. & Sear, R. A test of the intergenerational conflict model in Indonesia shows no evidence of earlier menopause in female-dispersing groups. *Proc. R. Soc. B Biol. Sci.* **281** , 20140580 (2014).
72. Augusto, J. F., Frasier, T. R. & Whitehead, H. Social structure of long-finned pilot whales (*Globicephala melas*) off Northern Cape Breton Island, Nova Scotia. *Behaviour* **154** , 509–540 (2017).
73. Alves, F. *et al.* Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **23** , 758–776 (2013).

74. Nishida, T. *et al.* Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *Am. J. Primatol.* **59** , 99–121 (2003).
75. Eriksson, J. *et al.* Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low male effective population size in bonobos (*Pan paniscus*). *Mol. Ecol.* **15** , 939–949 (2006).
76. Stokes, E. J., Parnell, R. J. & Olejniczak, C. Female dispersal and reproductive success in wild western lowland gorillas (<i>Gorilla gorilla gorilla</i>). *Behav. Ecol. Sociobiol.***54** , 329–339 (2003).
77. Chapman, S. N., Jackson, J., Htut, W., Lummaa, V. & Lahdenperä, M. Asian elephants exhibit post-reproductive lifespans. *BMC Evol. Biol.* **19** , 193 (2019).