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The potential fitness benefits of grandmothers in Long-Finned whale societies

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SWANSEA UNIVERSITY

Abstract

Contrary to life history theory suggesting individuals should reproduce until death, females of a small number of mammal species are known to live for a significant period after they cease reproduction. It is thought that this trait is facilitated by either female-biased dispersal or bisexual philopatry, leading to increased local relatedness throughout a female's lifetime, allowing greater inclusive fitness to be gained through kin selection. Currently, 3 non-exclusive hypotheses attempt to explain how females might gain this fitness: females halt reproduction to maximise investment in existing offspring (mother effects), females halt reproduction to aid in raising grandoffspring (grandmother effects) and females halt reproduction to minimise intergenerational reproductive competition with sexually mature daughters (reproductive conflict). Despite having similar relatedness and dispersal patterns to species possessing a post-reproductive lifespan, female long-finned pilot whales *(Globicephala melas)* do not halt reproduction significantly prior to death. This study investigates whether a lack of post-reproductive lifespan in long-finned pilot whales results from minimal benefits incurred from mother and grandmother presence or from a lack of costs incurred from mother-daughter co-reproduction. Using microsatellite data to conduct parentage analysis on a dataset collected at a legal drive fishery in the Faroe Islands between 1986-1988, I show that the size and pregnancy status of individuals is not influenced by mother effects or grandmother effects. Results show that individuals under 20 were more likely to have philopatric offspring assigned if their mother was present, indicating mothers may assist inexperienced daughters in raising offspring. No evidence of reproductive conflict between consecutive generations was found, indicating females are able to reproduce into old age whilst simultaneously aiding their daughters in reproduction. This highlights the importance of reproductive conflict in the evolution of a post-reproductive lifespan and demonstrates mother and grandmother effects alone do not predispose the decoupling of reproductive and somatic senescence.

Lay Summary

Menopause (described as the point at which women cease to be reproductive) usually occurs between the ages of 45 and 55 in humans, meaning women have an extended period in later life when they are unable to have offspring. The occurrence of this non-reproductive period (known as a post-reproductive lifespan) is very rare in nature, only being shared by a handful of whale species. In contrast, most species continue reproduction until the end of their lifespan in order to have the maximum number of offspring possible (and therefore pass on the maximum number of genes). Why then, do a handful of mammal species stop reproducing early?

Three main possibilities have been proposed to explain why it might benefit older females to stop reproducing: 1) females halt reproduction in order to focus on raising existing adult offspring, 2) females halt reproduction in order help raise their grandoffspring and 3) females halt reproduction to reduce the amount of competition their daughters experience whilst trying to have offspring of their own. While some evidence has been found for each of these possibilities, it is not clear which are the most important in governing the evolution of post-reproductive lifespan across mammals.

Interestingly, despite sharing the same social structures as whale species which halt reproduction early, long-finned pilot whales do not have a post-reproductive lifespan. This raises some intriguing questions about the relationships between female long-finned pilot whales and their offspring and grandoffspring; do mothers continue to care for their offspring throughout their lifetime? Do grandmothers care for their grandoffspring? Do daughters suffer costs when breeding alongside their mother?

To investigate these questions further, I used data collected between 1986-1988 from drive fisheries in the Faroe Islands to carry out 2 analyses. First, I used DNA samples to identify whether individuals had mothers or grandmothers present in their pod. Secondly, I carried out a series of analyses to determine whether the presence of a mother or grandmother benefitted offspring and whether the simultaneous reproduction of mothers and daughters lead to decreased offspring fitness.

Interestingly, despite finding no evidence that grandmothers actively increase the fitness of grandoffspring, I found that younger females were more likely to have offspring if they had a mother present. This suggests that mothers help their inexperienced daughters to raise their offspring. I also found that mother-daughter co-breeding did not reduce the fitness of individuals, suggesting that mothers somehow avoid competition with their daughters when breeding simultaneously. These results give a fascinating insight into long-finned pilot whale societies; females are able to aid adult offspring in raising offspring of their own and avoid reproductive competition with their daughters without the need to completely give up reproduction, as other whales with the same social structure do. In a wider context, these insights align with current literature which suggests that for a female to benefit from foregoing reproduction in later life, offspring must suffer fitness costs when mother-daughter co-breeding occurs.

University Declarations and Statements

This work has not been previously accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed: [redacted]

Date: 03/03/2022

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed: [redacted]

Date: 03/03/2022

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Dated: 03/03/2022

Statement of Expenditure

I can hereby confirm that no costs were incurred during the creation of this thesis.

Signature: [redacted]

Date: 25/05/2021

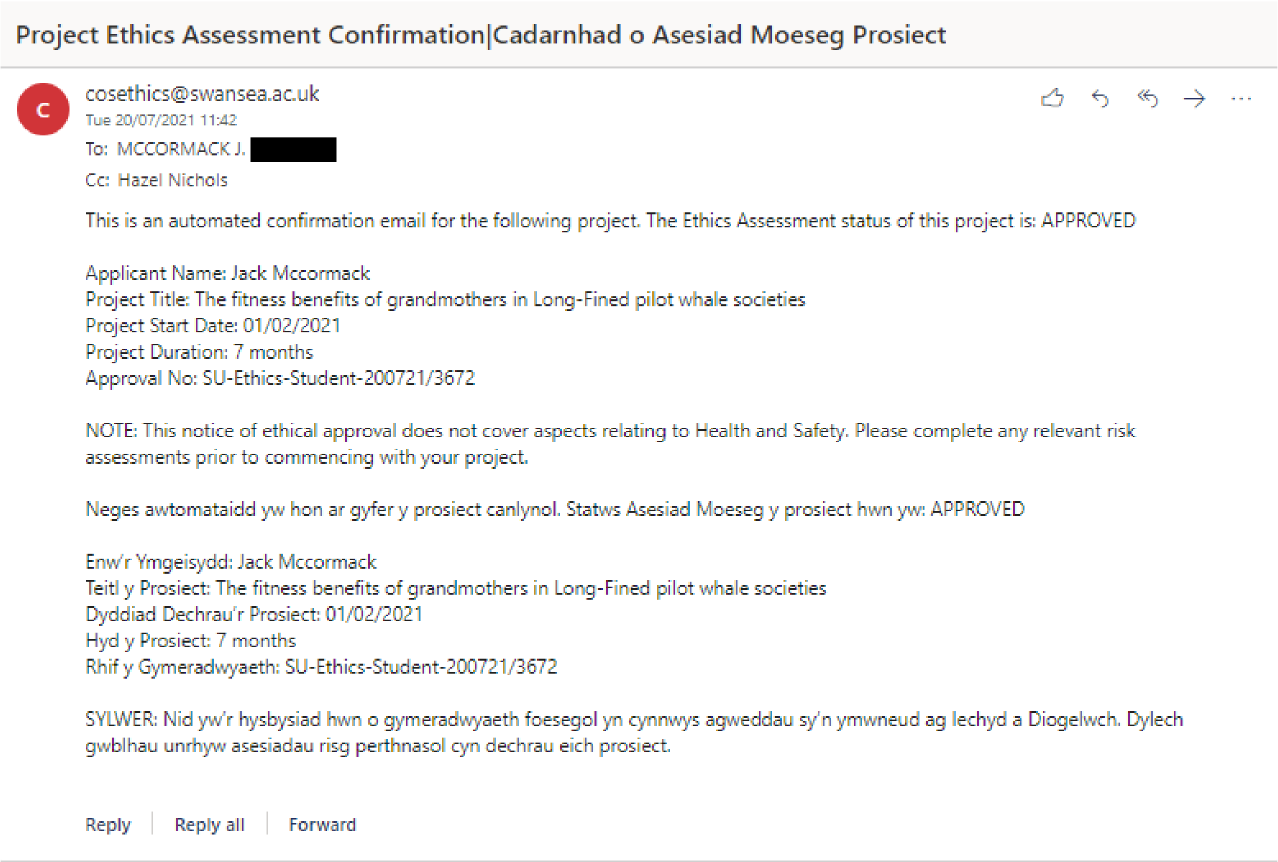
Authorship Statement

Candidate	Name and College	Percentage Contribution
Candidate 1	Jack McCormack, Swansea University	100%

Signed Candidate: [redacted]

Ethics Approval

The following is the confirmation of my Ethics Approval.



Project Ethics Assessment Confirmation|Cadarnhad o Asesiad Moeseg Prosiect

cosethics@swansea.ac.uk
Tue 20/07/2021 11:42
To: MCCORMACK J. [redacted]
Cc: Hazel Nichols

This is an automated confirmation email for the following project. The Ethics Assessment status of this project is: APPROVED

Applicant Name: Jack Mccormack
Project Title: The fitness benefits of grandmothers in Long-Fined pilot whale societies
Project Start Date: 01/02/2021
Project Duration: 7 months
Approval No: SU-Ethics-Student-200721/3672

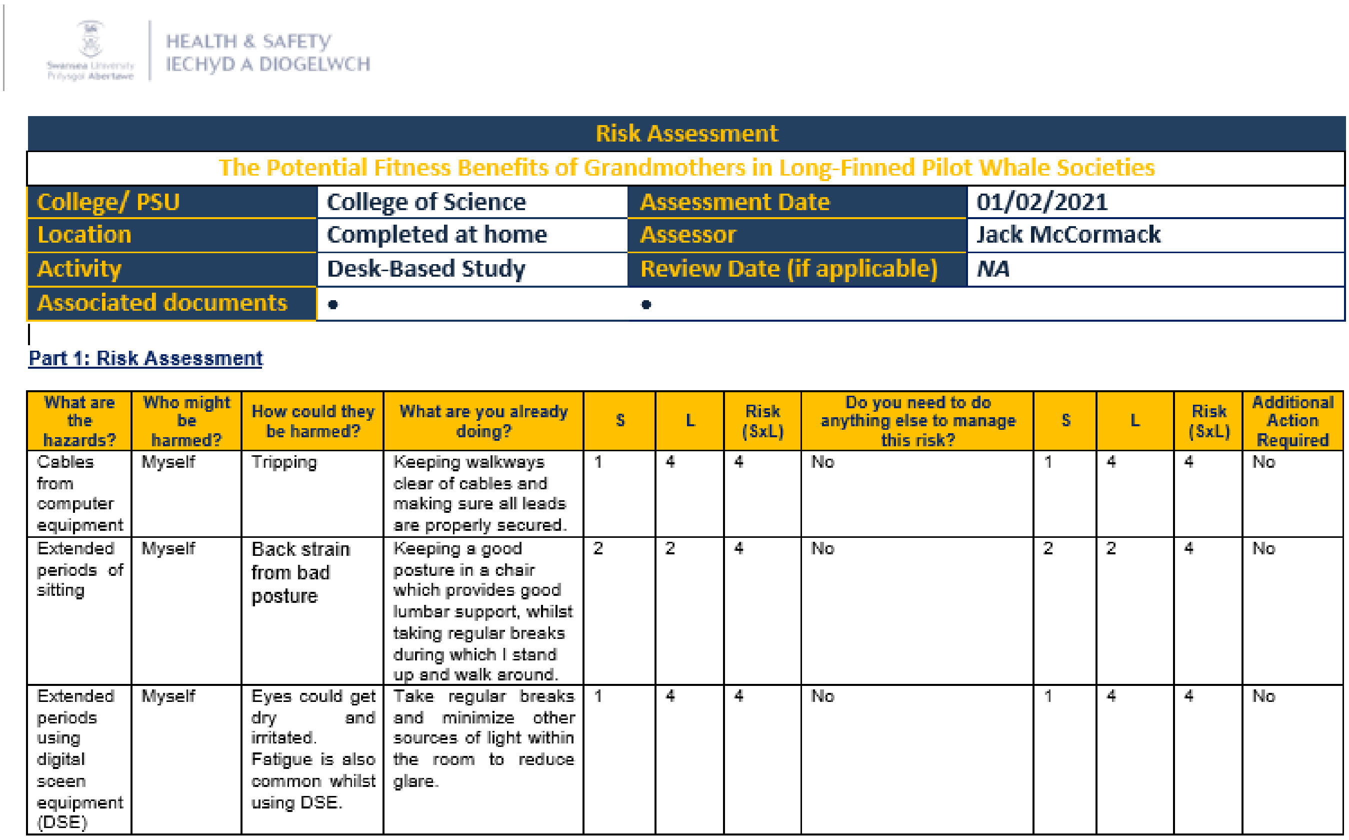
NOTE: This notice of ethical approval does not cover aspects relating to Health and Safety. Please complete any relevant risk assessments prior to commencing with your project.

Neges awtomataidd yw hon ar gyfer y prosiect canlynol. Statws Asesiad Moeseg y prosiect hwn yw: APPROVED

Enw'r Ymgeisydd: Jack Mccormack
Teitl y Prosiect: The fitness benefits of grandmothers in Long-Fined pilot whale societies
Dyddiad Dechrau'r Prosiect: 01/02/2021
Hyd y Prosiect: 7 months
Rhif y Gymeradwyaeth: SU-Ethics-Student-200721/3672

SYLWER: Nid yw'r hysbysiad hwn o gymeradwyaeth foesegol yn cynnwys agweddau sy'n ymwneud ag Iechyd a Diogelwch. Dylech gwblhau unrhyw asesiadau risg perthnasol cyn dechrau eich prosiect.

Risk Assessment



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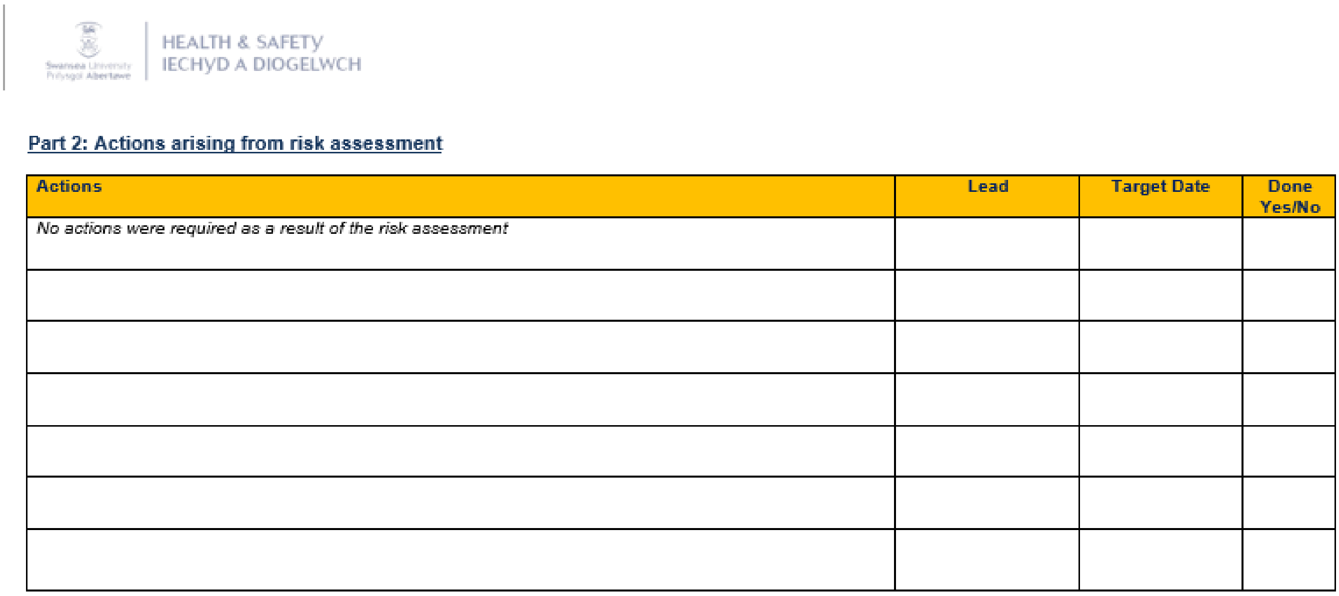
Risk Assessment			
The Potential Fitness Benefits of Grandmothers in Long-Finned Pilot Whale Societies			
College/ PSU	College of Science	**Assessment Date**	01/02/2021
Location	Completed at home	**Assessor**	Jack McCormack
Activity	Desk-Based Study	**Review Date (if applicable)**	*NA*
Associated documents	•	•	

Part 1: Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	S	L	Risk (SxL)	Do you need to do anything else to manage this risk?	S	L	Risk (SxL)	Additional Action Required
Cables from computer equipment	Myself	Tripping	Keeping walkways clear of cables and making sure all leads are properly secured.	1	4	4	No	1	4	4	No
Extended periods of sitting	Myself	Back strain from bad posture	Keeping a good posture in a chair which provides good lumbar support, whilst taking regular breaks during which I stand up and walk around.	2	2	4	No	2	2	4	No
Extended periods using digital sceen equipment (DSE)	Myself	Eyes could get dry and irritated. Fatigue is also common whilst using DSE.	Take regular breaks and minimize other sources of light within the room to reduce glare.	1	4	4	No	1	4	4	No



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Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
No actions were required as a result of the risk assessment			

Contents

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Tables and Figures

1. Introduction

Classical life history theory suggests that early cessation of reproduction should put an individual at a fitness disadvantage, and therefore reproduction should continue until death (Johnstone & Cant, 2019). Despite this, females in a handful of mammal species are known to live for a significant period after they cease reproduction (Ellis *et al.,* 2018). In humans, despite having their last child at approximately 38 years old, women regularly live into their 70s and 80s (Towner *et al.,* 2016). Many assume this decoupling of somatic and reproductive senescence, known as menopause in humans, to be an artefact of modern medicine, lifestyle and sanitation (Austad, 1994). This trait, however, is also reflected in modern day hunter-gatherer societies which are largely sheltered from modernisation. In the Hazda of Tanzania, for example, the 40% of females which live past 50 (the average age of menopause in humans) regularly survive into their 70s, indicating that this trait is a distinct feature of human life history (Blurton-Jones, 2016). Although menopause is a trait common to all women, patterns of reproduction vary across different cultures and time periods. For example, women in Japan tend to reproduce at older ages than African American women (Richard-Davis & Wellons, 2013). It is unclear, however, whether biological factors play a role, or whether these differences are related to lifestyle determinants (such as smoking and nutrition) and cultural differences, which are linked with geographical areas (Dratva *et al*., 2009).

Aside from humans, only 4 other mammal species are known to display a significant post-reproductive lifespan: killer whales *(Orcinus orca),* short-finned pilot whales *(Globicephala macrorhynchus),* beluga whales *(Delphinapterus leucas)* and narwhals *(Monodon monoceros)* (Nielsen *et al.,* 2021). Some evidence for a post-reproductive lifespan has also been found in false killer whales *(Pseudorca crassidens)* and Asian elephants *(Elephas maximus)* (Chapman *et al.,* 2019; Photopoulou *et al.,* 2017). Dalton (2021) highlights 4 main criteria applicable to all species with a post-reproductive lifespan: females have a lifespan of over 40 years, individuals live in social groups, female lifespans are at least 30% longer than males' (although this trait is not consistent with modern human life history, it is thought to be accurate for early hunter-gatherers) and adults have an encephalisation quotient (a measure of relative brain size) of at least 2.5. These commonalities suggest that an extended post-reproductive lifespan has a functional purpose within social groups. Adaptive theory suggests that by halting reproductive activity, an older female might gain greater inclusive fitness via kin selection (Reznick *et al.,* 2005). There are 3 proposed mechanisms via which post-reproductive females gain such inclusive fitness: the mother hypothesis, the grandmother hypothesis and the reproductive conflict hypothesis (Nattrass *et al.,* 2019).

The mother hypothesis describes the inclusive fitness gained by a post-reproductive female when reproduction is halted to maximise investment in living offspring (Pavard *et al.,* 2008). Strong evidence for such 'mother effects' have been found in killer whales, where mortality risk of adult offspring (over 30 years old) increases by 13.9-fold in sons and 5.4-fold in daughters the year proceeding the death of a post-reproductive mother (Foster *et al.,* 2012).

Much like the mother hypothesis, the grandmother hypothesis describes the inclusive fitness gained by halting reproduction to aid in the raising of grandoffspring (Whitehead, 2015). Such 'grandmother effects' are well studied in human populations. Data collected during the 18th and 19th century in Finland has revealed that the presence of a maternal or paternal post-reproductive grandmother significantly increased the lifetime reproductive success of grandoffspring (Lahdenperä *et al.,* 2004). Furthermore, data from pre-industrial French settlers in Quebec has shown that such grandmother effects decrease with increased geographical distance between grandmother and daughter, indicating that the physical presence of a post-reproductive grandmother can increase the fitness of her grandoffspring (Engelhardt *et al.,* 2019). Such grandmother effects have also been observed in killer whale societies, where the survival benefits provided by non-reproductive grandmothers surpass those provided by reproductive grandmothers (Nattrass *et al.,* 2019).

Aid from post-reproductive females is thought to come in the form of either 'depreciable' care, such as food sharing, or in the form of 'non-depreciable' care, such as the sharing of ecological knowledge or communal defence against predation (Péron *et al.,* 2019). In resident killer whale societies, which are heavily reliant on chinook salmon *(Oncorhynchus tshawytscha),* post-reproductive females are known to lead their pods to foraging grounds which vary considerably in space and time. Such leadership has been shown to be particularly strong during periods of low salmon abundance, suggesting that post-reproductive females act as repositories of ecological information (Brent *et al.,* 2015). It is unclear, however, whether the same pattern exists in other cetaceans (Nattrass *et al.,* 2019).

The sole benefits of grandmothering and caring for adult offspring are not sufficient to lead to the evolution of a post-reproductive lifespan. Reproductive female African elephants *(Loxodonta africana),* for example, are known to actively enhance the survival of their grandoffspring by acting as repositories of ecological information (Moss and Lee, 2011). Furthermore, the presence of mothers is shown to increase the reproductive success of adult sons in bonobos *(Pan paniscus)* despite remaining reproductive (Surbeck *et al.,* 2011). This suggests females are only likely to cease reproduction if it is at a cost to kin. The reproductive conflict hypothesis suggests that older females might halt reproductive activity to avoid intergenerational competition with their daughters, that may, on balance, reduce total fitness when losses of inclusive fitness are not compensated by direct fitness gains (Cant and Johnstone, 2008). Evidence for severe intergenerational conflict between non-related individuals has been found in pre-industrial Finnish society, where the simultaneous birth of offspring by consecutive generations of in-laws was seen to reduce offspring survival by up to 66% (Lahdenperä *et al.,* 2012). This study, however, found no evidence for reproductive conflict between mother-daughter pairings. Conversely, evidence for such conflict has been found in resident killer whale societies, where the mortality risk associated with co-breeding is 1.7 times higher in calves born to older generation females than those born to younger generation females (Croft *et al.,* 2017).

The combination of costs incurred through reproductive conflict and benefits gained by offspring and grandoffspring from the presence of older, non-reproductive females is likely to predispose the evolution of a post-reproductive lifespan (Lahdenperä *et al.,* 2012). This is reflected in a model developed by Johnstone and Cant (2010) to predict whether kin selection should favour a post-reproductive lifespan. It considers the reproductive activity of a female aged *a*, which results in the immediate gain of *b* fecundity for kin, and the immediate loss of *c* offspring for herself. It is stated that kin selection will only favour the evolution of a post-reproductive lifespan if the ratio of *c/b* is sufficiently small, i.e. if the inclusive fitness gained from eliminating reproductive conflict for descendant kin is greater than fitness gained from continued reproduction. As benefits imparted from foregoing reproduction are indiscriminate, however, and are therefore directed towards all local group members rather than just kin, selection is highly dependent on patterns of relatedness, and consequently patterns of mating and dispersal. In species which display bisexual philopatry with non-local mating, where females become increasingly related to other group members with age, the ratio of *c/b* decreases throughout a female's lifetime and she is more likely to undergo reproductive cessation (Croft *et al.,* 2021).

Interestingly, despite having similar social structures and relatedness patterns to their sister species, the short-finned pilot whale *(Globicephala macrorhynchus)*, which shows a substantial post-reproductive lifespan, female long-finned pilot whales *(Globicephala melas)* do not halt reproduction prior to complete somatic senescence (Nielsen *et al.,* 2021). Both species display bisexual philopatry and extra-pod mating, with groups being comprised of numerous related matrilines (Boran and Heimlich, 2019; Foote, 2008; Johnstone & Cant, 2010). This dispersal pattern is present in all cetaceans which are known to have a post-reproductive lifespan (Rendell *et al.,* 2019). In such a scenario, when females have more philopatric offspring, they become increasingly related to their pod. If reproduction is also at a cost to kin, kin selection may favour older females halting reproduction to aid younger relatives (Johnstone and Cant, 2010; Lahdenperä *et al.,* 2012). Long-finned pilot whales have been shown to become increasingly related to their pod members throughout their lifetime, meaning if reproductive conflict incurs fitness costs, then older females should benefit from halting reproduction early (Nichols *et al.,* 2020).

Here I will use physiological and genetic data from 1375 long-finned pilot whales of 25 pods collected during legal subsistence hunts between 1986-1988 to investigate whether a lack of post-reproductive lifespan in long-finned pilot whales is due to a lack of mother and grandmother effects or a result of minimal costs incurred during mother-daughter co-breeding. I first determined the maximum number of generations in each pod to ensure that mothers and grandmothers were present with offspring and grandoffspring, facilitating the potential for intergenerational fitness benefits and reproductive conflict. Secondly, to test whether mother and grandmother effects significantly contributed to offspring fitness, I investigated whether the presence of an individual's mother or grandmother in the pod had a significant effect on three fitness traits: an individual's size, the number of offspring females had and pregnancy status. Finally, to test whether reproductive conflict may reduce offspring fitness, I tested whether offspring born into mother-daughter co-reproduction were significantly different in size to those not born into intergenerational conflict. Given that long-finned pilot whales do not display a post-reproductive lifespan, I predict that older females do not impart fitness benefits to younger kin and/or that these fitness benefits may occur but a lack of costs associated with intergenerational co-breeding allows females to continue reproducing into old age without reducing the fitness of descendant kin.

2. Methods

2.1. Data collection

Data for this study originates from drive fisheries in the Faroe Islands, where researchers (D. Bloch, C. Lockyer, G. Desportes, R.Mouritsen and K Hoydal) commissioned by the International Whaling Commission (IWC) and the United Nations Environmental Programme (UNEP) conducted a survey of the local long-finned pilot whale population in a study initiated by the Faroese Government (Bloch *et al.,* 1993). The hunts, which were opportunistic in nature, involved the sightings of entire pods from land or boat which were driven into whaling bays for slaughter (Zachariassen, 1993). Pods are known to be highly cohesive, meaning that almost all pods were sampled in their entirety (Amos *et al.,* 1993).

The initial dataset was comprised of 1804 individuals, of which 1057 (58.59%) were female, 703 (38.97%) were male and 44 (2.44%) were unsexed. This biased sex ratio is likely a result of females having longer lifespans than males (Bloch *et al.,* 1993). These individuals were sampled from 26 pods, of which 3 pods (323, 819 and 829) were partially sampled due to the separation of pods during hunting (Bloch *et al.,* 1993). The size of these pods ranged from 17 to 194 individuals (median = 63). Each analysis used a different subset of these individuals, which is further explained in section 2.5.

2.2. Body length, sex, and age measurements

Length measurements, along with sex, were recorded for each individual along with a unique identity number. Body length was measured following the standard of Norris (1961), taking measurement to the nearest cm from the foremost part of the skull to the fluke notch, running parallel to the spine. To assess the reliability of length measurements, repeats were taken for 50 whales 3 times. Repeated measurements all varied within ≤5% of total length (Bloch *et al.,* 1993). Sex was determined via macroscopic observation. The reproductive status of females was recorded during on site dissection, and therefore all pregnancies were noted (Bloch *et al.,* 1993).

Where possible, age was calculated using growth rings in cementum and dentine in teeth. The tip of the lower mandible was severed and then allowed to rot in a heat pressured cabinet for 2 weeks before teeth were extracted. This prevented damage to cementum and dentine which might occur if this had been done using boiling. The 8 teeth which were in the best condition were defatted in a solution of 1/3 chloroform and 2/3 70% alcohol, before 2 of these teeth were mounted onto a wooden block with epoxy resin and bisected longitudinally using a diamond rotating saw, allowing for growth layers to be counted (Bloch *et al.*, 1993; Lockyer *et al.,* 1987). Due to time constraints, age data for 250 individuals (13.86%) was not obtained using this method. For the proportion of these individuals which had length data available, Nichols *et al.,* (2014) used quadratic regression of age against length to estimate age. Due to the rapid growth exhibited in the early lives of long-finned pilot whales, which is proceeded by a plateau in later life, this method was only applicable to individuals prior to full maturation. Therefore, instead of estimating an exact age for mature individuals, females larger than 400cm recorded as '10 years or older', and males larger than 500cm were noted as '15 years or older'. These 88 individuals were excluded from any subsequent analyses which required an exact age value, as were the ten individuals that had no age or length data noted. Individuals which had their age estimated based on their length (N = 170, 9.86% of individuals with age data) were removed from analyses for which length was the response variable. Ages range from 0 (representing the 154 unborn foetuses which were dissected from mothers upon capture) to 55 years.

2.3. Genetic data

Skin samples were taken from the posterior of the dorsal fin and tissues were preserved either at -20°C or using a 20% DMSO solution saturated with NaCl (Bloch *et al.,* 1993). A modified Chelex extraction protocol was used for DNA extraction (Walsh *et al.,* 1991). Tissues, which had been incubated overnight in a 320µL extraction buffer, were centrifuged at 10000g for 2 minutes, before 200µL of supernatant was transferred to 200µL of buffered Chelex solution (Fullard *et al.,* 2000). Polymerase chain reaction (PCR) amplification was then carried out on the following microsatellite primer pairs: 199/200, 409/470, 415/416, 417/418, 464/465, 468/469 (Amos *et al.,* 1993), EV37, EV94, EV1 (Valsecchi and Amos, 1996), D14, D22 (Shinohara *et al.,* 1997), FCB 6/17, FCB3, FCB1 (Buchanan *et al.,* 1996), SW10 (Richard *et al.,* 1996) and GM8 (Fullard *et al.,* 2000). Some individuals were genotyped at the later 7 loci where others were not, however it had previously been shown that this had no significant effect on patterns of maternity (Nichols *et al.,* 2014), so this was not considered in analyses.

2.4. Maternity assignment

The maternal assignment analysis was carried out following a similar analysis by Nichols *et al.,* (2020) using Cervus (Marshall *et al.,* 1998), a computer programme which uses microsatellite data and likelihood to assign parentage. Only a maternity analysis was carried out as long-finned pilot whales show extra-pod mating, with offspring remaining with their mother's pods, meaning that it is very rare for fathers to be present (Johnstone and Cant, 2010). Females were considered to be potential mothers if they were at least six years older than the offspring in question, as females are known to reach sexual maturity at a minimum of six years old (Anabella *et al.,* 2017). Furthermore, females were only listed as potential mothers if they were in the same pod as offspring, as long-finned pilot whales are known to display bisexual philopatry (Möller, 2011), and a previous study using the same dataset found that there was no evidence of dispersal between pods (Allen, 2020). 29 individuals had no potential mothers listed (as no individuals were at least six years older than them) and were therefore not included in the maternity analysis. Foetuses could be assigned to mothers they were dissected from without the need for genetic assignment. Individuals with less than 7 loci typed were also removed from the analysis as to ensure a more reliable maternity assignment. It is important to maximise the number of loci typed where related individuals are present with the true mother, as these related individuals often carry a set of alleles identical to that of the offspring in question, increasing the likelihood of inaccurate assignments (Marshall *et al.,* 1998). Although the pods sampled were mostly complete, it is likely that some mothers had escaped, died or emigrated (Nichols *et al.,* 2020). Therefore for this analysis, it was estimated that 50% of mothers had been sampled. An allele frequency analysis calculated that the proportion of loci genotyped was 0.73, whilst the average per-allele error rate was 0.01. These values were incorporated into simulations to calculate critical delta (the threshold probability used to assign parentage). No assumptions were made regarding the relatedness of candidate mothers to true mothers, as a previous study on this dataset had shown average relatedness between females in the same pod to be very low (Nichols *et al.,* 2020). Identity analysis indicated that one individual had been sampled twice, so one replicate of this individual was removed from the dataset.

Of the 1459 offspring listed, Cervus assigned mothers to 375 (27.3%) at a confidence level of ≥95% and a further 459 (33.4%) at a confidence level of ≥90%, leaving 916 (66.6%) individuals without an assigned mother (either due to the absence of a mother or insufficient genetic resolution). To remain conservative, subsequent statistical analyses were restricted to assignments made at ≥95% confidence.

2.5. Investigating mother effects, grandmother effects and reproductive conflict

Statistical analyses were carried out using RStudio version 1.1.463 (RStudio Team, 2015). The package 'lme4' (Bates *et al.,* 2015) was used to conduct a series of GLMMs, allowing for the addition of fixed effects which control for a variety of variables. The code for these models can be seen in **appendix 1.** Pod was added as a random factor for each analysis to account for any unknown variance between pods. Model assumptions were checked using the R package DHARMa, a package for interpreting residual diagnostics of mixed models (Harting, 2021). A residual Q-Q plot was created to check whether residuals showed a normal distribution, and a Residual vs Predicted plot was created to check for correlation between observations. Although model assumptions were met, a small number of outliers were detected. Models were rerun without these outliers, however the outcomes were quantitatively very similar, indicating that the influence of outliers on the original model was minimal. Models were not simplified from a 'full' model containing all possible variables, rather, they were constructed based on information which was thought to be biologically relevant. I ran two models for analyses investigating the mother and grandmother hypothesis – one investigating mother and grandmother effects in under 20s, and one investigating mother effects in under 35s. This was due to the fact that only a small number of individuals over the age of 35 had a mother present, and no individuals over the age of 20 had a grandmother present. P values were calculated using likelihood ratio tests (by comparing the fit of the model with and without each fixed term), and if interactions were found to be non-significant, they were removed from the model. Likelihood ratio tests were used as the resultant p values are more accurate than using model coefficients from R. Although p values from likelihood ratio tests are reported in **Table 1**, it should be noted that in this case qualitative outcomes did not change when using coefficients provided by R.

2.5.1. How many generations are found within pods?

Using maternal assignments obtained through Cervus, the maximum number of generations in each pod was counted. This was done to confirm that individuals were present in the same pods as their grandmothers, ensuring that there was the potential for grandoffspring to benefit from grandmother effects and for offspring to undergo intergenerational reproductive conflict.

2.5.2. Are whales larger for their age if their mother or grandmother is present?

To investigate the effects of the presence of a mother or grandmother on the size of offspring, and therefore test the mother and grandmother hypotheses, a GLMM with Gaussian error distribution was fitted with length as the response variable and mother presence, grandmother presence, age, age^2 and sex fitted as fixed effects. Sex was added as an interaction with age, age^2 and mother and grandmother presence to account for sex-specific growth rates and the likely disproportionate investment in male offspring required to facilitate such differences (Nichols *et al.,* 2014). For these analyses, individuals were removed if they were unsexed, as sex had to be controlled for due to sex specific growth rates, and individuals which had their age calculated from their length were removed as length was the response variable. Foetuses were also removed as all analyses were investigating the effect of mother presence, grandmother presence and reproductive conflict after an individual's birth. This left a final dataset of 1222 individuals for the analysis investigating effects in whales under the age of 35 (of which 726 (59.4%) were female and 496 (40.6%) were male) and 909 individuals in analyses investigating effects in whales under the age of 20 (of which 510 (56.1%) were female and 399 (43.9%) were male).

2.5.3. Does mother or grandmother presence affect the reproductive fitness of individuals?

Both the number of offspring a female had and the likelihood of pregnancy in females were studied. For all analyses into reproductive fitness, females below the age of 6 were removed as this is the minimum age of sexual maturity. To test whether females had more existing offspring for their age if their mother or grandmother was present, a GLMM with Poisson error distribution was fitted with number of offspring as the response variable and age, age^2, mother presence and grandmother presence as fixed effects.

Most individuals under the age of 20 only had one offspring present, making it difficult to use the number of offspring as a proxy for reproductive fitness. Therefore, I ran another model investigating the effect of mother and grandmother presence on the probability that individuals would have offspring present. I ran a binomial GLMM with offspring presence (coded as 1/0) as the response variable, and age, age^2, mother presence and grandmother presence as fixed effects, to see if the presence of a mother or grandmother increased the likelihood of an individual having offspring assigned.

To investigate whether females were more likely to be pregnant if their mother or grandmother was present, a GLMM with binomial distribution was fitted with pregnancy as the response variable and age, age^2, mother presence and grandmother presence as fixed effects. For both analyses looking at the effects of mother and grandmother presence on reproductive fitness, age was scaled (by subtracting the mean and dividing by the standard deviation) to avoid singularity issues during model fitting. These issues were a result of substantial differences in the scales of explanatory variables, which make it difficult to accurately assess the true impact of a term. Scaling age allowed the model to converge, therefore making model outputs more reliable.

For analyses investigating reproductive conflict, individuals with age estimated via quadratic regression were left in, as size was not the response variable. Individuals were only included, however, if they had a precise age estimated, which excluded females estimated to be over the age of 10 and males estimated to be over the age of 15. Males were removed as offspring were only present with mothers, and males could not be included in pregnancy analyses. This left a final dataset of 294 individuals in analyses studying effects in females under 20 and 510 individuals in analyses studying the effects in females under 35.

2.5.4. Does reproductive conflict affect offspring fitness?

To determine whether offspring were significantly affected by reproductive conflict, a GLMM with Gaussian error distribution was fitted with offspring length as the response variable and age, age^2, sex and whether the mother was in reproductive conflict (coded as 1/0) as the fixed terms. In this instance, reproductive conflict was defined as when an older generation female gave birth to offspring within 2 years of a younger generation female (or vice versa). Two years was selected to cover the period when females need to acquire energy for mate competition, gestation and birth - the period of most intense conflict. The same approach was used by Croft *et al.,* (2017) when investigating the effects of reproductive conflict in killer whales. Sex was added as an interaction with age, age^2 and reproductive conflict to account for differences in sex specific growth rates and the possible impact of disproportionate investment in sons on reproductive conflict. Analysis was run on individuals under 9 years old as the oldest individual known to be born into reproductive conflict was 8 years old.

A second analysis was carried out to investigate whether reproductive conflict disproportionately affected younger generation offspring or older generation offspring. A GLMM with Gaussian error distribution was fitted with size as the response variable and age and younger/older generation offspring (coded as 1/0) fitted as fixed variables. This analysis was also carried out on individuals under 9 years old.

Similarly to the analyses investigating mother and grandmother effects on size, individuals were removed if they were unsexed as sex specific growth rates had to be accounted for, and individuals with age calculated through quadratic regression were removed due to the fact length was the response variable. After removal of foetuses, this meant the final dataset for the analysis studying the effects of reproductive conflict in individuals under 9 had 565 individuals (of which 290 (51.3%) were female and 275 (48.7%) were male). For the analysis investigating whether reproductive conflict disproportionately affected younger generation offspring or older generation offspring, only individuals born into reproductive conflict were included, leaving a final dataset of 29 individuals.

2.6 Ethical note

Data were collected from dead whales during non-commercial subsistence hunts carried out between 1986-1988 in the Faroe Islands. The Faroese government approved this data collection, and no financial transaction was made for access to whale corpses or genetic samples, therefore this study did not contribute to the trade or consumption of whale meat. Full details of these hunts can be found in Bloch *et al.,* (1993). The IUCN classify the conservation status of the long-finned pilot whale as ‘Least Concern’ (Minton *et al.,* 2018). This study was approved by Swansea University College of Science Ethics Committee (approval number: SU-Ethics-Student-200721/3672.)

3. Results

3.1. How many generations were found within pods?

The maximum number of generations within pods ranged between 2-4 **(Figure 1)**. Of the initial 1459 offspring analysed using Cervus, 375 individuals were assigned mothers and 74 were assigned grandmothers. **Figure 2** shows that younger individuals were more likely to be assigned mothers and grandmothers, which is consistent with increased rates of mortality with age. A large proportion of younger individuals, however, are unassigned due to insufficient genetic resolution, meaning **figure 1** likely underestimates the number of generations within pods. **Figure 1** does, however, show that grandmothers are present in pods with grandoffspring in at least 13 of 25 pods (52%). **Figure 3** shows how pods are composed of several related matrilines, giving both mothers and grandmothers the opportunity to aid descendant kin.

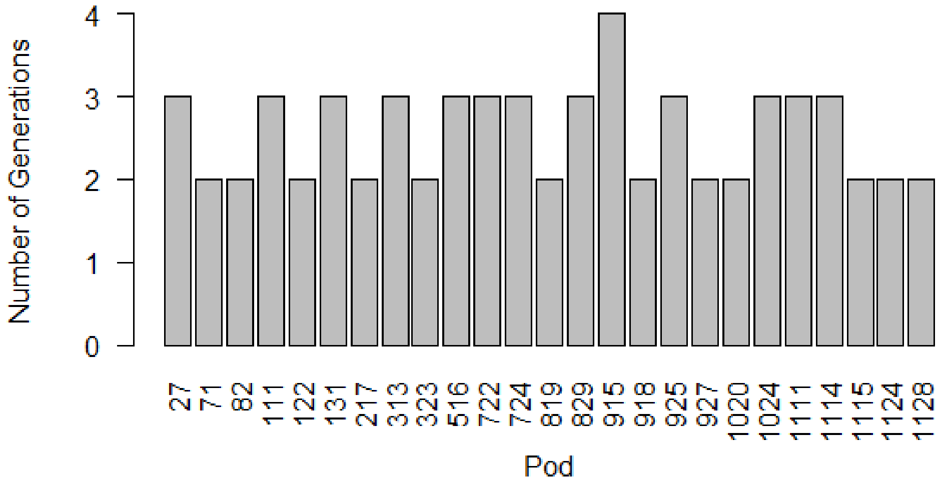

Figure 1 – The maximum number of generations within pods.

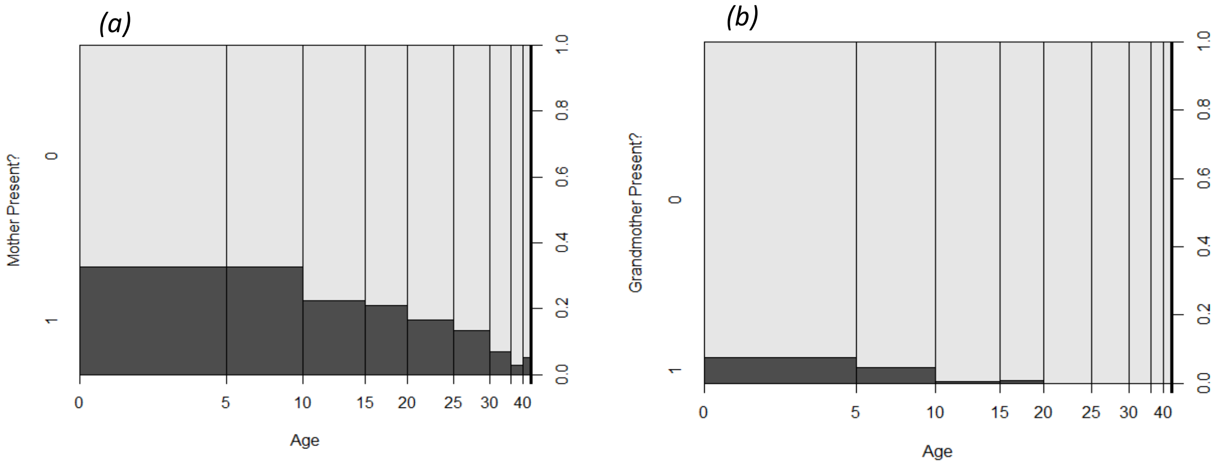

Figure 2 – The proportion of individuals with mothers (a) and grandmothers (b) present with age. Analyses for grandmother effects were studied in individuals under 20 as no individuals above this age had a mother present, and mother effects were studied in individuals under 35, as only 3 individuals above this age had mothers present. Bar width represents the number of individuals in each 5-year age bracket.

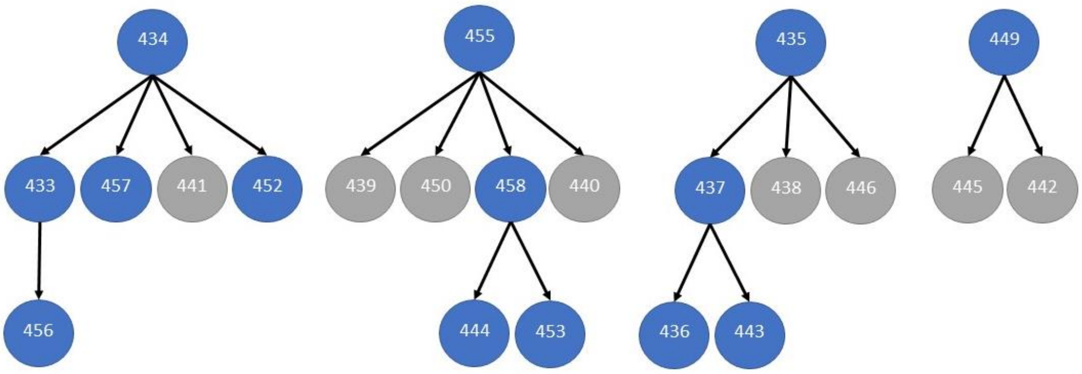

Figure 3 – The kin relationships of pod 131. The pod is seen to be made of multiple matrilines, with four older females with their offspring and grandoffspring. Blue nodes represent females whilst grey nodes represent males. This pedigree represents 22 out of the 25 individuals in this pod; 3 individuals were without

assigned offspring or an assigned mother. In total, 7 individuals were not assigned a mother.

3.2. Does mother and grandmother presence affect fitness?

Neither individuals under 20 (GLMM: $X^2 = 0.56$, df = 1, $P = 0.454$, **Figure 4b**, **Table 1**) or individuals under 35 (GLMM: $X^2 = 2.58$, df = 1, $P = 0.108$, **Table 1**) were larger for their age if their mother was present. Furthermore, individuals under 20 were not significantly larger if their grandmother was present (GLMM: $X^2 = 0.05$, df = 1, $P = 0.826$, **Figure 4a**, **Table 1**). Females under 20 did not have more offspring if their grandmother was present (GLMM: $X^2 = 0.31$, df = 1, $P = 0.579$, **Table 1**) and were not more likely to have offspring present (GLMM: $X^2 = 0.27$, df = 1, $P = 0.602$, **Figure 4c Table 1**). Individuals under 20 did, however, have more offspring present (GLMM: $X^2 = 4.69$, df = 1, $P = 0.030$ **Table 1**) and more likely to have any offspring assigned (GLMM: $X^2 = 5.65$, df = 1, $P = 0.018$, **Figure 4d**, **Table 1**) if their mother was present. Mother presence did not, however, affect the number of offspring individuals under 35 had (GLMM: $X^2 = 0.05$, df = 1, $P = 0.819$, **Table 1**). Females were not more likely to be pregnant if their mother (GLMM: $X^2 = 0.01$, df = 1, $P = 0.942$, **Figure 4f**, **Table 1**) or grandmother (GLMM: $X^2 =2.24$, df = 1, $P = 0.135$, **Figure 4e**, **Table 1**) were present.

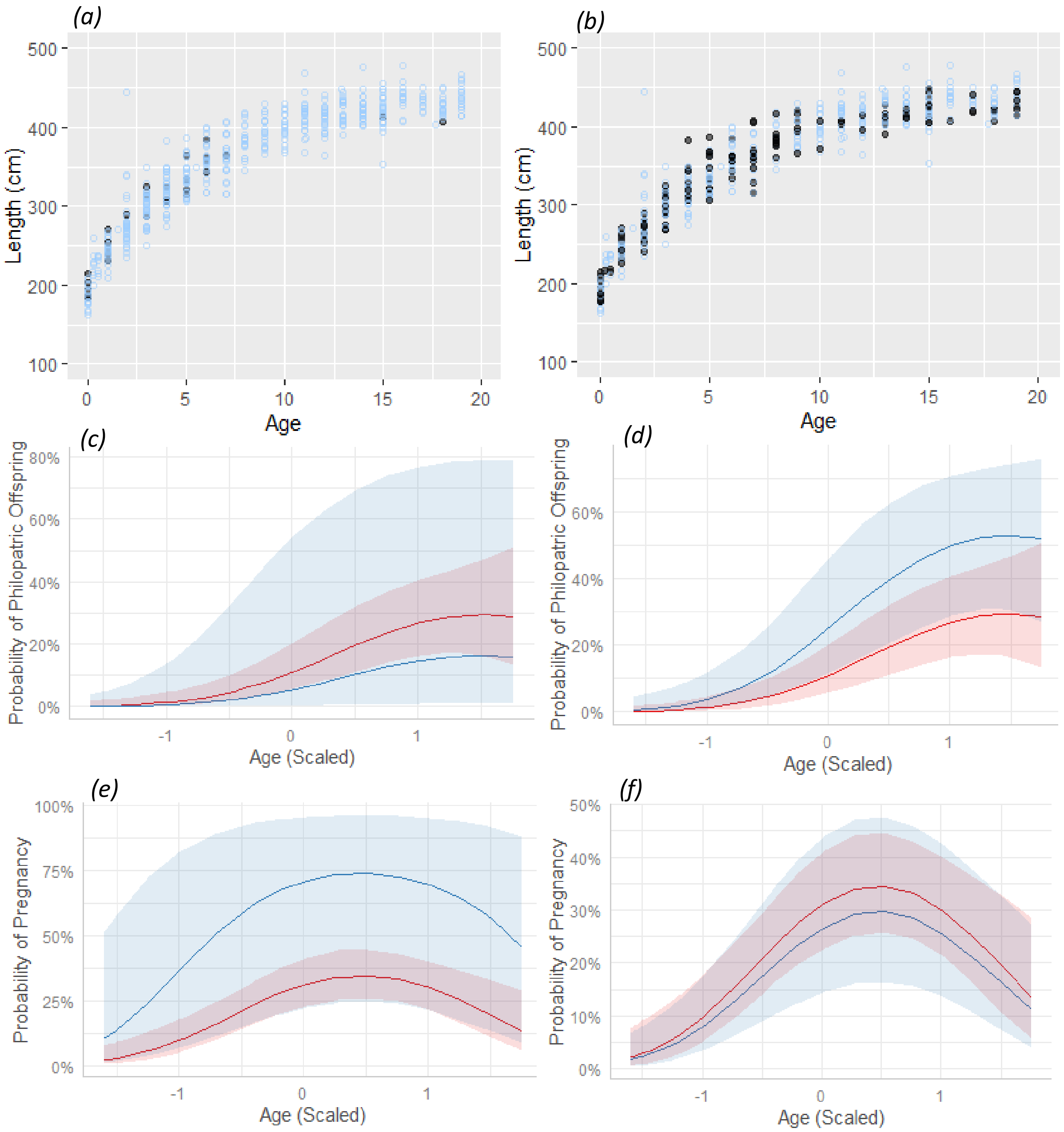

Figure 4 – Effects of grandmother and mother presence on offspring fitness. All plots are of models investigating effects in individuals under 20, as these models incorporated both grandmother and mother effects. Panels *a* and *b* show the effects of grandmother and mother presence on the length of female offspring respectively. Light blue points represent the individuals without grandmothers or mothers and black points represent those individuals with grandmothers or mothers genetically assigned. Individuals with grandmothers and mothers are not significantly different in size to those without. Panels *c* and *d* represent the effects of grandmother and mother presence on the probability a female having offspring present, with blue lines representing individuals with mothers and grandmothers present and red lines representing those without. Although grandmother presence

has no effect on the probability an individual will have offspring, mother presence is shown to increase this probability. Similarly to panels *c* and *d*, panels *e* and *f* represent the effects of grandmother and mother presence on the probability a female will be pregnant, with blue lines representing individuals with grandmothers and mothers present and red lines representing those without. There was no significant difference in the probability of pregnancy between individuals with grandmothers and mothers present, and those without. For models *c – f,* age was scaled (by subtracting the mean and dividing by the standard deviation) to avoid singularity during modelling, which is reflected on the axes. In panels *c-f*, shaded areas represent the upper and lower confidence bounds of the regression (which were set at 95%).

3.3. Does reproductive conflict affect offspring fitness?

Reproductive conflict did not influence offspring size (GLMM: $X^2 = 0.17$, df = 1, $P =$ 0.678, **Figure 5**, **Table 1**). To check if the effects of reproductive conflict were only detectable in younger individuals (where the period of conflict had been more recent), I ran this model again for individuals under 5 and results were concordant with the original model (GLMM: $X^2 = 0.37$, df = 1, $P = 0.545$, **Table 1**). A GLMM was run to investigate whether reproductive conflict affected offspring from older or younger generations disproportionately (**Table 1**). I found no evidence for such an effect, however even the most simplified version of this model would not converge (likely due to the small sample size in this model) so results should be interpreted cautiously.

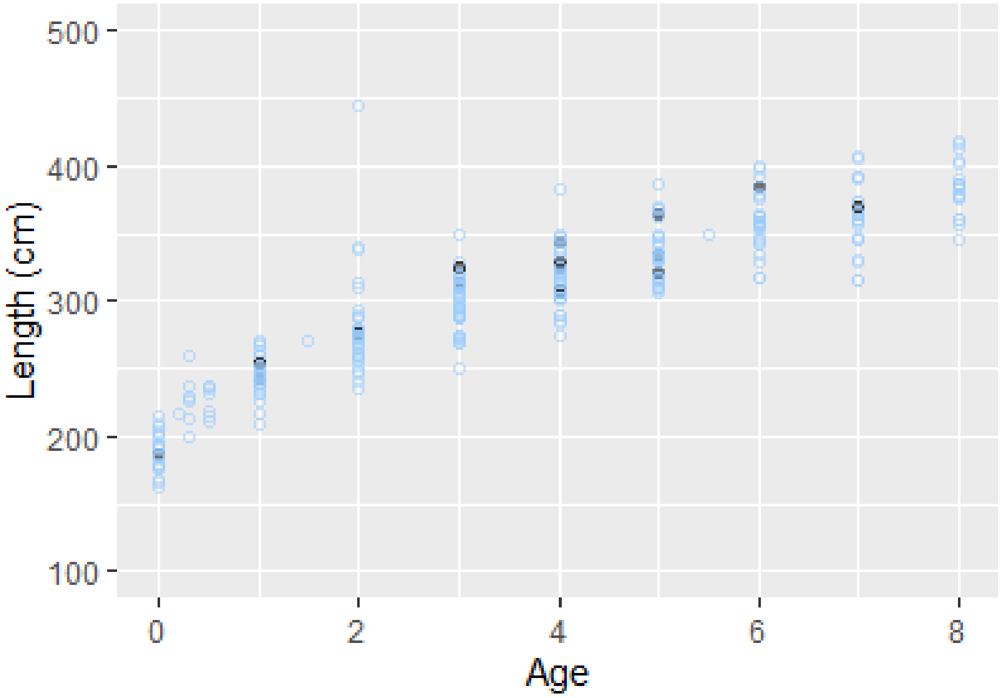

Figure 5 – The effects of reproductive conflict on the length of female offspring. Individuals born into reproductive conflict are shown in dark blue, and those not born into reproductive conflict are shown in light blue. It can be seen that individuals born into reproductive conflict are not significantly different in size to those not born into reproductive conflict.

Table 1 – A summary GLMMs carried out. Effect sizes, standard error and t/z values were taken from GLMM results, and P values were calculated using Likelihood Ratio Tests. P values are not reported for terms which are significant within interactions.

Model	Term	Effect Size	Std. Error	t/z value	P-value
Are individuals under 20 larger for their age if mother/grandmother is present?	**Intercept**	219.759	3.200	68.68	NA
(Response variable: length, number of individuals: 909, number of pods: 25.)	**Age**	27.358	0.717	38.18	NA
	Age^2	-0.881	0.038	-23.03	NA
	Sex	4.442	3.965	1.12	NA
	Mother	-1.520	2.012	-0.76	0.454
	Grandmother	-0.901	4.048	-0.22	0.826
	Age*Sex	2.559	1.112	2.30	0.021
	Age^2*Sex	0.165	0.061	2.73	0.006
Are individuals under 35 larger for their age if mother present?	**Intercept**	242.868	2.925	83.04	NA
(Response variable: length, number of individuals: 1222, number of pods: 25.)	**Age**	18.452	0.357	51.64	NA
	Age^2	-0.398	0.011	-34.81	NA
	Sex	-7.051	3.290	-2.14	NA
	Mother	-2.922	1.811	-1.61	0.108
	Age*Sex	7.318	0.573	12.77	<2x10^{-16}
	Age^2*Sex	-0.089	0.018	-4.89	1.110x10^{-6}
Do females under 20 have more offspring for their age if mother/grandmother present?	**Intercept**	-1.936	0.260	-7.45	NA
(Response variable: number of offspring, number of individuals: 294, number of pods: 25.)	**Age**	1.260	0.255	4.93	5.244x10^{-12}
	Age^2	-0.525	0.181	-2.90	0.001

	Mother	0.603	0.275	2.19	0.030
	Grandmother	-0.540	1.049	-0.52	0.579
Do females under 35 have more offspring for their age if mother is present?	**Intercept**	-1.145	0.177	-6.46	NA
(Response variable: number of offspring, number of individuals: 510, number of pods: 25.)	**Age**	0.960	0.111	8.66	<2x10^{-16}
	Age^2	-0.266	0.077	-3.43	3.96x10^{-4}
	Mother	0.040	0.170	0.23	0.819
Are females under 20 more likely to have offspring present if grandmother/mother present?	**Intercept**	-2.093	0.363	-5.76	NA
(Response variable: whether individual has offspring present, number of individuals: 294, number of pods: 25.)	**Age**	1.633	0.320	5.11	9.924x10^{-13}
	Age^2	-0.549	0.244	-2.25	0.016
	Mother	0.998	0.416	2.40	0.018
	Grandmother	-0.756	1.470	-0.51	0.602
Are females under 20 more likely to be pregnant if mother/grandmother present?	**Intercept**	-0.801	0.220	-3.64	NA
(Response variable: pregnancy status, number of individuals: 294, number of pods: 25.)	**Age**	0.697	0.206	3.39	1.990x10^{-4}
	Age^2	-0.738	0.200	-3.69	4.729x10^{-5}
	Mother	-0.221	0.385	-0.57	0.562
	Grandmother	1.676	1.054	1.59	0.135
Are females under 35 more likely to be pregnant if mother is present?	**Intercept**	-1.060	0.210	-5.06	NA
(Response variable: pregnancy status, number of individuals: 510, number of pods: 25.)	**Age**	0.097	0.134	0.72	0.471
	Age^2	-0.493	0.142	-3.47	2.25x10^{-4}
	Mother	-0.021	0.284	-0.07	0.942

Does reproductive conflict affect the size of individuals under 5? (Response variable: length, number of individuals: 353, number of pods: 25.)	**Intercept**	200.723	3.883	51.69	NA
	Age	47.468	3.370	14.09	<2x10^{-16}
	Age^2	-4.429	0.815	-5.44	NA
	Sex	2.030	3.875	0.52	NA
	In conflict	3.785	6.406	0.59	0.545
	Age^2*Sex	1.162	0.419	2.77	0.00540
Does reproductive conflict affect the size of individuals under 9? (Response variable: length, number of individuals: 565, number of pods: 25.)	**Intercept**	200.677	3.341	60.07	NA
	Age	38.120	1.524	25.01	<2x10^{-16}
	Age^2	-1.879	0.188	-10.02	<2x10^{-16}
	Sex	15.935	2.086	7.64	7.515x10^{-14}
	In conflict	2.010	4.963	0.41	0.678
Does reproductive conflict disproportionately affect the size of older/younger generation offspring? (Response variable: length, number of individuals: 29, number of pods: 7.) *(Model did not converge)*	**Intercept**	220.990	8.209	26.92	NA
	Age	24.178	1.742	13.88	1.57x10^{-14}
	Sex	-0.983	8.850	-0.11	0.905
	Younger/older generation	14.613	8.593	1.70	0.075

4. Discussion

This study aimed to investigate whether grandmother presence, mother presence and reproductive conflict effected several fitness traits in long-finned pilot whales. I show that grandmother presence did not have a significant effect on length, pregnancy status, the number of offspring an individual had, or the probability that an individual would have offspring present. Similarly, the presence of a mother had no effect on length or pregnancy status. Mother presence did, however, increase the likelihood of an individual under 20 having offspring present and the number of offspring they would have. This pattern was not reflected in older individuals, where no effect was found for mother presence. Finally, being born into reproductive conflict did not have a significant effect on the length of offspring. Despite some evidence for benefits typically associated with the evolution of a post-reproductive lifespan (mother effects), my results support the prediction that inter-generational competition resulting from reproductive conflict does not impose substantial costs, likely explaining why females do not have a post-reproductive lifespan. This is concurrent with Johnstone and Cant's (2010) model which suggests that reproductive senescence will only be selected for if inclusive fitness gained by reducing competition with kin outweighs the fitness cost of foregoing reproduction.

One possible explanation for a lack of costs incurred from reproductive conflict is that competition for resources between long-finned pilot whales is not as intense as other species which display a substantial post-reproductive lifespan. Long-finned pilot whales are known to have a sub-polar distribution, occupying cold-temperate waters, as opposed to their sister species, the short-finned pilot whale, which occurs in tropical and sub-tropical waters (Olson, 2009). Sub-polar waters are known to be more productive than that of the tropics and sub-tropics, meaning competition for resources, and therefore intergenerational reproductive conflict, is likely to be less intense (Péron *et al.,* 2019). Periods of resource scarcity are known to intensify reproductive competition in other species. Subordinate female banded-mongooses *(Mungos mungo)*, for example, are known to abort pregnancies during periods of climate-induced food scarcity if competition between her and the dominant, simultaneously reproducing females is too intense to support all resultant offspring (Inzani *et al.,* 2019). It should be noted that long-finned pilot whale populations found in the Faroe Islands are known to be larger than those found in Iceland and Newfoundland (Betty, 2019). This implies that resource abundance is particularly high for the individuals in this dataset compared to those distributed elsewhere, suggesting that if it is the greater ecological productivity of the North-East Atlantic that reduces reproductive conflict within this population, then offspring in other populations may still incur costs as a consequence of mother daughter co-breeding.

Even if some level of cost is incurred through intergenerational reproductive conflict, it is possible that they may be offset by potential benefits of mother-daughter co-breeding if reproductive conflict is minimal. Some evidence for benefits associated with mother-daughter co-breeding have been found in killer whales *(Orcinus orca),* however the costs associated with reproductive competition outweigh these benefits (Croft *et al.,* 2017). In African elephants *(Loxodonta africana)*, however, the presence of a mother reproducing simultaneously with her daughter has been shown to increase the daughter's reproductive rate, despite having a costly 22-month gestation period, suggesting that younger females may gain some advantage from co-residence with older, breeding females during reproduction (Lee *et al.,* 2016). Mother-daughter co-breeding has also been shown to positively influence offspring survival in lions *(Panthera leo)* and bushy tailed woodrats *(Neotoma cinerea)* (Moses & Millar, 1994; Packer *et al.,* 1998). I found that young females were more likely to have offspring (and an increased number of offspring) if their mother was present, indicating that long-finned pilot whales do benefit from mother-daughter co-breeding. These benefits may mitigate the pressures associated with reproductive conflict.

It is also possible that the lack of costs associated with mother-daughter reproductive conflict in long-finned pilot whales results from large group sizes. Due to the fact that foregoing reproduction reduces competition for all local breeders, rather than just kin, the benefits of foregoing reproduction, and therefore the costs of co-reproduction, are indiscriminate, equally benefitting all reproductive females in the group (Johnstone and Cant, 2010). Since long-finned pilot whales are known to live in pods with several unrelated matrilines, therefore, this means that such benefits and costs will also be directed towards non-kin (Oremus *et al.,* 2013). Furthermore, in mammalian societies, smaller social groups tend to have a higher average relatedness compared to that of larger groups (Croft *et al.,* 2021). When comparing the range of group sizes of the long-finned pilot whales studied in this dataset (17-194) to datasets of short-finned pilot whales (2-34 in Heimlich-Boran (1993)) or transient killer whales (1-15 in Baird & Dill (1996)), it can be seen that long-finned pilot whales tend to live in larger groups than their close relatives which display a substantial post-reproductive lifespan. This is seen to translate to average relatedness within pods, which, for example, is estimated to be 0.06 for the long-finned pilot whales within this dataset and has been estimated at 0.11 for short-finned pilot whales (Nichols *et al.,* 2020; Van Cise *et al.,* 2017). For long-finned pilot whales, therefore, the costs incurred by kin as a result of co-reproduction are likely to be more dilute than that of other species which have a higher average relatedness within groups. Greater group sizes, and potentially therefore lower direct costs incurred by kin via reproductive conflict, may be facilitated by more favourable ecological conditions as discussed in previous paragraphs. To test this hypothesis, however, it would be necessary to examine populations of long-finned pilot whales which occupy less productive waters.

I found that mothers increased the number of offspring assigned and the probability of having offspring assigned to individuals under 20, but not to individuals under 35, suggesting that either mothers may help younger, inexperienced daughters to raise offspring or facilitate their daughters' first reproduction at an earlier age. It has been shown that in African elephants, females which reproduce early (younger than 12.5 years old) had higher age specific fertility rates, and therefore greater lifetime reproductive output, than those which commenced reproduction later (older than 15 years of age) (Lee *et al.,* 2016). A similar pattern has also been seen in semi-captive Asian elephants *(Elephas maximus)*, however in this case individuals which reproduce earlier suffer lower rates of later life survival (Mumby *et al.,* 2015; Robinson *et al.,* 2012). Therefore, it is possible that by facilitating reproduction at a younger age, and subsequently increasing the lifetime reproductive output of their daughters, mothers may gain greater inclusive fitness. This may explain why the results from this study seem to suggest an initial investment from mothers into the reproductive fitness of their younger daughters, which is reduced as daughters age. Earlier reproduction could be facilitated by mothers via forms of alloparental care such as allonursing, whereby females suckle young of other females. Although this behaviour has not been observed in long-finned pilot whales, the collection of such data is difficult as it requires substantial observational data where the mother and grandmother of a calf can be identified by sight (Augusto *et al.,* 2016). Allonursing has been observed in other odontocetes, however, such as sperm whales *(Physeter macrocephalus)* and captive beluga whales *(Delphinapterus leucas)* (Konrad *et al.,* 2019; Leung *et al.,* 2010). Alternatively, mothers could babysit the offspring of their daughters, allowing for younger females to hunt and acquire more energy to offset the costs associated with raising offspring at a younger age. Again, although this behaviour has not been observed in long-finned pilot whales, it has been observed in sperm whales (Whitehead, 1996).

The results of this study did not find the presence of a grandmother to have a significant effect on the size or reproductive fitness of individuals. It is possible this is due to a lack of opportunities for grandmothers to aid in the raising of their grandoffspring. In some species, such as killer whales and African elephants, grandmothers play an important role as ‘repositories’ of ecological information which is learnt throughout their lifetime (Brent *et al.,* 2015; McComb *et al.,* 2011). This allows older females to lead groups to resources which vary spatially and temporally, and therefore increase the survival rates of grandoffspring (Greve *et al.,* 2009). Although analyses of stomach contents have shown that long-finned pilot whales do feed on prey which vary geographically and seasonally, it is possible that these prey species are followed over large distances, meaning grandmothers would not need to impart ecological information to descendant kin about the location and timings of such resources (Nichols *et al.,* 2020; Santos *et al.,* 2014). Alternatively, if older females do lead their pods to spatially and temporally varying resources based on learned ecological knowledge, it is likely that all younger individuals within the pod will equally benefit from this, not just grandoffspring, as this behaviour cannot be directed at specific individuals. Therefore, this is not likely to be reflected in the size of individuals with grandmothers assigned compared to those without, rather, it would be reflected in pods which have older females present compared to those which do not. Conversely, it is possible that grandmothers do convey fitness benefits to their grandoffspring, but they contribute more to the survival of these offspring rather than to their size or reproductive output, meaning such effects could not be detected in my study. For example, older African elephants are known to be more sensitive to cues of predatory threat, and therefore engage in longer periods of listening and more intense bunching behaviour in reaction to such cues, consequently improving the survival of young (McComb *et al.,* 2011).

This study, in line with current literature which predicts that a combination of mother and grandmother effects and intergenerational reproductive conflict would predispose a post-reproductive lifespan, has demonstrated that long-finned pilot whales do not incur substantial fitness costs as a result of mother-daughter co-breeding. Although this study has revealed much about the roles of grandmothers, mothers and reproductive conflict in long-finned pilot whales societies, there is still further work that could be done to better our understanding. Effects in other populations remain largely unstudied, despite long-finned pilot whales having a vast, bipolar distribution. Investigations into the mother, grandmother and reproductive conflict hypotheses in other populations of long-finned pilot whales are likely to better our understanding of the social behaviour of this species and go further in revealing why long-finned pilot whales do not have a substantial species wide post-reproductive lifespan. Furthermore, long-term observational datasets are likely to uncover more about specific social behaviours, for example, whether mothers or grandmothers improve the fitness of descendant kin in ways not identified within this study, such as defence against predation.

5. Conclusion

Despite having patterns of dispersal and relatedness that suggest that they might benefit from a post-reproductive lifespan, female long-finned pilot whales do not live for a significant period of time after the cessation of reproduction. Using a combination of maternity assignment and morphological data, this study aimed to test 3 non-exclusive hypotheses for the evolution of a substantial post-reproductive lifespan (the mother hypothesis, grandmother hypothesis and reproductive conflict hypothesis) in long-finned pilot whales. In doing this, I aimed to identify why this unusual life history trait was not present in this species, but present in other species with similar social conditions. My results suggest that potential benefits of older relatives that might favour a post-reproductive lifespan exist in long-finned pilot whales: although no benefit of grandmothers was detected, young females were more likely to have offspring present (and have more offspring) when their mother was present. However, I found no evidence that offspring incur costs as a result of mother-daughter co-breeding, meaning benefits can be conferred without the mother avoiding reproduction herself. This is concurrent with literature that suggests that benefits from mothering and grandmothering are not sufficient in themselves to drive the evolution of a prolonged post-reproductive lifespan, and that the inclusive fitness gained from reducing intergenerational reproductive conflict with descendant kin must outweigh the costs associated with halting reproduction.

Future research should investigate the effects of mother presence, grandmother presence and reproductive conflict in other populations of long-finned pilot whale to investigate whether the results found are applicable to the whole species, or whether these results are a product of favourable ecological conditions found in the North- East Atlantic. Furthermore, the collection of long-term, observational data on long-finned pilot whales to complement data from drive fisheries would reveal more about the specific social behaviours between kin, adding to our understanding of the roles of mothers and grandmothers in long-finned pilot whale societies.

6. Appendices

Appendix 1 – R code used for running GLMMs

```
##### ANALYSIS 2 - ARE WHALES LARGER FOR THEIR AGE IF THEIR MOTHER OR GRANDMOTHER IS PRESENT? ##############

library(readr)

datasheet_without_non_exact_age_and_122_137 <- read_csv("FINAL DATA (teeth only).csv")

View(datasheet_without_non_exact_age_and_122_137)

onlyexactage <- datasheet_without_non_exact_age_and_122_137

library(lme4)

############## ANALYSES OF INDIVIDUALS UNDER 20 ########################

u20<- onlyexactage[which(onlyexactage$best_age<20),]

u20size <- u20$length

u20AGE <- u20$best_age

u20mother <- factor(u20$`Mother Present?`)

u20GM <- factor(u20$`Grandmother Present?`)

u20offspring <- u20$`Number of offspring`

u20whale <- u20$`whale ID`

u20pod <- u20$pod

u20sex <- factor(u20$sex)


m5 <- lmer(u20size ~ u20AGE*u20sex +I(u20AGE^2)*u20sex +u20mother*u20sex  + u20GM*u20sex +  (1|u20pod))

library(lmerTest)

summary(lmer(m5))


install.packages("DHARMa")

library("DHARMa")

plot(simulateResiduals(m5,n=1000))
```

```
#### OBTAINING P VALUES ####

m5.1 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2)*u20sex +u20mother*u20sex
+ (1 | u20pod))

anova(m5, m5.1)


m5.2 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2)*u20sex + u20GM*u20sex +
(1|u20pod))

anova(m5, m5.2)


m5.3 <- update(m5, ~ u20AGE +I(u20AGE^2) +u20mother  + u20GM+  (1|u20pod))

anova(m5, m5.3)


m5.4 <- update(m5, ~ u20AGE*u20sex +u20mother  + u20GM +  (1|u20pod))

anova(m5, m5.4)


m5.5 <- update(m5, ~ I(u20AGE^2)*u20sex +u20mother*u20sex  + u20GM*u20sex
+  (1|u20pod))

anova(m5, m5.5)


m5.6 <- update(m5, ~ u20AGE +I(u20AGE^2)*u20sex +u20mother*u20sex  +
u20GM*u20sex +  (1|u20pod))

anova(m5, m5.6)


m5.7 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2) +u20mother*u20sex  +
u20GM*u20sex +  (1|u20pod))

anova(m5, m5.7)


m5.8 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2)*u20sex +u20mother  +
u20GM*u20sex +  (1|u20pod))

anova(m5, m5.8)
```

```
m5.9 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2)*u20sex +u20mother*u20sex + u20GM +  (1|u20pod))

anova(m5, m5.9)

m5 <- lmer(u20size ~ u20AGE*u20sex +I(u20AGE^2)*u20sex +u20mother  + u20GM +  (1|u20pod))

library(lmerTest)

summary(lmer(m5))


library("DHARMa")

plot(simulateResiduals(m5,n=1000))


m5.1 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2)*u20sex +u20mother  + (1 | u20pod))

anova(m5, m5.1)


m5.2 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2)*u20sex + u20GM + (1|u20pod))

anova(m5, m5.2)


m5.3 <- update(m5, ~ u20AGE +I(u20AGE^2) +u20mother  + u20GM+  (1|u20pod))

anova(m5, m5.3)


m5.4 <- update(m5, ~ u20AGE*u20sex +u20mother  + u20GM +  (1|u20pod))

anova(m5, m5.4)


m5.5 <- update(m5, ~ I(u20AGE^2)*u20sex +u20mother  + u20GM +  (1|u20pod))

anova(m5, m5.5)


m5.6 <- update(m5, ~ u20AGE +I(u20AGE^2)*u20sex +u20mother  + u20GM + (1|u20pod))

anova(m5, m5.6)
```

```
m5.7 <- update(m5, ~ u20AGE*u20sex +I(u20AGE^2) +u20mother  + u20GM +
(1|u20pod))

anova(m5, m5.7)



################## ANALYSES OF INDIVIDUALS UNDER 35
###########################

u35<- onlyexactage[which(onlyexactage$best_age<35),]


u35size <- u35$length

u35AGE <- u35$best_age

u35mother <- factor(u35$`Mother Present?`)

u35GM <- factor(u35$`Grandmother Present?`)

u35offspring <- u35$`Number of offspring`

u35whale <- u35$`whale ID`

u35pod <- u35$pod

u35sex <- factor(u35$sex)


m6 <- lmer(u35size ~ u35AGE*u35sex +I(u35AGE^2)*u35sex + u35mother*u35sex +
(1|u35pod))

library(lmerTest)

summary(lmer(m6))


library("DHARMa")

plot(simulateResiduals(m6,n=1000))



### OBTAINING P VALUES ###

m6.1 <- update(m6, ~u35AGE*u35sex +I(u35AGE^2)*u35sex + (1 | u35pod))

anova(m6, m6.1)
```

```
m6.2 <- update(m6, ~ u35AGE +I(u35AGE^2) + u35mother +  (1|u35pod))

anova(m6, m6.2)


m6.3 <- update(m6, ~u35AGE*u35sex + u35mother*u35sex +  (1|u35pod))

anova(m6, m6.3)


m6.4 <- update(m6, ~ I(u35AGE^2)*u35sex + u35mother*u35sex +  (1|u35pod))

anova(m6, m6.4)


m6.5 <- update(m6, ~ u35AGE +I(u35AGE^2)*u35sex + u35mother*u35sex + (1|u35pod))

anova(m6, m6.5)


m6.6 <- update(m6, ~ u35AGE*u35sex +I(u35AGE^2) + u35mother*u35sex + (1|u35pod))

anova(m6, m6.6)


m6.7 <- update(m6, ~ u35AGE*u35sex +I(u35AGE^2)*u35sex + u35mother + (1|u35pod))

anova(m6, m6.7)



m6 <- lmer(u35size ~ u35AGE*u35sex +I(u35AGE^2)*u35sex + u35mother + (1|u35pod))

library(lmerTest)

summary(lmer(m6))


library("DHARMa")

plot(simulateResiduals(m6,n=1000))


m6.1 <- update(m6, ~u35AGE*u35sex +I(u35AGE^2)*u35sex + (1 | u35pod))

anova(m6, m6.1)
```

```
m6.2 <- update(m6, ~ u35AGE +I(u35AGE^2) + u35mother +  (1|u35pod))

anova(m6, m6.2)


m6.3 <- update(m6, ~u35AGE*u35sex + u35mother +  (1|u35pod))

anova(m6, m6.3)


m6.4 <- update(m6, ~ I(u35AGE^2)*u35sex + u35mother +  (1|u35pod))

anova(m6, m6.4)


m6.5 <- update(m6, ~ u35AGE +I(u35AGE^2)*u35sex + u35mother +  (1|u35pod))

anova(m6, m6.5)


m6.6 <- update(m6, ~ u35AGE*u35sex +I(u35AGE^2) + u35mother +  (1|u35pod))

anova(m6, m6.6)



################################################################################


###### ANALYSIS 3 - EFFECTS OF MOTHER AND GRANDMOTHER PRESENCE ON NUMBER/PROBABILITY OF ASSIGNED OFFSPRING ########

library(readr)

datasheet_without_non_exact_age_and_122_137 <- read_csv("FINAL DATA.csv")

View(datasheet_without_non_exact_age_and_122_137)

install.packages("lme4")

library("lme4")


###################### ANALYSES ON INDIVIDUALS UNDER 20 #####################
```

```
onlyexactage <- datasheet_without_non_exact_age_and_122_137
females <- subset(onlyexactage, sex == 'female')
posmothers <- subset(females, best_age>5)
posmothersu20s <- subset(posmothers, best_age<20)

age20 <- posmothersu20s$best_age
mother20 <- factor(posmothersu20s$`Mother Present?`)
GM20 <- factor(posmothersu20s$`Grandmother Present?`)
offspring20 <- posmothersu20s$`Number of offspring`
whale20 <- posmothersu20s$`whale ID`
pod20 <- posmothersu20s$pod
size20 <- posmothersu20s$length
offspring20.1 <- factor(posmothersu20s$`Offspring?`)
sex20 <- posmothersu20s$sex

age20sc<-scale(age20, scale = T, center = T)
m1 <- glmer(offspring20~age20sc+I(age20sc^2)+mother20+GM20+(1|pod20),family=poisson(link = "log"), glmerControl(optimizer = "bobyqa"), data = posmothersu20s)
summary(m1)

install.packages("DHARMa")
library("DHARMa")
plot(simulateResiduals(m1,n=1000))

###### OBTAINING P VALUES #######
m1.1 <- update(m1, ~age20sc+I(age20sc^2)+mother20+(1|pod20),family=poisson(link = "log"))
anova(m1, m1.1)

m1.2 <- update(m1, ~age20sc+I(age20sc^2)+GM20+(1|pod20),family=poisson(link = "log"))
```

```
anova(m1, m1.2)


m1.3 <- update(m1, ~age20sc+mother20+GM20+(1|pod20), family=poisson(link = "log"))

anova(m1, m1.3)


m1.4 <- update(m1, ~I(age20sc^2)+mother20+GM20+(1|pod20),family=poisson(link = "log"))

anova(m1, m1.4)




#################### ANALYSES ON INDIVIDUALS UNDER 35 ######################

posmothersu35s <- subset(posmothers, best_age<35)

age35 <- posmothersu35s$best_age

mother35 <- factor(posmothersu35s$`Mother Present?`)

GM35 <- factor(posmothersu35s$`Grandmother Present?`)

offspring35 <- posmothersu35s$`Number of offspring`

whale35 <- posmothersu35s$`whale ID`

pod35 <- posmothersu35s$pod

size35 <- posmothersu35s$length


age35sc<-scale(age35, scale = T, center = T)

m2 <- glmer(offspring35~age35sc+I(age35sc^2)+mother35+(1|pod35),family=poisson(link = "log"))

summary(m2)

plot(simulateResiduals(m2,n=1000))


##### OBTAINING P VALUES #####

m2.1 <- update(m2, ~age35sc+I(age35sc^2)+(1|pod35),family=poisson(link = "log"))

anova(m2, m2.1)
```

```
m2.2 <- update(m2, ~age35sc+mother35+(1|pod35),family=poisson(link = "log"))

anova(m2, m2.2)


m2.3 <- update(m2, ~I(age35sc^2)+mother35+(1|pod35),family=poisson(link = "log"))

anova(m2, m2.3)


########## ANALYSES ON THE PROBABILITY OF INDIVIDUALS UNDER 20 HAVING OFFSPRING ASSIGNED ######



m3 <- glmer(offspring20.1~age20sc+I(age20sc^2)+mother20+GM20+(1|pod20), family = binomial(link = "logit"), control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=1e4)))

summary(m3)

plot(simulateResiduals(m3,n=1000))


###### OBTAINING P VALUES ######

m3.1 <- update(m3, ~age20sc+I(age20sc^2)+mother20+(1|pod20), family = binomial(link = "logit"))

anova(m3, m3.1)


m3.2 <- update(m3, ~age20sc+I(age20sc^2)+GM20+(1|pod20), family = binomial(link = "logit"))

anova(m3, m3.2)


m3.3 <- update(m3, ~age20sc+mother20+GM20+(1|pod20), family = binomial(link = "logit"))

anova(m3, m3.3)


m3.4 <- update(m3, ~I(age20sc^2)+mother20+GM20+(1|pod20), family = binomial(link = "logit"))
```

```
anova(m3, m3.4)


###########################################################################


############ ANALYSIS 4 - EFFECTS OF MOTHER AND GRANDMOTHER PRESENCE ON THE PROBABILITY OF PREGNANCY ##############

library(readr)

datasheet_without_non_exact_age_and_122_137 <- read_csv("FINAL DATA.csv")

View(datasheet_without_non_exact_age_and_122_137)


install.packages("lme4")

library("lme4")

females <- subset(datasheet_without_non_exact_age_and_122_137, sex == "female")

posmothers <- subset(females, best_age>5)


######################### ANALYSES ON FEMALES UNDER 20 ###################

posmothersu20s <- subset(posmothers, best_age<20)


age20 <- posmothersu20s$best_age

preg20 <- factor(posmothersu20s$'Pregnant?')

mother20 <- factor(posmothersu20s$`Mother Present?`)

GM20 <- factor(posmothersu20s$`Grandmother Present?`)

whale20 <- posmothersu20s$`whale ID`

pod20 <- posmothersu20s$pod


age20sc<-scale(age20, scale = T, center = T)

m5 <- glmer(preg20 ~ age20sc+I(age20sc^2) + mother20 + GM20 + (1|pod20), family = binomial(link=logit))

summary(m5)
```

```
install.packages("DHARMa")

library("DHARMa")

plot(simulateResiduals(m5,n=1000))


####### OBTAINING P VALUES ######

m5.1 <- update(m5, ~age20sc+I(age20sc^2) + mother20 + (1|pod20), family = binomial(link=logit))

anova(m5, m5.1)


m5.2 <- update(m5, ~ age20sc+I(age20sc^2) + GM20 + (1|pod20))

anova(m5, m5.2)


m5.3 <- update(m5, ~ age20sc + mother20 + GM20 + (1|pod20), family = binomial(link=logit))

anova(m5, m5.3)


m5.4 <- update(m5, ~ I(age20sc^2) + mother20 + GM20 + (1|pod20), family = binomial(link=logit))

anova(m5, m5.4)


##################### ANALYSES ON FEMALES UNDER 35 #######################

posmothersu35s <- subset(posmothers, best_age<35)


age35 <- posmothersu35s$best_age

preg35 <- factor(posmothersu35s$'Pregnant?')

mother35 <- factor(posmothersu35s$`Mother Present?`)

GM35 <- factor(posmothersu35s$`Grandmother Present?`)

whale35 <- posmothersu35s$`whale ID`

pod35 <- posmothersu35s$pod
```

```
age35sc<-scale(age35, scale = T, center = T)

m6 <- glmer(preg35 ~ age35sc+I(age35sc^2) + mother35 + (1|pod35), family = binomial(link=logit))

summary(m6)


library("DHARMa")

plot(simulateResiduals(m6,n=1000))


####### OBTAINING P VALUES ##########

m6.1 <- update(m6, ~ age35sc+I(age35sc^2) + (1|pod35), family = binomial(link=logit))

anova(m6, m6.1)


m6.2 <- update(m6, ~ age35sc+ mother35 + (1|pod35), family = binomial(link=logit))

anova(m6, m6.2)


m6.3 <- update(m6, ~ I(age35sc^2) + mother35 + (1|pod35), family = binomial(link=logit))

anova(m6, m6.3)


##############################################################################


####### ANALYSIS 5 - THE EFFECT OF REPRODUCTIVE CONFLICT ON SIZE OF OFFSPRING #######

library(readr)

datasheet_without_non_exact_age_and_122_137 <- read_csv("FINAL DATA (teeth only).csv")

View(datasheet_without_non_exact_age_and_122_137)

data <- datasheet_without_non_exact_age_and_122_137
```

```
######################## EFFECTS ON INDIVIDUALS UNDER 5
####################

u5s <- subset(data, best_age<5)

pod5 <- u5s$pod

size5 <- u5s$length

mother5 <- factor(u5s$`Mother Present?`)

gm5 <- factor(u5s$`Grandmother Present?`)

age5 <- u5s$best_age

conflict5 <- factor(u5s$`Reproductive conflict`)

mo5 <- factor(u5s$`Mother Offspring`)

do5 <- factor(u5s$`Daughter Offspring`)

sex5 <- factor(u5s$sex)


m2 <- lmer(size5~age5*sex5+I(age5^2)*sex5+conflict5*sex5+(1|pod5))

summary(lmer(m2))


install.packages("DHARMa")

library("DHARMa")

plot(simulateResiduals(m2,n=1000))


############## OBTAINING P VALUES ########################

m2.1 <- update(m2, ~age5*sex5+I(age5^2)*sex5+(1|pod5))

anova(m2,m2.1)


m2.2 <- update(m2, ~age5+I(age5^2)+conflict5+(1|pod5))

anova(m2, m2.2)


m2.3 <- update(m2, ~age5*sex5+conflict5*sex5+(1|pod5))

anova(m2, m2.3)


m2.4 <- update(m2, ~I(age5^2)*sex5+conflict5*sex5+(1|pod5))
```

```
anova(m2, m2.4)

m2.5 <- update(m2, ~age5+I(age5^2)*sex5+conflict5*sex5+(1|pod5))
anova(m2, m2.5)

m2.6<- update(m2, ~age5*sex5+I(age5^2)+conflict5*sex5+(1|pod5))
anova(m2, m2.6)

m2.7 <- update(m2, ~age5*sex5+I(age5^2)*sex5+conflict5+(1|pod5))
anova(m2, m2.7)

m2 <- lmer(size5~age5+I(age5^2)*sex5+conflict5+(1|pod5))
summary(lmer(m2))

library("DHARMa")
plot(simulateResiduals(m2,n=1000))
m2.1 <- update(m2, ~age5+I(age5^2)*sex5+(1|pod5))
anova(m2,m2.1)

m2.2 <- update(m2, ~age5+I(age5^2)+conflict5+(1|pod5))
anova(m2, m2.2)

m2.3 <- update(m2, ~age5+I(age5^2)+conflict5+sex5+(1|pod5))
anova(m2, m2.3)

m2.4 <- update(m2, ~I(age5^2)*sex5+conflict5+(1|pod5))
anova(m2, m2.4)

m2.5 <- update(m2, ~age5+conflict5+sex5+(1|pod5))
anova(m2, m2.5)
```

```
###########################################################################

################ MODEL INVESTIGATING THE EFFECTS OF REPRODUCTIVE CONFLICT IN INDIVIDUALS UNDER 9 #########################
u9s <- subset(data, best_age<9)


pod9 <- u9s$pod
size9 <- u9s$length
mother9 <- factor(u9s$`Mother Present?`)
gm9 <- factor(u9s$`Grandmother Present?`)
age9 <- u9s$best_age
conflict9 <- factor(u9s$`Reproductive conflict`)
mo9 <- factor(u9s$`Mother Offspring`)
do9 <- factor(u9s$`Daughter Offspring`)
sex9 <- factor(u9s$sex)


m6<-lmer(size9~age9*sex9+I(age9^2)*sex9+conflict9*sex9+(1|pod9))
library(lmerTest)
summary(lmer(m6))


library("DHARMa")
plot(simulateResiduals(m6,n=1000))


######### OBTAINING P VALUES #########
m6.1 <- update(m6, ~age9*sex9+I(age9^2)*sex9+(1|pod9))
anova(m6, m6.1)


m6.2 <- update(m6, ~age9+I(age9^2)+conflict9+(1|pod9))
anova(m6, m6.2)
```

```
m6.3 <-update(m6, ~age9*sex9+conflict9*sex9+(1|pod9))
anova(m6, m6.3)

m6.4 <- update(m6, ~I(age9^2)*sex9+conflict9*sex9+(1|pod9))
anova(m6, m6.4)

m6.5 <- update(m6, ~age9+I(age9^2)*sex9+conflict9*sex9+(1|pod9))
anova(m6, m6.5)

m6.6 <- update(m6, ~age9*sex9+I(age9^2)+conflict9*sex9+(1|pod9))
anova(m6, m6.6)

m6.7 <- update(m6, ~age9*sex9+I(age9^2)*sex9+conflict9+(1|pod9))
anova(m6, m6.7)

m6<-lmer(size9~age9+I(age9^2)+conflict9+sex9+(1|pod9))
library(lmerTest)
summary(lmer(m6))

library("DHARMa")
plot(simulateResiduals(m6,n=1000))

m6.1 <- update(m6, ~age9+I(age9^2)+sex9+(1|pod9))
anova(m6, m6.1)

m6.2 <- update(m6, ~age9+I(age9^2)+conflict9+(1|pod9))
anova(m6, m6.2)

m6.3 <- update(m6, ~age9+sex9+conflict9+(1|pod9))
```

```
anova(m6, m6.3)

m6.4 <- update(m6, ~I(age9^2)+sex9+conflict9+(1|pod9))
anova(m6, m6.4)
```

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