Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

THOMAS HENRY HUXLEY REVIEW

No time to die: Evolution of a post-reproductive life stage

P. Monaghan & E. R. Ivimey-Cook

School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow, UK

Keywords
menopause; sterility; mitochondria; brain size; oogonia; reproductive senescence; gametogenesis.

Correspondence
Pat Monaghan, School of Biodiversity, One Health and Veterinary Medicine, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, UK.
Email: pat.monaghan@glasgow.ac.uk

Editor: Nigel Bennett

Received 27 November 2022; revised 19 May 2023; accepted 14 June 2023

doi:10.1111/jzo.13096

Abstract

In some species, permanent curtailment of reproduction part-way through the life-span of adult females is a feature of their evolved life history. The existence of such a post-reproductive life stage is apparently rare; reasonably robust evidence for this is confined to only six species (humans, Asian elephants and four whales). That it occurs at all appears to contradict our view of natural selection operating to maximize fitness and special circumstances must exist to explain its occurrence. We evaluate the main hypotheses posited to explain the evolution of this life stage, why it occurs in a restricted group of animals, and why only in females. We bring together literature from multiple biological disciplines and levels of enquiry, ranging through evolutionary ecology, developmental biology, physiology, neuroscience, molecular biology, and human medicine. We conclude that while time-limited fertility is not in itself adaptive, the duration of subsequent survival is likely to be linked to inclusive fitness benefits. We present a new hypothesis which posits that the duration of female fertility in certain long-lived, highly encephalised species, with no post-natal oogenesis, is limited by the need for intense screening of oocyte mitochondria. This is required to support endothermy coupled with the very high energy requirement for the development and maintenance of the exceptionally large brain size required for complex social living. This limits the number and shelf-life of oocytes, creating an antagonistically pleotropic effect that is beneficial to the production of high performing offspring but carries the later life cost of time-limited female fertility. But the end of the fertile period is no time to die. Inclusive fitness benefits arising from protracted parental care of offspring, overlapping generations, and kin group structures means that continued survival of post-reproductive females is favoured by selection. We suggest further lines of research to test these ideas.

Introduction

Our understanding of the evolution of animal life histories is rooted in the premise that traits are shaped by natural selection acting to maximize an individual's genetic contribution to the next generation. Given the overwhelming importance of reproductive strategies in this context, it is surprising to find that a non-reproductive adult phenotype is an integral part of the life history in some species. This can involve no reproduction throughout adulthood, as in the sterile castes of many social insects (Williams & Williams, 1957), or the forms of self-sacrificing parental care as shown by female gall aphids. These aphids protect their clonally produced offspring by becoming a post-reproductive 'glue bomb' whose explosion when the offspring are threatened destroys both themselves and any potential predators (Foster, 2010). We can understand the evolution of such extreme life histories from the high inclusive fitness benefits individuals obtain (e.g. Olejarz et al., 2015). Much harder to understand are cases such as the menopause in humans, where all women transition from a reproductive to an irreversible, non-reproductive state part-way through adult life. Women spend on average 43% of 'lived years' in a state of permanent sterility (around a quarter of their adult life), which, along with the age at menarche, shows remarkably low variability across populations (Gavrilova et al., 2012) and high heritability (40–60%; Peccei, 2001a, 2001b). In contrast, men can retain reproductive capacity throughout adulthood. Why does this occur? In this review, we bring together a literature that is scattered across a wide variety of disciplines, and combine information from evolutionary ecology with developmental biology, physiology, neuroscience, molecular biology, and human medicine. We critically examine the current evidence for the occurrence of a Post-Reproductive Life Stage in animals (hereafter PRLS), summarize the main hypotheses that have been put forward to explain its occurrence, discuss the evidence for and against these hypotheses and how they apply

 © 2023 The Authors. *Journal of Zoology* published by John Wiley & Sons Ltd on behalf of Zoological Society of London. This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

to different taxa and to males and females. We then provide a new, speculative synthesis of what we see as the most likely explanation. Throughout, we highlight the key gaps and contradictions in our current knowledge, and end by identifying important lines for future research.

PRLS definition and distribution

A PRLS can occur due to age-specific changes in the *inclination*, *opportunity*, or *capacity* to breed. Respectively, these involve:

(1) Age-specific changes in an individual's motivation to breed, for example due to a lack of appropriate resources for successful reproduction (Bunce et al., 2005; Rauset et al., 2015);
(2) Age-specific changes in the ability to attract a reproductive partner in sexually reproducing species (Kuo et al., 2012);
(3) Predictable, age-related changes in physiology that render a previously fertile individual sterile (Lim & Tsakok, 1997).

The first two can be considered transient sterility, which is potentially reversible should access to resources or partners change. There are other reasons for transient sterility that do not involve age-related changes. For example, removal of a dominant female who subsequently becomes a grandparental helper at the nests of her offspring in the Seychelles warbler (*Acrocephalus sechellensis*; Richardson et al., 2007), or where a failed breeding attempt leads to the transition into helping kin in long-tailed tits (*Aegithalos caudatus*; Hatchwell et al., 2001). However, the third is a life history transition to a state of permanent sterility, involving an irreversible loss of reproductive capability. It is with this third pathway that we are concerned in this review. While survival of some individuals for a period after reproduction has been shown across multiple taxa (Jones et al., 2014), an inevitable transition to a permanent and lasting sterile state appears to occur in only a very small number of species, and only in females. Why only these species, and if males can retain some reproductive capacity to the end of life, why cannot females do the same?

Reproduction is not usually suicidal, and most animals survive for at least a short time following breeding even if semelparous. This may be simply by chance, or until they become food for their mate as in male praying mantises, or food for their young as in the matrivorous moth, *Andesobia jelskii* (Schmidt & Freina, 2011), or until their existing young become fully independent, or they may simply be between breeding events with interbirth interval increasing with age, or take a variable time to eventually die. Therefore, rather than the more commonly used term 'Post-Reproductive Lifespan', we prefer to use the term 'Post-Reproductive Life Stage' (PRLS) indicating a predictable, age-related transition to a lasting state of permanent sterility. This is similar to the conclusion reached by Levitis et al. (2013) in their discussion of post-reproductive survival. Hence, for this review, our definition of a PRLS is as follows: *An age-associated, later life stage of variable duration where all surviving individuals exhibit a permanent and irreversible cessation of reproduction after having reached functional sexual maturity.* Post-reproductive lifespan is then the duration of this post-reproductive life stage. This transition to sterility is not a feature of only a few exceptional individuals nor is it associated with pathology. In theory, the transition can be abrupt or be preceded by a gradual decline in fertility, as illustrated in Fig. 1. However, there is always a final 'cliff edge' and once over this, individuals cannot reascend.

There are two opposing views on the prevalence of PRLSs across the animal kingdom. Some authors argue that the evidence is overwhelmingly in favour of the presence of PRLSs, largely in the mammals (Cohen, 2004). More recent papers however suggest that several previously quoted examples do not exhibit a true post-reproductive life stage (Ellis, Franks, Nattrass, Cant, et al., 2018) and instead a few individuals survive for a significant period after their last reproductive event simply by chance, or that a state of *permanent* sterility does not in fact occur. Establishing that sterility is permanent can be difficult. Numerous species have been put forward as exhibiting a PRLS, including the Bali mynah bird (*Leucopsar rothschildi*, Holmes & Ottinger, 2003; Jones et al., 2014), a viviparous gall-forming aphid that reproduces via parthenogenesis (*Quadrartus yoshinomiyai*; Uematsu et al., 2010; Uematsu & Shibao, 2018), the classic model species *Drosophila melanogaster* (Klepsatel et al., 2013), the guppy (*Poecilla reitculata*; Reznick et al., 2005), the nematode worm *Caenorhabditis elegans* (Mendenhall et al., 2011; Kern et al., 2021). In all of these cases, there is no assessment of the proportion of individuals reaching this post-reproductive state, and it might well involve only a very few exceptional individuals (see Levitis & Lackey, 2011 for a more thorough discussion).

It is of course especially challenging to collect age-specific data in wild systems and some species present greater challenges than others, such as those that are harder to track and/or have small body sizes (Ellis, Franks, Nattrass, Cant, et al., 2018). Accordingly, some studies have applied a minimum time period for individuals to be considered post-reproductive, such as two standard deviations (or 90th percentile; Reznick et al., 2005) of a species' average interbirth interval. Figure 2 (data from Lahdenperä et al., 2014) shows data from a pre-industrial human population. While an individual's interbirth interval often increases with age, the average duration of the PRLS in this population was more than 10 times the average interbirth interval. Other studies use a population-level measure known as post-reproductive representation (hereafter, PrR as proposed by Levitis & Lackey, 2011; see also Croft et al., 2015; Ellis, Franks, Nattrass, Cant, et al., 2018). This is a useful indicator that incorporates the prevalence of the PRLS and is calculated as the proportion of adult female years in the population that are lived by females who have become permanently sterile. All of these measures are difficult to obtain, especially in the wild. For harvested and hunted species, data may come from dissected animals in which ovarian tissue can be examined as can be the case with cetaceans.

To illustrate the usefulness of the PrR measure, we searched the literature and found 157 PrR values for 114 species. These values were based on information from 26 papers that include both general reviews of PRLSs and species-specific

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

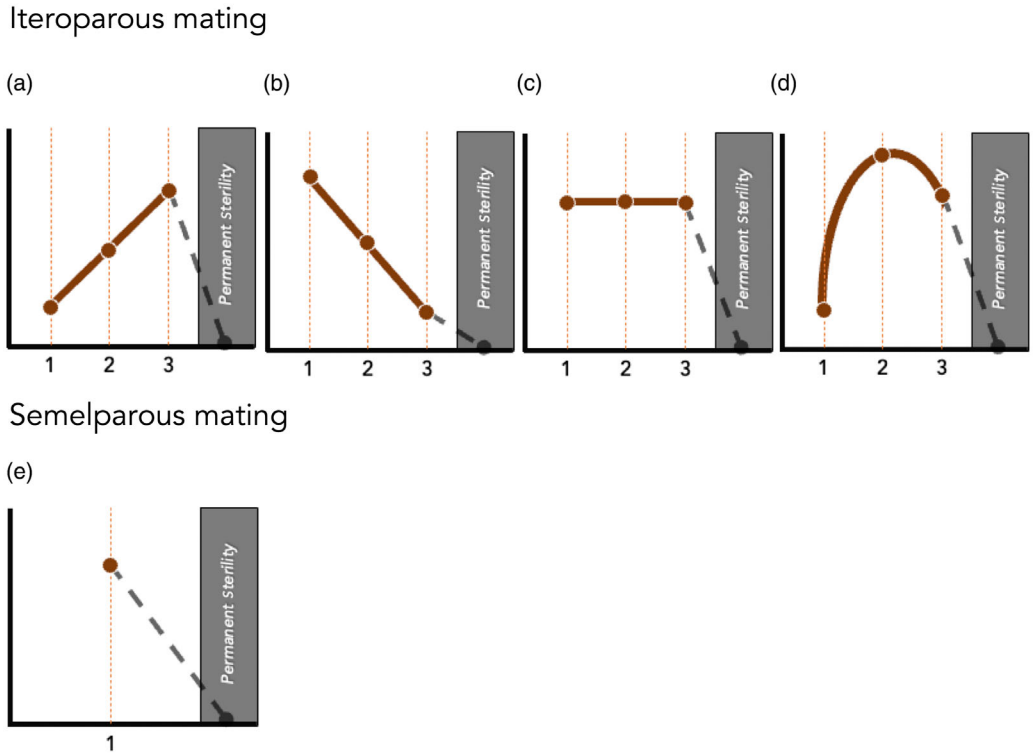

Figure 1 Potential patterns for the onset of a Post-Reproductive Life Stage (PRLS) in females, depicted by the grey box marked 'Permanent Sterility'. We here show the PRLS as a fixed duration for simplicity, but obviously this duration can vary. Individual reproductive performance prior to the PRLS might increase steadily with age (a), decline (b), remain constant (c) or show a quadratic relationship (d). (e) illustrates the potential pattern for a semelparous breeder. The numbers on the *x* axis refer to a fictional reproductive lifetime of an iteroparous (a–d) or a semelparous breeder (e). The *y* axis refers to offspring number, the trend reflects the reproductive schedule, but the values are arbitrary (hence no scale).

observations. Of these 114, 67 species had PrR values less than 0.10 (this measure captures both duration and frequency). While 0.10 is of course a somewhat arbitrary cut off, we have used this to avoid inclusion of species where only a small number of females are involved and/or the duration of the PRLS is very short. It is of course possible that subsequent data from the wild will be available for more species (Fig. S1 gives a full phylogenetic tree of species that have been suggested so far to possess some form of a PRLS, however short this may be). Figure 3 shows the taxonomic distribution of the 52 species whose PrR values were estimated as greater than 0.10, indicative of post-reproductive survival being common and relatively long. These are all mammals, mostly primates, involve exclusively females, and are populations predominantly studied in captivity, probably because of some reporting bias and ease of recording data from captive populations. There are data from only five non-human species showing evidence of a PRLS in their natural or semi-natural environment (Fig. 3). Notably, these values are much greater than the average PrR across all wild populations, which, in comparison to what has been recorded in captive or semi-captive conditions and in humans, is generally very low. For the 52 species having PrR value of over 0.10, simulations that enable confidence limits for the PrR to be calculated (see Appendix S1 for details) indicate that only six of the 52 have PrR values significantly different from 0 and originate from wild or semi-natural populations; humans (*Homo sapiens*, from multiple populations), the killer whale (*Orcinus orca*), the short-finned pilot whale (*Globicephala macrorhynchus*), the narwhal (*Monodon monoceros*), the Asian elephant (*Elephas maximus*), and the beluga whale (*Delphinapterus leucas*) with values of 0.52 (±0.11), 0.26 (±0.06), 0.23 (±0.07), 0.24, 0.17 (±0.04), 0.27 PrR values, respectively (values given are means with or, in the case of the beluga whale and narwhal, without standard deviation). Caution is particularly needed with two of these listed species, the narwhal and beluga whale, as the data may be too sparse to accurately detect PRLS and instead could simply provide an example of a extremely long reproductive lifespan (see appendix A from Péron et al., 2019), and the physiological state of the post reproductive Asian elephant females needs more investigation (Chapman et al., 2019). Furthermore, the false killer whale (*Psuedorca crassidens*) is notably absent from this list. Whilst it has been suggested that this species has a significant PrR (see Photopoulou et al., 2017; Peron et al., 2019), Ellis, Franks, Nattrass, Currie, et al. (2018) found contrasting evidence both through pregnancy or ovarian data and suggested the need for further conclusive evidence to be collected. We found no robust evidence for the existence of a

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

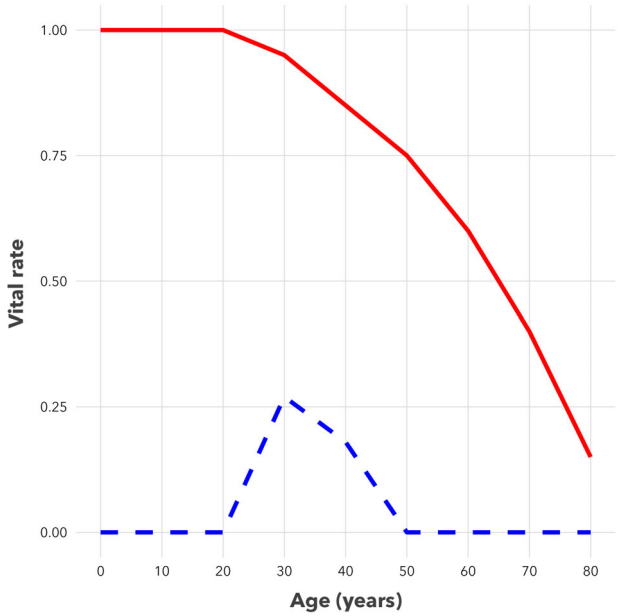

Figure 2 Age-specific survival in a population of 5336 pre-industrial women who survived to reproductive age (proportion alive at age x; solid, red) and age-specific fertility in the same group (average number of offspring born in the population at age x; dashed, blue). Adapted from Lahdenperä et al. (2014); in this population mean age of last reproduction = 37.66 years, standard deviation (SD) = 6.27 years; mean longevity = 60.07 years, SD = 16.50 years; mean interbirth interval = 2.72 years, 2 × SD = 2.46 years. Data used for this graph was extracted from the source paper using the shinyDigitise (v. 0.1.0) add-on for metaDigitise (v. 1.0.1) (Pick et al., 2019; Ivimey-Cook and Pick, 2023).

substantial PRLS in other relatively well studied taxonomic groups such as birds, reptiles, amphibians, and insects. Although we note that an apparent PRLS has been reported in some of these taxonomic groups (for example in several captive bird species in Ricklefs et al., 2003), the Japanese quail (*Coturnix japonica*; Holmes et al., 2003) and those mentioned previously, but PrR values are lacking.

As is evident from Fig. 3, most studies enabling a PrR value to be calculated are from captivity, generally zoos. Apart from humans, the largest average PrR across all populations are from studies in captivity (Fig. 4). Environmental conditions in captivity have been found to alter the probability of observing a PRLS. For example, chimpanzees (*Pan troglodytes*) and other primate species have, in captive zoo environments, been shown to exhibit a PRLS, which was not evident when the same species was studied in the wild (Fig. 5; Thompson et al., 2007). This may be due to more favourable conditions in captivity, with *ad libitum* food, access to veterinary care and reduced predation enabling individuals to survive longer than they would in their natural environment thus increasing the likelihood of an individual reaching a PRLS (see Section Environmental artefact for further discussion of this). Interestingly, the duration of reproductive life in males is extended in captivity in tandem with increased longevity, whereas that of females is not (Ricklefs et al., 2003), illustrating the sex difference in time limitation. In humans, where most data occur, despite male fertility declining with age there is no convincing evidence of an upper limit to the age at which men are fertile. The oldest age at which paternity is reported to have been verified in men (by DNA testing) is 65.4 years (Kaufman et al., 2019), though unverified paternity has been reported in much older men, up to 96 years. Sperm have been detected in the testes of men in their 90s, and the rarity of fatherhood in very old men seems to be related to general somatic ageing (Kaufman et al., 2019), involving changes in inclination and opportunity to breed. There is a decline in male gamete quality with age, albeit with considerable inter-individual variation, but importantly, no reproductive cliff-edge (Kaufman et al., 2019; Vinicius et al., 2014). In women on the other hand, there is a relatively narrow range in the age of onset of the menopause; this shows very little cross-population variation with females exhibiting an extremely low probability of remaining fertile into the fifth decade of life (Broekmans et al., 2009; Gavrilova et al., 2012; Shanley & Kirkwood, 2001). It is also the case that post-reproductive life stages in animals have only been reported in females as in humans (Gaulin, 1980), and the references listed below Fig. 3 support this. Thus, an age-dependent loss in reproductive function is steeper and more decoupled from somatic deterioration in females than in males (Fig. 6). Hypotheses to explain PRLS therefore also need to also account for the sex difference, but this has rarely been addressed.

We therefore centre our further discussion on the six species for which there is reasonably robust evidence of a significant PRLS: humans, killer whales, short-finned pilot whales, narwhals, Asian elephants, and beluga whales (although note the caveats mentioned above) often verified by ovarian tissue. All of these belong to the Class Mammalia. The four species of cetaceans are all members of the super family *Delphinoidea* and the data come from wild populations. The Asian elephant data are from a semi-captive, but relatively natural environment. We appreciate of course additional species could be included and that other species may yet be identified, but this seems the most rigorous approach at present.

Several hypotheses have been put forward to explain the occurrence of a PRLS (e.g. Cant & Johnstone, 2008; Gems, 2014; Hawkes et al., 1998; Moorad & Walling, 2017; Shanley et al., 2007; Williams, 1957). We consider the main hypotheses here; additional hypotheses are covered in several of the excellent reviews cited above. This includes the cancer-avoidance hypothesis, where reproductive cessation is seen as an adaptive anticancer mechanism (Thomas et al., 2019) and the mate-choice theory (Morton et al., 2013), where male preference for younger females, coupled with increased mutation accumulation with female age, is posited to lead to the non-adaptive evolution of a post-reproductive life stage. Below, we have divided the main hypotheses into those which consider the early cessation of fertility in itself to be adaptive and those which consider it non-adaptive, including those that posit that a PRLS is an outcome of much stronger selection for some other physiological or life history trait (Austad, 1994; Croft et al., 2015; Hawkes et al., 1998; Peccei, 2001b; Shanley et al., 2007; Williams, 1957). We stress that the selection pressures responsible for the emergence of a PRLS may be different from those that influence its duration.

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

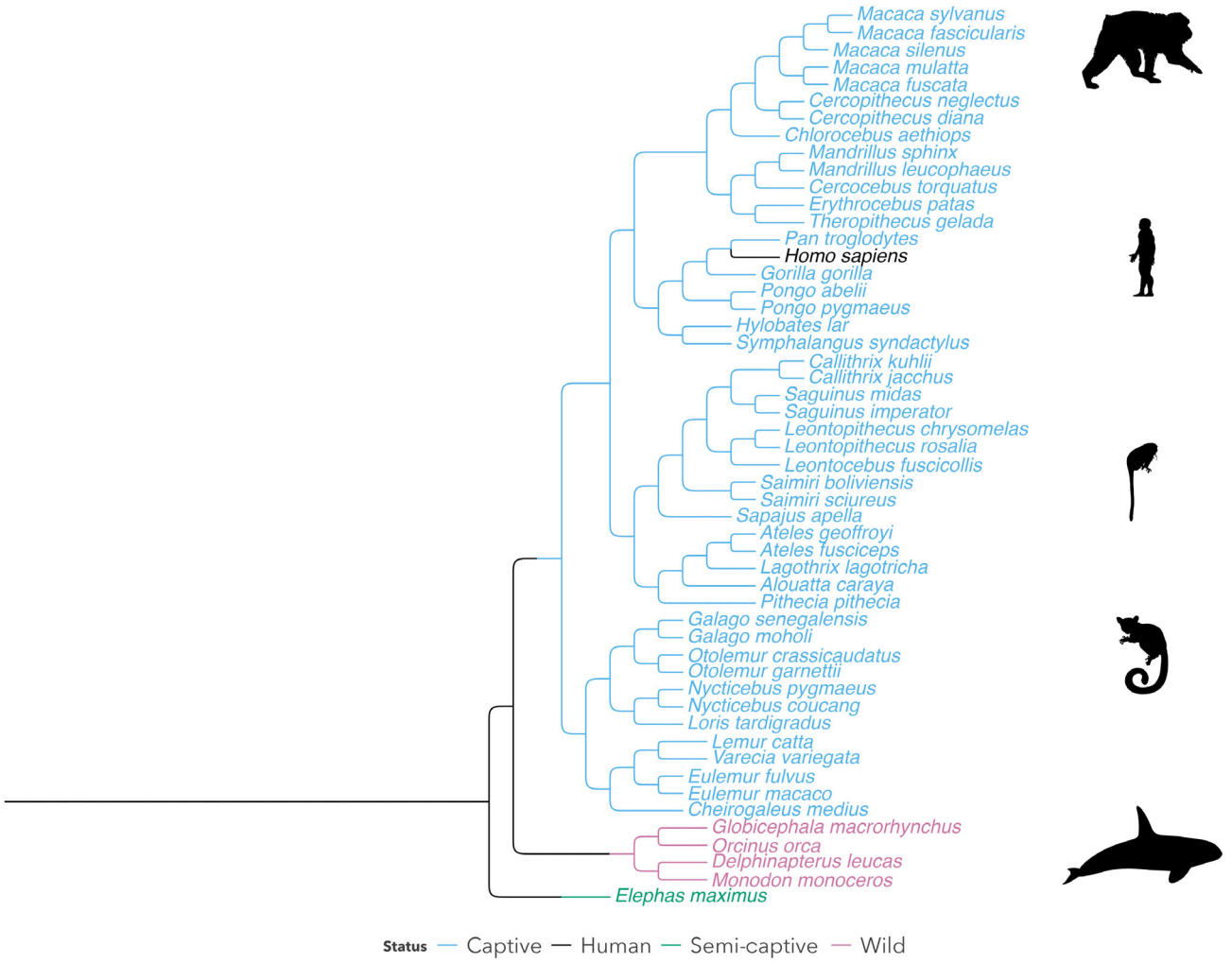

Figure 3 Phylogenetic tree of 52 species showing Post-reproductive Representation (PrR) values above 0.10 coloured by their captivity status (wild = Pink, semi-captive = Green, human = Black, and captive = Blue). Significant PrR values (discussed in the Appendix S1) are found in *Elephas maximus*, *Orcinus orca*, *Monodon monoceros*, *Delphinapterus leucas*, *Globicephala macrorhynchus*, and *Homo sapiens* (References: Alberts et al., 2013; Atwood et al., 2017; Auld, 2018; Austad, 1994; Chapman, Jackson, et al., 2019; Cohen, 2004; Croft et al., 2015; Ellis, Franks, Nattrass, Cant, et al., 2018; Ellis, Franks, Nattrass, Currie, et al., 2018; Finch & Holmes, 2010; Foote, 2008; Foster et al., 2012; Jervis et al., 1994; Kasuya et al., 1988; Kern et al., 2021; Klepsatel et al., 2013; Lahdenperä et al., 2014; Levitis et al., 2013; Levitis & Lackey, 2011; Nichols et al., 2016; Reznick et al., 2005; Uematsu et al., 2010); Walker & Herndon, 2008; Weadick & Sommer, 2016.

Adaptive hypotheses

PRLS is linked to an unusual combination of life history traits

The occurrence of a PRLS could be associated with an unusual combination of life history traits. The most obvious commonalities among the six cases are that they are all endothermic, viviparous, iteroparous, mammalian females with primarily female-based parental care at least in early post-natal life. These are traits of virtually all mammals, most of whom do not show a PRLS, and so in itself this combination is not particularly informative. Five of the six species have very large body sizes, four are aquatic and two are terrestrial, and all six are long-lived. Again, they are not 'special' in these respects. All have litters that usually comprise only one offspring, requiring intense and protracted parental care and relatively complex dispersal patterns and mating systems (Cohen, 2004; Croft et al., 2015; Ellis, Franks, Nattrass, Cant, et al., 2018; Ellis, Franks, Nattrass, Currie, et al. (2018); Finch & Holmes, 2010; Lemaître, Ronget, & Gaillard, 2020; Nichols et al., 2016). All six PRLS species show a substantial degree of parental care provided both during the pre-natal period and over a prolonged post-natal period, primarily due to the non-independence of offspring until near sexual maturity. However, extended parental care occurs in many mammalian species. Mammals are characterized by low frequencies of bi-parental care (Stockley & Hobson, 2016), with fathers contributing in

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

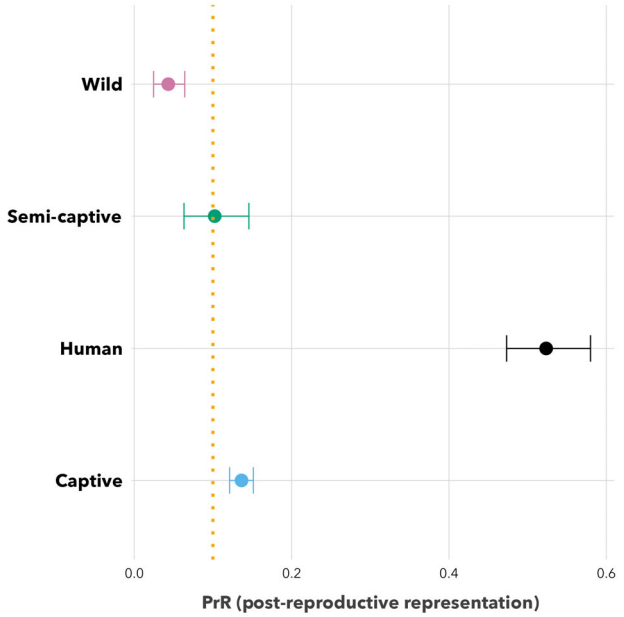

Figure 4 Average Post-reproductive Representation (PrR) in relation to captivity status. Points shown are means with 95% confidence intervals for all populations and coloured by their captivity status (wild = Pink, semi-captive = Green, human = Black, and captive = Blue). The dotted orange line denotes an PrR cut-off of 0.10, which represents populations where females spend 10% of life in a post-reproductive state. References are given below Fig. 3.

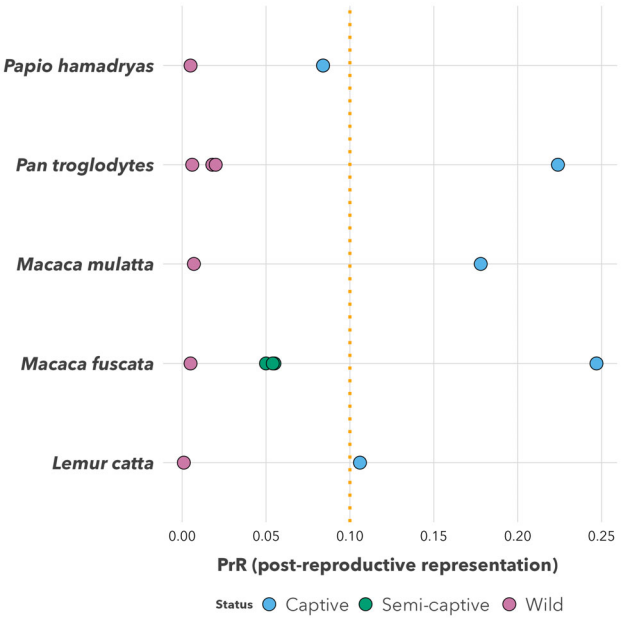

Figure 5 Post-reproductive Representation (PrR) for species where multiple values are available for different environments. Points are coloured by their captivity status (wild = Pink, semi-captive = Green, and captive = Blue). The dotted orange line denotes an PrR cut-off of 0.10, which represents populations where females spend 10% of life in a post-reproductive state. References are given below Fig. 3.

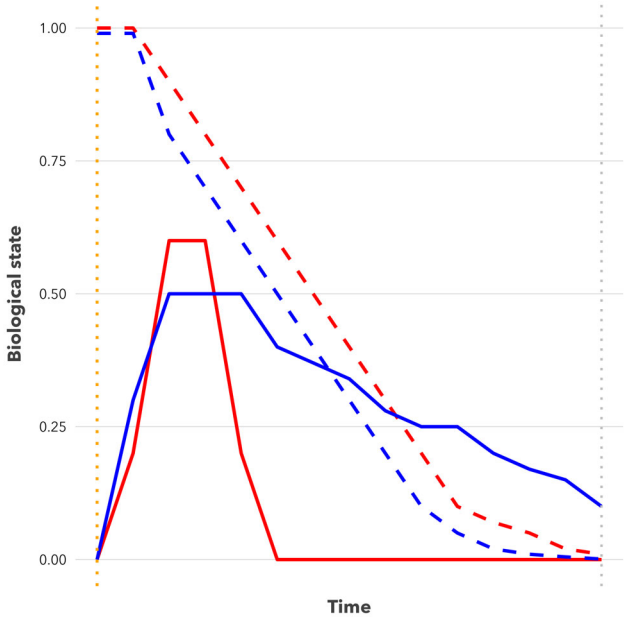

Figure 6 Schematic representation of the difference in the age-specific patterns of reproductive (solid line) and somatic (dashed line) function in males (blue) and females (red). Note that these lines are purely arbitrary and are meant to simply serve as a diagrammatic representation of hypothetical differences in male and female reproductive/somatic function.

just 10% of known mammalian genera. It is possible that a decline in the ability of females to provide an adequate level care to offspring later in life may be part of the picture for those mammals showing PRLS. Nonetheless, if this was the case, one would have expected evolution to adjust the scheduling of reproduction to increase investment earlier in life. However, all of the PRLS mammals usually give birth to only a single offspring at each reproductive event. Therefore, the high investment of females in each offspring might constrain their capacity to invest more in reproduction early in life since they cannot easily reduce the inter-birth interval or number of young per event. In addition, they have a prolonged gestation period (e.g. in humans this is ca 280 days, in elephants this ranges from 644 to 690 days and in killer whales and other cetaceans, this is ca 450 days; data from AnAge; De Magalhaes & Costa, 2009). This is in stark contrast to many other taxonomic groups where offspring number is higher per reproductive event (Werner & Griebeler, 2011) and gestation length appears shorter (Needham, 1930). Interestingly, parental care duration appears to scale with body mass, but relatively little information is available for the very large eutherian mammals (Thompson, 1987).

No convincing cases of a PRLS have yet been documented in birds despite detailed long-term studies (e.g. Richardson et al., 2007). Some of the same life history traits as observed in the PRLS mammals also occur in some bird species, such as long-lived seabirds, except for viviparity, large body size, and female-biased parental care. Bi-parental care is common in

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

birds (Cockburn, 2006) with between 80 and 90% of all bird species providing this form of care. However, while seabirds often lay only a single egg, and invest heavily during the prenatal incubation and nestling periods, intense parental care does not extend much beyond fledging. Maternal age effects operating on offspring pre-adult survival in wild birds have been found to differ from that of wild mammals, with the former showing an overall average effect that was positive and the latter exhibiting a negative effect of advancing maternal age (Ivimey-Cook & Moorad, 2020). However, birds in general do show overwhelming evidence of reproductive declines with age, manifesting in reduced egg quality and offspring number (Jones et al., 2014; Lemaître & Gaillard, 2017). A further factor is that, while seabirds are colonial breeders, they do not live in highly cohesive social groups in the same way as the PRLS mammals, which may be very important (see below and Section A speculative synthesis). However, some bird species, such as the vulturine guineafowl (*Acryllium vulturinium)* and the Seychelles warbler (*Acrocephalus sechellensis)*, do live in complex societies on a par with those of primates and in which intergenerational helping can occur, but PRLSs in such bird species have not been found (Richardson et al., 2007; Papageorgiou et al., 2019).

Dispersal patterns and mating systems

Kinship dynamics and the change in age-specific group relatedness have been suggested as important drivers of the evolution of a PRLS (Croft et al., 2015; Johnstone & Cant, 2010; Nichols et al., 2016, 2020), potentially favouring a social structure that promotes intergenerational helping rather than conflict. However, dispersal patterns differ markedly among the species that exhibit a demonstrable PRLS, and no obvious trend is apparent. Humans show female-biased dispersal, elephants show male-biased dispersal, whilst in the cetaceans, both males and females show limited dispersal (Nichols et al., 2016). However, it is interesting to note that those non-human species that exhibit a significant PRLS *in the wild* are those that show limited dispersal by both sexes coupled with extra-group mating and increased within-group relatedness with age (Croft et al., 2017; Johnstone & Cant, 2010). This is postulated to result in selection for reduced reproductive effort by older females of both whale and ape species (although the effects of intergenerational conflict in humans are potentially more pronounced in comparison to other primates; Croft et al., 2017). Although exceptions do exist, for instance, in another species of pilot whale (the long-finned pilot whale; *Globicephala melas*) which has a similar relatedness structure but an apparent lack of a PRLS. In this particular case (see Nichols et al., 2020), the authors note, in addition to several other potential reasons, that the average within-pod relatedness is generally lower than in other cetaceans that show a significant PRLS. This could suggest a threshold of relatedness that is required for the promotion of intergenerational helping or to trigger a plastic cessation of reproduction (Nichols et al., 2020). Furthermore, in many co-operatively breeding birds, there is also the potential for such intergenerational conflict but no evidence of a PRLS (although we note that relatedness in these species tends to decrease with age in contrast to the increase shown by many cetacean species that exhibit a PRLS; Dierkes et al., 2005; Riehl, 2013). Such a life stage in cooperatively breeding birds is yet to be found.

Complex social networks and behaviour

All six of the PRLS species live in stable social groups, involving overlapping generations, variable kin associations, individual recognition, strong networks, and social bonds. A complex social structure exists in other species including some other mammals, birds, and social insects in which no PRLS appears to occur. However, social complexity can require a high level of cognitive function. The 'social brain' hypothesis posits that the effect of the social environment on brain size is stronger than that of the physical environment and explains the very large degree of encephalisation seen in primates, cetaceans and hominids in particular (Dunbar & Shultz, 2007; Fox et al., 2017). Indeed, it has been suggested that a high Encephalization Quotient (EQ), the ratio between observed and expected brain mass (with values above 1 suggesting that the species has a larger brain than expected for its body size; Jerison, 1975), could be a prerequisite for determining whether individuals possess a PRLS (Dalton, 2022). The very high energetic costs associated with large brains may be very important in the development of a PRLS and we develop this idea further in Section A speculative synthesis.

Large body mass

The average body mass of females in the non-human species with a PRLS is in the region of 1500 kg (average adult weights calculated from Lemaître, Ronget, Tidière, et al., 2020; Ridgway et al., 2017). Human females have a substantially smaller average weight than the other five species (53.6 kg; Smith & Cheverud, 2002), yet the longest PRLS, and there are many other large-bodied mammals in which PRLS does not appear to occur. This suggests large body mass *per se* is not driving PRLS. Body size is linked, either directly or indirectly, with a variety of life history traits, including a positive relationship with gestation length, birth weight, and the duration of parental care, so it is difficult to tease traits apart (Sikes & Ylönen, 1998; Tuomi, 1980). Furthermore, in all six of the PRLS species, males are larger than females, yet PRLS is a female-only trait. It may be, however, that certain aspects of body size are particularly important. The six PRLS species identified here have an exceptionally large brain size for their taxonomic group in absolute and relative terms, and all belong to four of the five mammalian groups that a recent analysis of the evolution of mammalian brain size singled out as such (elephants, hominins, toothed whales, delphinids and great apes; Smaers et al., 2021). Note that one further suggestion, which is only applicable to the four cetacean species, is that these species live in oceans. Suspension in water was once thought to reduce the constraints on body size seen in terrestrial environments. This has been subsequently refuted, as there are thought to be number of constraints on body size that also apply to mammals in aquatic environments (Gearty et al., 2018).

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

With the exception of brain size, the life history traits listed above, either in themselves or in combination, are unlikely to drive PRLS evolution, since in all cases there are species exhibiting the trait(s) that do not possess a PRLS. Based on our present knowledge, closely related species with broadly similar life history traits can differ in whether they have a PRLS or not, as illustrated in Fig. 7. In all three closely related species pairs shown here, within which many life history traits are shared, the PRLS species have proportionally larger brains. The six species identified here as having a PRLS all have high EQs (*Homo sapiens*: 5.72; *Elephas maximus*: 1.46; *Orcinus orca*: 2.76; *Monodon monoceros*: 1.79; *Delphinapterus leucas*: 2.24; *Globicephalas macrorhynchus*: 3.01; EQs from Boddy et al., 2012, Montgomery et al., 2013, and Montgomery pers. comms.). This is based simply on overall brain size, and more information relating to which aspects of brain size might be most important could be illuminating. We return to this in Sections A speculative synthesis and Future research.

Mother effect

One of the most obvious and well-known hypotheses to explain the occurrence of a PRLS is the so-called 'Mother Effect' (Williams, 1957). One aspect of this hypothesis posits that, in species where the period of parental dependency is greater than the inter-birth interval, there will come a point where somatic senescence of the mother means that she cannot effectively care for offspring from more than one breeding event simultaneously. At this point, it then pays in fitness terms for the mother to divert resources to her own survival rather than engage in further reproduction. This is an intuitively attractive hypothesis. Nonetheless, where litter size cannot be reduced if only a single offspring is produced per event, extending the interbirth interval is likely to be a better option in fitness terms. A second aspect is based on an age-related increase in the risk of maternal death during parturition in viviparous species (Jasienska, 2020). In addition, somatic ageing can reduce the capacity of the older female to sustain the demands of pregnancy, thereby debilitating the female's capacity to provide adequate parental care for all her dependent offspring. Age-related sterility would prevent maternal death or debilitation, known in humans to be higher when women are older (Pavard et al., 2008; Restrepo-Méndez & Victora, 2014; Saccone et al., 2022; Shanley & Kirkwood, 2001). However, when individuals exist in social groups, death or poor health of the mother does not necessarily

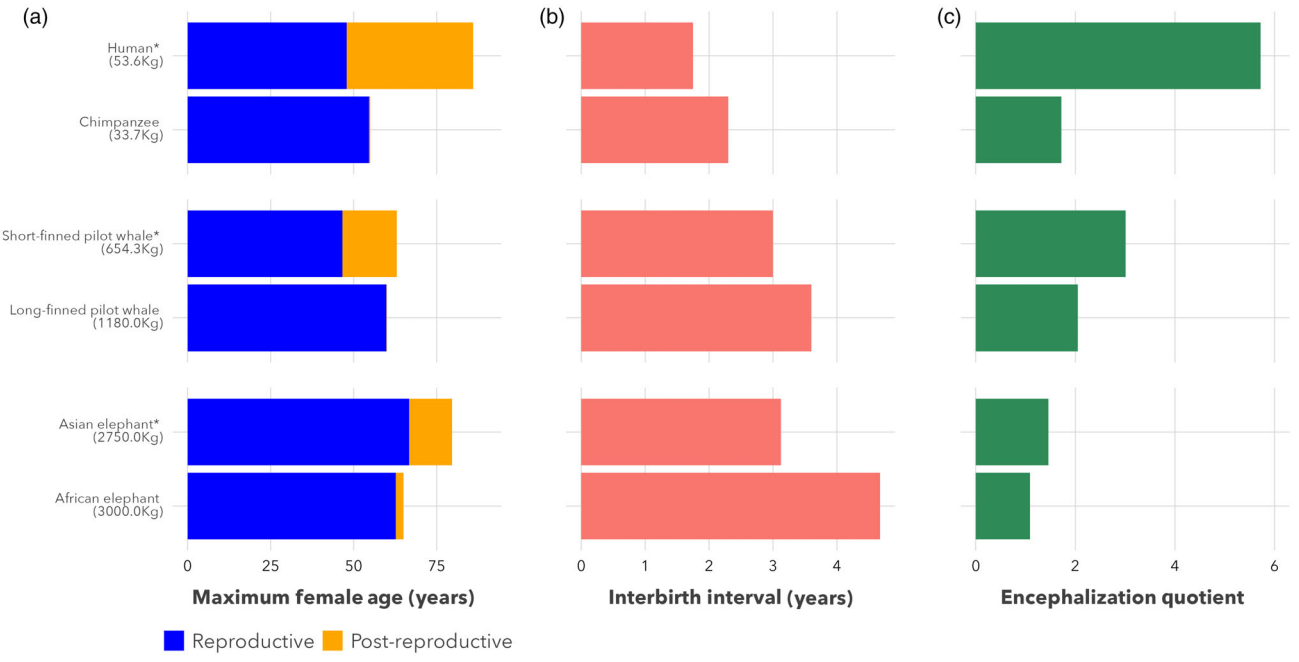

Figure 7 Comparisons of species in the same family with similar life histories, one of which has a demonstrable Post-reproductive Representation value (denoted by an asterisk). (a) Estimated proportion of female years lived in a reproductive (blue) and post-reproductive state (yellow) for populations of each species; the length of each bar reflects maximum female age. Values of maximum lifespan and proportions of lived years taken from Ellis, Franks, Nattrass, Cant, et al. (2018), Lahdenperä et al. (2014), and Chapman, Jackson, et al. (2019). Note that for humans, the PRLS displayed is the Hadza hunter-gatherers from Ellis, Franks, Nattrass, Cant, et al. (2018). (b) Length of interbirth interval in years. All values were obtained from AnAge (De Magalhaes & Costa, 2009) aside from the long-finned pilot whale, which was obtained from Verborgh et al. (2021). (c) Encephalization quotients (EQ). Values were taken from Montgomery et al. (2013) and Boddy et al. (2012). The value of EQ for short-finned pilot whales was obtained from Montgomery (pers. comms.). Also given (below each species name on the left side of the figure) are estimates of average female body mass taken from Lemaître, Ronget, and Gaillard (2020; for both species of elephant), Ridgway et al. (2017; for short- and long-finned pilot whales), and Smith and Cheverud (2002; for humans and chimpanzees).

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

influence survival of her dependent offspring to a large enough extent to favour complete reproductive cessation (Shanley & Kirkwood, 2001) and the mother hypothesis has limited support from empirical data both in humans and non-humans (Lahdenperä et al., 2011, 2016b; Rogers, 1993; although see Andersson et al., 1996), despite several theoretical models suggesting otherwise (Pavard et al., 2008; Shanley & Kirkwood, 2001). In humans, mortality risk is heavily dependent on offspring age, and rapidly decreases after weaning; other group and family members also help care for offspring, especially when the mother dies or is incapacitated (Lahdenperä et al., 2011; Sear & Mace, 2008). In non-human species, including some other primates, early maternal death can contribute to reduced offspring survival (Zipple et al., 2021). Recent research in populations of killer whales has suggested that survival of male offspring is increased when mothers are present, owing largely to maternal assistance during food acquisition and during potentially harmful encounters (Brent et al., 2015; Foster et al., 2012). Social structure is likely to play a role in determining the strength of any such effect.

A further consideration is whether effects via somatic ageing might also apply to fathers. Obviously, the risk of paternal death or ill health is not linked to pregnancy or birth. The absence of a father effect might be due to the sex bias in parental care provision in mammals (Kleiman & Malcolm, 1981; Stockley & Hobson, 2016). However, in the species in which a PRLS is observed, males do sometimes contribute to offspring survival (although often limited to temporary allocare, or babysitting, such as in male killer whales; Woodroffe & Vincent, 1994). In humans, there is usually significant paternal investment in providing resources and defence (Peccei, 2001a, 2001b) and as a result, paternal death can have an adverse effect on offspring survival (Kuhle, 2007). The importance of the father's presence for offspring survival has been demonstrated experimentally in other monogamous mammals (Gubernick & Nordby, 1992). Indeed, it has been further suggested that impaired parental performance in older women could be exacerbated by an 'absent father' effect due to an increased likelihood of the father having died or defected to a younger female (Kuhle, 2007). The fertility of men does decrease with age (Kaufman et al., 2019) and there is increased risk of mutations in sperm DNA being passed to offspring (Kong et al., 2012). It has been suggested that in order for paternal presence to be a major factor in the evolution of a PRLS in humans, the so-called 'market value' of an older woman as a marriage partner (Vinicius & Migliano, 2016) needs to already be substantially lower than that of an older man. However, this requires that age-related cessation of female fertility is already in place. There is therefore a clear need to investigate further why we do not see evidence of permanent sterility and an analogous version of the 'mother hypothesis' existing for paternal caregivers.

Grandmother effect

An essentially inclusive-fitness based hypothesis and one which has attracted a large amount of attention over the years, is the 'Grandmother Effect'. First suggested by Peter Medawar in 1952, this hypothesis is based on the fitness benefit of increasing the number of grand-offspring (Cant & Croft, 2019; Hawkes et al., 1998; Medawar, 1952). Extensive discussions of this hypothesis have been published (see Peccei, 2001b; Sear & Mace, 2008) with some studies suggesting that grandmothering has been a key component to extending human longevity (Chan et al., 2016; Kim et al., 2012, 2014). This idea requires a very particular form of social structure to work, with limited dispersal of kin, significant post-natal parental care, and the presence of overlapping generations in which intergenerational transfer of resources can occur (Davison & Gurven, 2022; Hooper et al., 2015; Kaplan & Robson, 2002). There are two interlinked grandmother hypotheses relating the evolution of sterility to the duration of the post-reproductive stage: (1) that because the fitness benefits of producing children decline with maternal age due to somatic ageing, the indirect fitness benefits of helping rear grandchildren eventually outweigh the direct fitness effects from producing 'own' children leading to the evolution of a sterile life stage that allows more resources to be devoted to grandchildren; (2) that while age-related sterility itself arises for other reasons, prolonged survival of post-reproductive females has been favoured because of the additional inclusive fitness gains from helping more grandchildren survive, given that continued reproduction is not possible. Both 1 and 2 require a protracted period of coexistence of grandparents and grandchildren, which it has been suggested might actually be a relatively recent occurrence. To examine the duration of the generational overlap, Chapman et al. (2017) used data from a Finnish population across the demographic transition, spanning a period of 170 years. Their data show that prior to industrialisation, this overlap was much less than it is now. They show that before the demographic transition, *ca* 75% of children had at least one grandmother alive when they were born, rising to 93.9% in the 1950s. For grandfathers, the comparable figure is 63.4 and 83%. The average number of years for which a grandchild has at least one grandmother alive was *ca* 5 years pre-transition, due to lower child survival and higher adult mortality; this changed with the demographic transition increasing to an average of 24 years by the 1950s. Furthermore, grandfathers were rarely present during the life of their grandchildren in later 18th century. This suggests that in humans, the observed beneficial effect of grandparents is a relatively recent phenomenon. But note that the very early post-natal years are the most important for child survival, and this would have been much more so in the past when infant mortality was high.

It is difficult to distinguish between the two grandmother hypotheses, since both make the prediction that the presence of grandmothers will be associated with higher grand-offspring survival. For the second hypothesis, we still need an explanation of why sterility occurs (see Section The cost of quality control: constraints on female fertility imposed by trade-offs between high quality oocytes and fertility duration). Several studies have found evidence that the presence of a grandparent does increase grand-offspring survival in several species that exhibit PRLSs, in humans (Engelhardt et al., 2019; Lahdenperä et al., 2004; Sear & Mace, 2008), Asian elephants (Lahdenperä et al., 2016a), and killer whales (Nattrass et al., 2019).

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Nonetheless, models of fitness effects suggest this form of intergenerational assistance is not sufficient to compensate for the fitness loss arising from cessation of reproduction (Hill & Hurtado, 1991; Pavard et al., 2008; Shanley & Kirkwood, 2001), which would favour the second hypothesis. Furthermore, intergenerational transfer of resources later in life need not involve late life sterility. Indeed in African lions, grandmothers can only help via lactation if they have a cub themselves (Packer et al., 1998). For a state of permanent sterility to evolve under the first hypothesis, continued reproduction in old age needs to carry substantial fitness costs (Davison & Gurven, 2022), such as those produced by intergenerational conflict between kin (see Section Avoidance of intergenerational competition (or the reproductive conflict hypothesis) below). Central to the grandmother hypothesis is that grandmothers gain more fitness benefits investing in grand-offspring while in a post-reproductive state in comparison with what they would be able to do *at the same age* had they continued to reproduce themselves. This is not supported in Asian elephants, where the grandmothers' reproductive status was found to have no impact on grand-calf survival, irrespective of grandmaternal age and did not reduce the benefits of grandparental care (Lahdenperä et al., 2016a). However, the effects in this study are somewhat blurred by the categorisation of grandmothers into only two broad age categories (young, 25.7–44.63 years and old = 44.64–79.00 years). Furthermore, the act of grandmothering is also present in a variety of species that do not possess a PRLS (e.g. in several mammals, including African lions (*Panthera leo*; Packer et al., 1998) and Olive baboons (*Papio anubis*; Packer et al., 1998) and in some birds (Richardson et al., 2007)).

We need also to explain why such intergenerational helping might apply only to females. In species with long-term pair bonds and/or non-dispersal of adults, surviving grandfathers will still be present in the group alongside the grandmother, though as mentioned above this might not have always been the case in humans. In practice, there is little empirical support for a significant grandfather effect (Lahdenperä et al., 2016b). In a philopatric society, it is possible that problems with paternity assurance are important here (Coall & Hertwig, 2010); grandfathers would be less likely to help rear their grandchildren, grandmothers more likely to help their daughters rear children than their sons, and maternal grandmothers would help more than paternal grandmothers. However, in a patriarchal society, daughters will have undergone dispersal prior to breeding and thus not be present in the same population as their parents. Sear and Mace (2008) found in humans that maternal grandmothers are only a little more likely than paternal grandmothers to help with rearing of grandchildren; in the statistically valid studies they evaluated, 64% of studies reported that presence of maternal grandmother improved child survival, with a similar figure of 60% of studies examining paternal grandmothers. Nichols et al. (2016) examined the duration of post-reproductive lifespans in relation to female and male philopatry using a phylogenetic approach with data from 26 mammalian species in the wild. They found a significant association between post-reproductive survival and male philopatry, but the data suggested that the former evolved first, followed by the latter. They also found that 50% of the species without male philopatry showed some evidence of survival post-reproduction. The authors concluded that post-reproductive survival in females is likely to have arisen from non-adaptive processes.

A further issue is the potentially confounding effect of mother and grandmother quality, which are likely to be highly correlated; high-quality females with high reproductive success and survival, thereby having a greater probability of living to become grandmothers, are likely to have similarly high-quality daughters who produce offspring that are more likely to survive. The experimental data needed to exclude this quality effect (removal of grandmothers to create unbiased control and experimental groups) are almost impossible to obtain, although in some cases, simultaneously estimating the genetic contribution of both grandmothers and mothers has been possible with sufficient high quality data (see Moorad & Walling, 2017). Here, in this case, the authors found no evidence of any genetic contributions, by grandmothers or mothers, on survival to age 16 in humans (Moorad & Walling, 2017).

Importantly, the core idea that a transition to a permanently sterile state increases the capacity of females to invest in grandchildren (and to some extent, their own already born children) is not supported by closer examination of what happens in the female menopause. The transition into this post-reproductive state is associated with accelerated somatic deterioration. Menopause in women brings with it multiple adverse effects on health related to hormonal changes, including reduced energy levels, sleeplessness, increased anxiety, reduced bone density, and other adverse effects that are all likely to decrease rather than increase the capacity for intergenerational helping (Monteleone et al., 2018; Peccei, 2001a; Whiteley et al., 2013). For certain age-related pathologies, such as cancer risk, transition to a non-reproductive state might be favourable as reproduction is known to exacerbate certain types of tumour growth, although more data are needed to confirm that age-related changes in such an effect would be strong enough (Thomas et al., 2019). In contrast, the detrimental effects of the female menopause on ageing are supported in recent work by Levine et al. (2016) who found that this age-related somatic deterioration was reflected in an acceleration of the DNA methylation clock in women following menopause, as measured from blood samples. In addition, this study also found some evidence that menopausal hormone therapy (oestrogen and progesterone hormone replacement) slows epigenetic ageing, while early surgical induction of menopause increases methylation levels, providing quasi-experimental evidence of the link between menopause and ageing rate. Interestingly, in a meta-analysis investigating the oxidative costs of reproduction in females across a range of homeothermic species, Blount et al. (2016) found that being in a reproductive state was associated with reduced oxidative damage compared with non-reproductive females. This led the authors to develop the idea that reproduction induces protective effects, which they termed 'reproductive shielding' of the mother and her offspring from oxidative damage. Experimental data from other species might help to provide further insight. It is also important to bear in mind that it is not just grandmothers that help in rear young in

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

complex social groups; this can involve other kin such as siblings, aunts and uncles; in some human societies most provisioning help actually comes from younger and unmarried males (Hill & Hurtado, 2009). Overall, the current body of evidence suggests that intergenerational helping is unlikely to have been a driver of the cessation of sterility, but inclusive fitness benefits might have then favoured extension of the post-reproductive period as in the second of the two hypotheses described at the start of this section.

Avoidance of intergenerational competition (or the reproductive conflict hypothesis)

This hypothesis is based on the inclusive fitness benefits of reducing within-group resource competition between generations in social species that experience age-related increases in group relatedness (Cant & Johnstone, 2008; Croft et al., 2015; Johnstone & Cant, 2010). The main premise of this hypothesis is that the cessation of reproduction in middle-aged females reduces the overlap in the timing of reproduction between mothers and their offspring (i.e. with her sons or daughters depending on the dispersal pattern). There is some evidence in support of this hypothesis from both human and cetacean populations (Cant & Johnstone, 2008; Croft et al., 2017; Lahdenperä et al., 2012). It is thought to be linked closely to dispersal patterns (female-biased in humans and limited dispersal by both sexes in killer whales and short-finned pilot whales) and the age-specific increase in relatedness in males and females. These costs and particular dispersal patterns are also suggested to act in concert with the potential benefits associated with (grand-)maternal care (Cant & Johnstone, 2008; Croft et al., 2017). It may be that these particular species show the greatest degree of generational overlap and therefore possess the largest opportunity for intergenerational conflict. In practice however, this is difficult to evaluate, as many species show overlapping generations without having a PRLS, with entire fields of research devoted to understanding how gene flow operates in populations with fluctuating age structure (Charlesworth, 1973; Charlesworth & Giesel, 1972). Furthermore, a similar argument pertains to fathers, which would favour the avoidance of competition between the father's own offspring and those of his sons or daughters.

Reduced quality of later-life offspring

In considering the fitness costs of cessation of reproduction in later life, no account is generally taken of the fact that offspring produced by older parents can be of poorer quality and have reduced lifespan (termed the Lansing effect) and reproductive value (Comfort, 1953; Ivimey-Cook et al., 2023; Lansing, 1947; Monaghan et al., 2020; Monaghan & Metcalfe, 2019). A recent meta-analysis by Ivimey-Cook et al. (2023) found that there was an average reduction in offspring lifespan of 17–22% per unit increase in maternal age, across 15 species (however note that the effect sizes were dominated by laboratory invertebrates). Whilst we lack an evolutionary model to explain the Lansing effect (Ivimey-Cook et al., 2023), substantial reduction in offspring quality with maternal age could be sufficient in some circumstances to favour a cessation in reproduction by mothers. However, such a reduction in offspring longevity might drive a shift towards more investment in earlier reproduction (Kroeger et al., 2020; Monaghan et al., 2020). The extent to which this can occur will be limited in species where other factors delay maturation and/or where only single offspring with long periods of dependency is produced per breeding event. In addition, there is also no reason for Lansing effects to be confined to mothers as paternal age is also associated with a variety of negative outcomes for offspring (Fay et al., 2016; Ivimey-Cook et al., 2023; Vuarin et al., 2021). We currently lack a detailed comparative analysis of a paternal Lansing effect.

On balance, based on current information, none of the above adaptive hypotheses are likely to provide a sufficient benefit to offset the fitness disadvantage of becoming non-reproductive for a substantial part of adult life. All five processes could act in concert, and indeed might do so in human populations and other species with a significant PRLS (for instance in killer whales and the other cetaceans where costs of intergenerational conflict and grand-(maternal care) benefits are closely linked; see Cant & Johnstone, 2008; Croft et al., 2017). While this link might also occur in other species without a PRLS, evidence is lacking. Nor do any of these theories provide a convincing explanation of why a post-reproductive life stage should occur in females but not males, nor why it should be confined to mammals. We therefore need to examine what factors might constrain the duration of female fertility in some species, uncoupling it from age-related survival.

Non-adaptive hypotheses

An alternative suite of theories provides a different approach. Age-related sterility could simply be an artefact that emerges under atypical environmental conditions or an unavoidable outcome of a trade-off that favours another trait under stronger selection due to the higher fitness benefits it confers. There are a number of different hypotheses as to why this might occur.

Environmental artefact

This hypothesis posits that a PRLS arises as a consequence of an 'unnatural' lifespan extension in benign environments due to protection from food shortage, disease, and predation in advanced human civilisations or animals in captivity. Often termed the 'extended lifespan hypothesis' and typically applied to describe the occurrence of menopause in human populations, the suggestion is that the female reproductive system cannot change in tandem with the rapid extension of lifespan resulting from modern access to medicine and other lifestyle improvements (Austad, 1994; Corbett et al., 2018). The existence of a post-reproductive life stage in human females might therefore be because they now live 'beyond their (reproductive) means'. However, historically, in non-industrial human societies the chances of living to the 6th decade for females who survive childhood appears to have been relatively high (Chapman, Pettay, et al., 2019), and full

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

reproductive cessation in females is seen in a diversity of historic and contemporary human societies (Vinicius et al., 2014). Furthermore, the timing and duration of menopause in humans seem to have a strong genetic component (Levine et al., 2016) and relatively little phenotypic plasticity, which does not support the suggestion that it is environmentally driven. Moreover, the duration of the fertile period in women appears to vary less than the age of its onset or end, and both the age of menarche and menopause show low variability across human populations (Gavrilova et al., 2012; Zhang et al., 2019). All of this suggests some inbuilt constraint in the female reproductive system that is absent in males. We need to understand where this constraint occurs and why it is phenotypically manifested as a PRLS in only a very few species.

As mentioned earlier, many species show evidence of a PRLS in captivity (Figs 3 and 4). As can be seen in Fig. 5, where the same species is observed both in the wild and in captivity, a much larger proportion of individuals reach a post-reproductive life stage in captivity. A comparison between wild and captive populations of chimpanzees (Atsalis & Videan, 2009) suggests that captive primates in particular experience an earlier depletion of ovarian stock and high oocyte loss due to earlier ages at menarche (7–8 years in captivity, 10–11 years in the wild) and shorter interbirth intervals (2–3 years in captivity, 5–6 years in the wild). This is coupled with a faster age-related decline in fertility reported in captive chimpanzee females, although data on wild populations are limited (Atsalis & Videan, 2009) Therefore, while captive females have increased longevity, they also experience an earlier onset of sexual maturity, faster fertility declines and an earlier age at last reproduction. Importantly, the reproductive window is not extended in captivity despite the lifespan extension. This suggests a finite reproductive resource that cannot be replenished regardless of the beneficial conditions of captivity.

Males exhibit a similar lifespan extension when kept in captivity in comparison to wild conditions (Tidière et al., 2016) and presumably also experience more human-managed breeding events but, as mentioned earlier, do not become sterile. Therefore, as other authors have also questioned (e.g. Reiber, 2010), we need also to ask why is it only the female reproductive period that is limited?

Female PRLS as a by-product of selection for male longevity

Often termed the 'Patriarch Hypothesis' (Marlowe, 2000), this suggests that the female post-reproductive life stage is a by-product of selection for longer life in males (see also Tuljapurkar et al., 2007). If the genes that increase lifespan in males are autosomal, and strongly selected for, this could also cause increased longevity in females. If, as Marlowe posits, there is no direct reproductive benefit associated with this increased lifespan for females, for example due to reproductive constraints, female inclusive fitness could then be enhanced to a degree by helping kin, either their own offspring or grand-offspring. For this to work, there must be a constraint on the duration of the female fertile period that nonetheless confers a sufficiently high fitness benefit to have been favoured by selection. We describe where this constraint is likely to come from in the next section. However, relationships with brain and body mass in catarrhine primates suggest that the lifespan of human females is predicted to be at least 20 years longer than the age of menopause (Judge & Carey, 2000). This suggests that the long lifespan of human females is an ancestral trait rather than a consequence of recent selection on males. This hypothesis also lacks an explanation for why female longevity is often far greater than that of males across mammalian and human populations (Colchero et al., 2016; Lemaître, Ronget, Tidière, et al., 2020; Marais et al., 2018). Furthermore, there is no reason given for the cessation of reproduction in females associated with this male increase in reproduction (Croft et al., 2015).

The cost of quality control: constraints on female fertility imposed by trade-offs between high quality oocytes and fertility duration

In sexually reproducing eukaryotic animals, most of the zygote cytoplasm, including key organelles such as the mitochondria, is derived from the female gamete. This maternal inheritance of mitochondria is thought to have arisen largely to preserve compatibility between the nuclear genome and the mitochondrial genome, since this concerted dual control by both genomes is essential to mitochondrial function (Lane, 2018). Eukaryote gametes are produced from primordial germ cells (PGCs) formed during embryogenesis. In most sexually reproducing species, gametogenesis can occur throughout adult life. In birds and mammals however, such continual production of gametes only occurs in males; in females, no new germ cells are formed after reaching a peak usually around half-way through embryonic development. In both sexes two meiotic divisions give rise to the haploid gametes. In males, gametogenesis is a tale of proliferation. Meiosis begins in males at puberty and occurs continuously in adult life in cells derived from the mitotically dividing PGC population. The two meiotic divisions produce symmetrical gametes and the four haploid cells resulting from each PGC are shaped into spermatogonia, with most of the cytoplasm being ejected. In contrast, in female birds and mammals, gametogenesis is triggered only at the embryonic stage and the number of oocytes is fixed very early in life. In females, PGCs first divide mitotically in the embryonic genital ridge, increasing substantially in number. Thereafter, female gametogenesis is a tale of loss on an astonishing scale. Significant germ cell death occurs prior to the onset of meiosis. A further substantial drop in number arises from the formation of so-called germ cell cysts in which groups of usually eight germ cells form cytoplasmic bridges through which macromolecules and organelles are transferred to a single germ cell destined to become a primary oocyte. The remaining seven cytoplasm-depleted cells become so-called 'nurse' cells and eventually die. This cytoplasmic pooling is thought to include a clearing out of defective or unsuitable organelles, especially mitochondria containing DNA

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

mutations that impair mitochondrial function or reduce compatibility with the nuclear genome (Melvin & Ballard, 2017). Modelling suggests that this may be the most important process that gives rise to the drop in oocyte number (Colnaghi et al., 2021), as a consequence of which, only one eighth of the germ cells in the ovary enter the first phase of meiosis. These are now termed 'oogonia' and are arrested at the first meiotic prophase, when recombination between the sister chromatids has occurred; the first meiotic division has not yet occurred and the oogonia are still diploid. These arrested cells are then enclosed by specialized ovarian somatic cells (pregranulosa cells) and become primordial follicles. This oogonia resting stage can last for decades in long-lived species, and these cells, held in a kind of suspended animation, outlive almost all other cells in the female body, leading a sheltered life until required. Groups of follicles are progressively reactivated when meiosis resumes at puberty. The meiotic divisions in oogenesis are asymmetrical; at each of the two meiotic divisions, one cell retains most of the cytoplasm and the other becomes a depleted polar body. Thus, only one haploid gamete is produced from the two meiotic divisions in females, in contrast to the four in males, again substantially reducing female gamete proliferation. Cell death is estimated to claim up to 99.9% of cells in the mammalian female germline, where most studies have taken place (Tilly, 2001). In humans around 1000 or so PGCs reach the embryonic ovary, increasing between the 2nd and 7th month of gestation to between 5 and 7 million, and then reducing to *ca* 1 million by birth. This loss is thought to ensure that only oocytes with sufficient levels of cytoplasm and cytoplasmic organelles are stored, and that these organelles are the best of the bunch. Loss continues relentlessly after birth. In humans, the number of oocytes drops at a more or less constant rate to around 400 000 by puberty and continues at a similar rate to around age 37–40 years, by which time follicle number has fallen to around 25 000. The rate of loss then increases and by the human menopause at *ca* age 51 years, only around 1000 remain (Faddy et al., 1992). Importantly, this loss is irreversible. In women, only a small number of oocytes (ca 400) are actually ovulated during the fertile period and it has been estimated that if the rate of loss not increase around age 37 years, women could remain fertile until their early 70s (Faddy et al., 1992). There is a mechanistic association between the onset of menopause in women and the much-reduced number of ovarian follicles (Broekmans et al., 2009). Support cells in the ovarian follicles secret various substances, such as Anti-Mullerian Hormone (AMH), which have a role in determining female fertility. As follicular number drops, the level of circulating AMH also drops. Once this reaches a critically low level, thought to be about 150 follicles in women (Finch, 2014; Finch & Holmes, 2010), the lack of AMH triggers the beginning of the menopausal process.

The huge loss of potential germ cells during oogenesis in female birds and mammals is neither random nor wasteful. It is part of a massive screening process that results in a supply of high-quality oogonia containing high-quality mitochondria. Both the size of the follicular pool and the rate of oocyte loss are strongly influenced by mitochondria (May-Panloup et al., 2016). There is what has been termed a 'mitochondrial bottleneck' in primordial oocytes, each of which contains only a small number of copies of mitochondrial DNA (mtDNA), estimated in humans at about 30–35 copies (Rebolledo-Jaramillo et al., 2014). Screening out mutated copies that might cause malfunction or mismatches with the nuclear DNA is thought to occur at this stage, and species with the smallest litters have the narrowest bottleneck and greatest cull of oocytes during development (Lane, 2018). Mature oocytes can have several hundred thousand mtDNA copies depending on the species, these being one of the most mitochondrial rich cell types in the body (Otten & Smeets, 2015). The enormous amount of mitochondrial biogenesis needed to achieve this level in the mature oocyte can lead to mtDNA replication errors (Colnaghi et al., 2021; Kauppila & Stewart, 2015; Lane, 2006) necessitating some further screening. During the long period of storage in the ovary, mutations can also accumulate in mtDNA in oocytes of older females (Arbeithuber et al., 2022) again resulting in discarding of some oocytes and failure of others to implant after fertilization. Techniques being developed during *In Vitro Fertilization* (IVF) in which the transfer of mitochondria from oocytes of younger women appears to rejuvenate aged oocytes and increase implantation success, further evidences the importance of mitochondria in oocyte ageing, but such techniques remain controversial for a variety of reasons (Otten & Smeets, 2015).

In most Eukaryotic organisms other than birds and mammals, females produce oocytes *de novo* throughout their adult life in much the same way as males, despite having the same requirement for high-quality mitochondria in the female gamete. What makes birds and mammals different? The answer may lie with endothermy. In birds and mammals, the mitochondria perform a highly demanding dual function, the production of both energy and heat, the latter being required even when the animal is at rest. They achieve this by having more, possibly five times as many, mitochondria per cell (Lane, 2018). Thus, the screening out of incompatible and defective mitochondria may be even more ruthless in these species and best done at the embryonic stage, but more research is needed to understand why this is so. Still, most avian and mammalian females do not have a PRLS. Where then does this leave us in understanding the existence of a PRLS in the few species where it does occur?

A speculative synthesis

What follows now is partly speculative but an explanation that we think warrants further investigation. Based on the current evidence, the most likely explanation of a PRLS is that this is a consequence of a coming-together of a suite of physiological and life history traits (see Fig. 8): (1) maternal inheritance of mitochondria, (2) an endothermic physiology coupled with an exceptionally large brain that is very energetically expensive to develop and maintain, which necessitates very stringent quality control of oocyte mitochondria and culling of oocytes with damaged or nuclear-incompatible mitochondria, (3) long adult life, which means that deterioration of oocyte mitochondria occurs during the long term storage in long-lived species with

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

no *de novo* oogenesis after birth, and (4) intense and protracted maternal investment in offspring during their long development time required for high level cognition, which limits plasticity in reproductive scheduling. What we have then is akin to an antagonistically pleiotropic effect; in order to provide offspring that grow and develop successfully and thrive in complex social environments, the number and shelf life of oocytes, and hence the duration of the female fertile period, is limited. Where the opportunity to achieve inclusive fitness benefits after the cessation of fertility exists, this gives rise to a protracted PRLS in females.

But why then do we not see a PRLS in some bird species to which many of the same arguments pertain? The apparent absence of a PRLS in birds might be because we lack data from relevant wild bird species, such as long-lived seabirds like albatrosses with their low reproductive rates or from highly social,

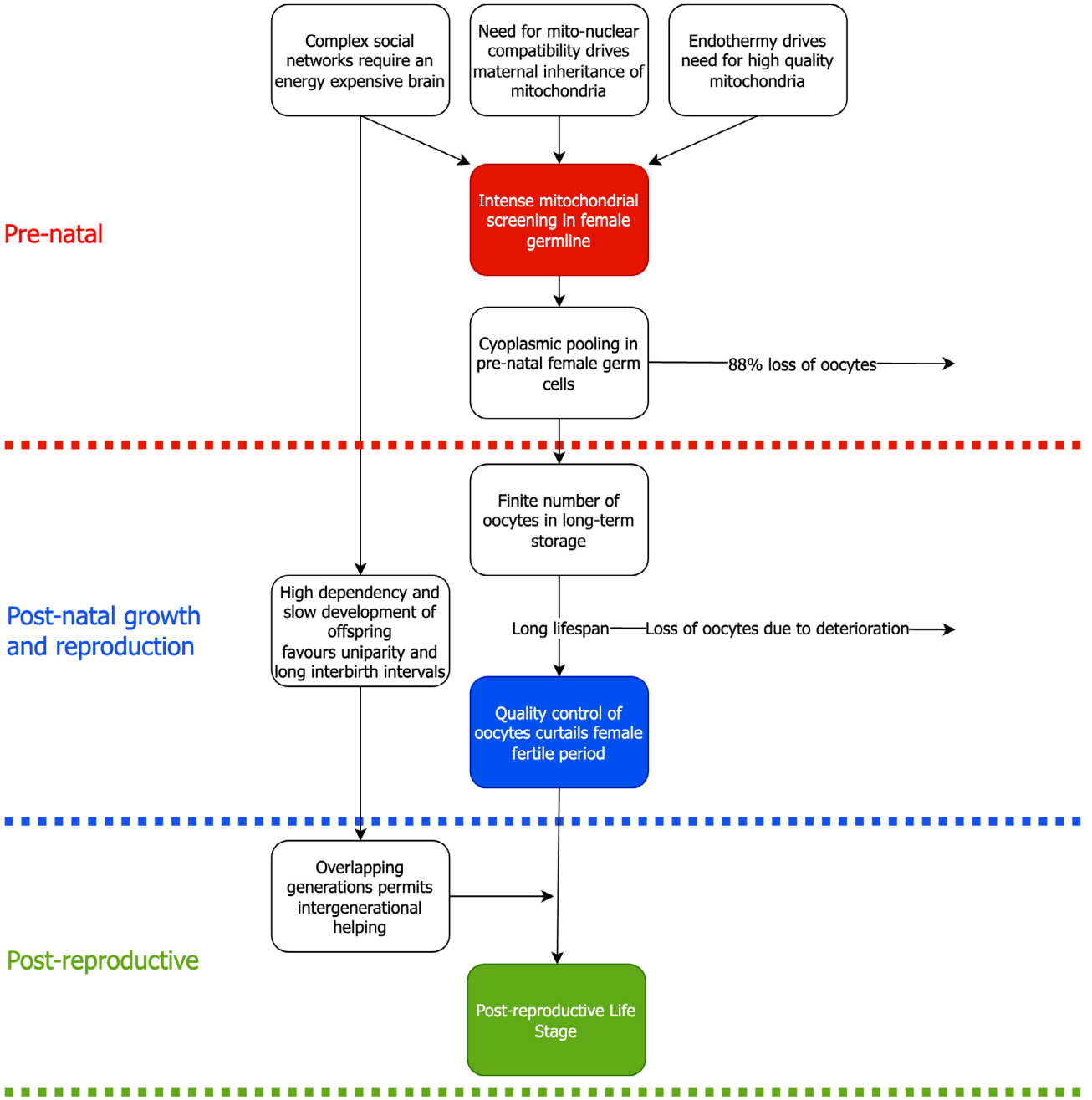

Figure 8 A diagrammatic representation of factors explaining the transition to female sterility and the evolution of a Post-reproductive Life Stage, as per the section, 'A speculative synthesis'. Flowchart diagram drawn using draw[dot]io.

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

co-operatively breeding species such as some corvids. Interestingly, dissection of 18 of the occasional 'dark-faced' puffins sometimes seen around breeding colonies was carried out during large puffin culls that took place in summer on the Faroe Islands; all 18 were old birds as indicated by the number of grooves on the bill, all were female, and all had regressed ovaries and oviducts (Birkhead, 2022). Whether such birds have permanently ceased reproduction or are skipping a breeding season and retaining their winter physiology is not known (see Birkhead, 2022). As mentioned earlier, some highly social birds do not appear to show a PRLS. More importantly however is that, while some birds, especially parrots and corvids, have a high level of cognitive power, both their brains and their body sizes are compressed in order to facilitate flight. The nidopallium of birds is functionally equivalent to the pre-frontal cortex of mammals but in songbirds and parrots has twice the number of neurons per gram compared with mammals (Güntürkün et al., 2021). Recent work has shown that avian neurones consume three times less glucose than mammalian neurons (von Eugen et al., 2022). This may mean that bird brains are much cheaper to run and that aspects of the mitochondrial screening programme are less stringent.

Future research

There remains much that we do not know about the occurrence, nature, and evolution of PRLSs. We have highlighted gaps in our knowledge throughout this review. However, the long-term studies necessary to fill these gaps are difficult to carry out in the wild, and some of the information needed requires invasive studies that are often incompatible with long-term individual-based field programmes. The work needed is very interdisciplinary, and collaborative ventures could be very promising. Below, we provide a by no means exhaustive list of potential avenues of research that could be addressed.

(1) More information is needed on the taxonomic spread of PRLS, since robust data remain largely confined to harvested or charismatic species, species in captivity and humans. We have, in this review, attempted to highlight species that exhibit significant PRLS based upon values of PrR. Data from a greater breadth of species would therefore be extremely valuable and extend our knowledge of PRLS beyond captive populations and the current handful of wild species. Species of special interest are those birds and mammals with exceptionally large brains and body sizes, long lifespans, and complex social networks. Co-operatively breeding corvids would be of particular interest, as would those mammals highlighted by Smaers et al. (2021) as having especially large brain sizes for their taxonomic group.

(2) Whilst several studies do exist that investigate the loss of ovarian function with age (for instance see Ellis, Franks, Nattrass, Currie, et al., 2018; Finch & Holmes, 2010), more research is needed to offer a more comparative view of follicular and reproductive loss across multiple taxonomic groups, and how this relates to mitochondrial state. However, much of the work investigating ovarian structure is cross-sectional, in part because obtaining ovarian tissue is very invasive and in order to gain insight, a sufficient number of samples are needed across a wide variety of ages. Advanced scanning techniques might help but it would be very difficult to employ these in the field, though technology is improving. More work could potentially be done on follicular reserves at the end of life in species that are long-lived, and which do or do not show a PRLS. Obtaining samples would inevitably be adventitious, but could be done in collaboration with veterinary practices, wildlife rescue operations, and zoos. In some cases, farmed animals might be used, for example ostriches or unusually long-lived species such as donkeys. More cross-species comparisons to examine how the supply of ovarian follicles scales with body size, brain size and lifespan would also be of great interest.

(3) Mitochondria are likely to play an important role in facilitating the evolution of PRLS. Most of the detailed data are from humans. Clearly an essential step would be to examine changes in mitochondrial functioning and mtDNA in oocytes with age in a variety of species.

(4) Further work to examine changes in mitochondrial functioning in male gametes would also be very interesting given their enormous proliferation. Changes in mitochondrial performance in sperm, while not inherited by their offspring, could be important for the maintenance or not of male fertility.

(5) The brain is a complex organ whose energetic costs are unlikely to be fully captured when just considering brain size. Simple measures of relative brain size, including encephalisation quotients, do not capture this complexity. Rather than using overall brain size in examining the link with PRLS, gametogenesis, energy requirements and mitochondrial screening, it would be worth examining whether particular brain structures are more relevant/expensive. Elephants for example, while they have a large cortex, appear to have a lower density of neurons than primates. They do however excel in long-term spatio-temporal and social memory and have a very large cerebellum (Hart et al. 2008). The study of the energetics of brain function is still in its infancy, and it might vary with brain structure and complexity. Estimates of the proportion of energy expenditure devoted to brain function could be very informative. More comparative work, including comparisons of species known from robust studies to be with and without PRLS, could be illuminating. For example, short- and long-finned pilot whales differ in body and brain size, and potentially also in key aspects of brain structure and energetic requirements. Obtaining good data on body and brain size is difficult and estimates in cetaceans in particular vary widely. Certain species (such as dolphins, which have very high EQs; Fox et al., 2017) could be examined in more detail.

(6) The pre- and post-natal development of a brain with high cognitive power may be very energetically expensive and underpin the slow maturation typical of the offspring of species that show a PRLS. More comparative work on brain energetics during development and the role of mitochondrial functionality in this context could be very revealing.

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(7) More work is needed to examine the cause of accelerated follicular loss in women over 37 years and whether this applies to other PRLS species.
(8) It remains unclear why female birds and mammals have no *de novo* oogenesis after birth, why embryonic determination of oocytes number is advantageous, and what changes in mitochondrial function in oocytes during storage occur in species with and without PRLS.

Acknowledgements

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (AdG Grant agreement No. 101020037). We thank Jean-Francois Lemaitre, Hazel Nichols, Jacob Moorad, and one anonymous reviewer for their invaluable comments on the manuscript. We also thank Steve Montgomery for his help in sourcing more information on cetacean encephalisation quotients.

References

Alberts, S. C., Altmann, J., Brockman, D. K., Cords, M., Fedigan, L. M., Pusey, A., Stoinski, T. S., Strier, K. B., Morris, W. F., & Bronikowski, A. M. (2013). Reproductive aging patterns in primates reveal that humans are distinct. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 13440–13445.

Andersson, T., Hogberg, U., & Åkerman, S. (1996). Survival of orphans in 19th century Sweden—The importance of remarriages. *Acta Paediatrica*, **85**, 981–985.

Arbeithuber, B., Cremona, M. A., Hester, J., Barrett, A., Higgins, B., Anthony, K., Chiaromonte, F., Diaz, F. J., & Makova, K. D. (2022). Advanced age increases frequencies of de novo mitochondrial mutations in macaque oocytes and somatic tissues. *Proceedings of the National Academy of Sciences of the United States of America*, **119**, e2118740119.

Atsalis, S., & Videan, E. (2009). Reproductive aging in captive and wild common chimpanzees: Factors influencing the rate of follicular depletion. *American Journal of Primatology*, **71**, 271–282.

Atwood, C. S., Hayashi, K., Meethal, S. V., Gonzales, T., & Bowen, R. L. (2017). Does the degree of endocrine dyscrasia post-reproduction dictate post-reproductive lifespan? Lessons from semelparous and iteroparous species. *GeroScience*, **39**, 103–116.

Auld, J. R. (2018). The effects of diet and mating system on reproductive (and post-reproductive) life span in a freshwater snail. *Ecology and Evolution*, **8**, 12260–12270.

Austad, S. N. (1994). Menopause: An evolutionary perspective. *Experimental Gerontology*, **29**, 255–263.

Birkhead, T. (2022). *Birds and Us: A 12,000-Year History from Cave Art to Conservation*. Princeton University Press.

Blount, J. D., Vitikainen, E. I. K., Stott, I., & Cant, M. A. (2016). Oxidative shielding and the cost of reproduction: Oxidative shielding and the cost of reproduction. *Biological Reviews*, **91**, 483–497.

Boddy, A. M., McGowen, M. R., Sherwood, C. C., Grossman, L. I., Goodman, M., & Wildman, D. E. (2012). Comparative analysis of encephalization in mammals reveals relaxed constraints on anthropoid primate and cetacean brain scaling. *Journal of Evolutionary Biology*, **25**, 981–994.

Brent, L. J. N., Franks, D. W., Foster, E. A., Balcomb, K. C., Cant, M. A., & Croft, D. P. (2015). Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Current Biology*, **25**, 746–750.

Broekmans, F. J., Soules, M. R., & Fauser, B. C. (2009). Ovarian aging: Mechanisms and clinical consequences. *Endocrine Reviews*, **30**, 465–493.

Bunce, A., Ward, S. J., & Norman, F. I. (2005). Are age-related variations in breeding performance greatest when food availability is limited? *Journal of Zoology*, **266**, 163–169.

Cant, M. A., & Croft, D. P. (2019). Life-history evolution: Grandmothering in space and time. *Current Biology*, **29**, R215–R218.

Cant, M. A., & Johnstone, R. A. (2008). Reproductive conflict and the separation of reproductive generations in humans. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 5332–5336.

Chan, M. H., Hawkes, K., & Kim, P. S. (2016). Evolution of longevity, age at last birth and sexual conflict with grandmothering. *Journal of Theoretical Biology*, **393**, 145–157.

Chapman, S. N., Jackson, J., Htut, W., Lummaa, V., & Lahdenperä, M. (2019). Asian elephants exhibit post-reproductive lifespans. *BMC Evolutionary Biology*, **19**, 193.

Chapman, S. N., Lahdenperä, M., Pettay, J. E., & Lummaa, V. (2017). Changes in length of grandparenthood in Finland 1790-1959. *The Finnish Yearbook of Population Research*, **52**, 3–13.

Chapman, S. N., Pettay, J. E., Lummaa, V., & Lahdenperä, M. (2019). Limits to fitness benefits of prolonged post-reproductive lifespan in women. *Current Biology*, **29**, 645–650.e3.

Charlesworth, B. (1973). Selection in populations with overlapping generations. V. Natural selection and life histories. *The American Naturalist*, **107**, 303–311.

Charlesworth, B., & Giesel, J. T. (1972). Selection in populations with overlapping generations. II. Relations between gene frequency and demographic variables. *The American Naturalist*, **106**, 388–401.

Coall, D. A., & Hertwig, R. (2010). Grandparental investment: Past, present, and future. *The Behavioral and Brain Sciences*, **33**, 1–19; discussion 19–40.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1375–1383.

Cohen, A. A. (2004). Female post-reproductive lifespan: A general mammalian trait. *Biological Reviews*, **79**, 733–750.

Colchero, F., Rau, R., Jones, O. R., Barthold, J. A., Conde, D. A., Lenart, A., Nemeth, L., Scheuerlein, A., Schoeley, J., Torres, C., Zarulli, V., Altmann, J., Brockman, D. K., Bronikowski, A. M., Fedigan, L. M., Pusey, A. E., Stoinski,

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

T. S., Strier, K. B., Baudisch, A., … Vaupel, J. W. (2016). The emergence of longevous populations. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, E7681–E7690.

Colnaghi, M., Pomiankowski, A., & Lane, N. (2021). The need for high-quality oocyte mitochondria at extreme ploidy dictates mammalian germline development. *eLife*, **10**, e69344.

Comfort, A. (1953). Absence of a Lansing effect in *Drosophila subobscura*. *Nature*, **172**, 83–84.

Corbett, S., Courtiol, A., Lummaa, V., Moorad, J., & Stearns, S. (2018). The transition to modernity and chronic disease: Mismatch and natural selection. *Nature Reviews. Genetics*, **19**, 419–430.

Croft, D. P., Brent, L. J. N., Franks, D. W., & Cant, M. A. (2015). The evolution of prolonged life after reproduction. *Trends in Ecology & Evolution*, **30**, 407–416.

Croft, D. P., Johnstone, R. A., Ellis, S., Nattrass, S., Franks, D. W., Brent, L. J. N., Mazzi, S., Balcomb, K. C., Ford, J. K. B., & Cant, M. A. (2017). Reproductive conflict and the evolution of menopause in killer whales. *Current Biology*, **27**, 298–304.

Dalton, D. (2022). How evolutionary biology can explain why human and a few marine mammal females are the only ones that are menopausal. *Journal of Theoretical Biology*, **543**, 111123.

Davison, R., & Gurven, M. (2022). The importance of elders: Extending Hamilton's force of selection to include intergenerational transfers. *Proceedings of the National Academy of Sciences of the United States of America*, **119**, e2200073119.

De Magalhaes, J. P., & Costa, J. (2009). A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology*, **22**, 1770–1774.

Dierkes, P., Heg, D., Taborsky, M., Skubic, E., & Achmann, R. (2005). Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. *Ecology Letters*, **8**, 968–975.

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, **317**, 1344–1347.

Ellis, S., Franks, D. W., Nattrass, S., Cant, M. A., Bradley, D. L., Giles, D., Balcomb, K. C., & Croft, D. P. (2018). Postreproductive lifespans are rare in mammals. *Ecology and Evolution*, **8**, 2482–2494.

Ellis, S., Franks, D. W., Nattrass, S., Currie, T. E., Cant, M. A., Giles, D., Balcomb, K. C., & Croft, D. P. (2018). Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. *Scientific Reports*, **8**, 12833.

Engelhardt, S. C., Bergeron, P., Gagnon, A., Dillon, L., & Pelletier, F. (2019). Using geographic distance as a potential proxy for help in the assessment of the grandmother hypothesis. *Current Biology*, **29**, 651–656.e3.

Faddy, M. J., Gosden, R. G., Gougeon, A., Richardson, S. J., & Nelson, J. F. (1992). Accelerated disappearance of ovarian follicles in mid-life: Implications for forecasting menopause. *Human Reproduction*, **7**, 1342–1346.

Fay, R., Barbraud, C., Delord, K., & Weimerskirch, H. (2016). Paternal but not maternal age influences early-life performance of offspring in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20152318.

Finch, C. E. (2014). The menopause and aging, a comparative perspective. *The Journal of Steroid Biochemistry and Molecular Biology*, **142**, 132–141.

Finch, C. E., & Holmes, D. J. (2010). Ovarian aging in developmental and evolutionary contexts: Finch & Holmes. *Annals of the New York Academy of Sciences*, **1204**, 82–94.

Foote, A. D. (2008). Mortality rate acceleration and post-reproductive lifespan in matrilineal whale species. *Biology Letters*, **4**, 189–191.

Foster, E. A., Franks, D. W., Mazzi, S., Darden, S. K., Balcomb, K. C., Ford, J. K. B., & Croft, D. P. (2012). Adaptive prolonged postreproductive life span in killer whales. *Science*, **337**, 1313.

Foster, W. A. (2010). Behavioural ecology: The menopausal aphid glue-bomb. *Current Biology*, **20**, R559–R560.

Fox, K. C. R., Muthukrishna, M., & Shultz, S. (2017). The social and cultural roots of whale and dolphin brains. *Nature Ecology and Evolution*, **1**, 1699–1705.

Gaulin, S. J. (1980). Sexual dimorphism in the human post-reproductive life-span: Possible causes. *Journal of Human Evolution*, **9**, 227–232.

Gavrilova, N. S., Gavrilov, L. A., Severin, F. F., & Skulachev, V. P. (2012). Testing predictions of the programmed and stochastic theories of aging: Comparison of variation in age at death, menopause, and sexual maturation. *Biochemistry*, **77**, 754–760.

Gearty, W., McClain, C. R., & Payne, J. L. (2018). Energetic tradeoffs control the size distribution of aquatic mammals. *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 4194–4199.

Gems, D. (2014). Evolution of sexually dimorphic longevity in humans. *Aging (Albany NY).*, **6**(2), 84–91. https://doi.org/10.18632/aging.100640

Gubernick, D. J., & Nordby, J. C. (1992). Parental influences on female puberty in the monogamous California mouse, *Peromyscus californicus*. *Animal Behaviour*, **44**, 259–267.

Güntürkün, O., von Eugen, K., Packheiser, J., & Pusch, R. (2021). Avian pallial circuits and cognition: A comparison to mammals. *Current Opinion in Neurobiology*, **71**, 29–36.

Hart, B. L., Hart, L. A., & Pinter-Wollman, N. (2008). Large brains and cognition: where do elephants fit in? *Neurosci Biobehav Rev.*, **32**(1), 86–98. https://doi.org/10.1016/j.neubiorev.2007.05.012

Hatchwell, B. J., Ross, D. J., Fowlie, M. K., & McGowan, A. (2001). Kin discrimination in cooperatively breeding long–tailed tits. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 885–890.

Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

evolution of human life histories. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 1336–1339.

Hill, K., & Hurtado, A. M. (1991). The evolution of premature reproductive senescence and menopause in human females. *Human Nature*, **2**, 313–350.

Hill, K., & Hurtado, A. M. (2009). Cooperative breeding in South American hunter–gatherers. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3863–3870.

Holmes, D. J., & Ottinger, M. A. (2003). Birds as long-lived animal models for the study of aging. *Experimental Gerontology*, **38**, 1365–1375.

Holmes, D. J., Thomson, S. L., Wu, J., & Ottinger, M. A. (2003). Reproductive aging in female birds. *Experimental Gerontology*, **38**, 751–756.

Hooper, P. L., Gurven, M., Winking, J., & Kaplan, H. S. (2015). Inclusive fitness and differential productivity across the life course determine intergenerational transfers in a small-scale human society. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20142808.

Ivimey-Cook, E., & Moorad, J. (2020). The diversity of maternal-age effects upon pre-adult survival across animal species. *Proceedings of the Royal Society B: Biological Sciences*, **287**, 20200972.

Ivimey-Cook, E. R., & Pick, J. (2023). shinyDigitise: Extract and Summarise Data from Published Figures. R package version 0.1.0.

Ivimey-Cook, E. R., Shorr, S., & Moorad, J. A. (2023). The distribution of the Lansing Effect across animal species. *Evolution*, **77**, 608–615.

Jasienska, G. (2020). Costs of reproduction and ageing in the human female. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, **375**, 20190615.

Jerison, H. J. (1975). Evolution of the brain and intelligence. *Current Anthropology*, **16**, 403–426.

Jervis, M. A., Kidd, N. A. C., & Almey, H. E. (1994). Post-reproductive life in the parasitoid Bracon hebetor (Say) (Hym., Braconidae). *Journal of Applied Entomology*, **117**, 72–77.

Johnstone, R. A., & Cant, M. A. (2010). The evolution of menopause in cetaceans and humans: The role of demography. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3765–3771.

Jones, O. R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C. G., Schaible, R., Casper, B. B., Dahlgren, J. P., Ehrlén, J., García, M. B., Menges, E. S., Quintana-Ascencio, P. F., Caswell, H., Baudisch, A., & Vaupel, J. W. (2014). Diversity of ageing across the tree of life. *Nature*, **505**, 169–173.

Judge, D. S., & Carey, J. R. (2000). Postreproductive life predicted by primate patterns. *The Journals of Gerontology: Series A*, **55**, B201–B209.

Kaplan, H. S., & Robson, A. J. (2002). The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 10221–10226.

Kasuya, T., Sergeant, D. E., & Tanaka, K. (1988). Re-examination of life history parameters of long-finned pilot whales in the Newfoundland waters. *The Scientific Reports of the Whales Research Institute*, **39**, 103–119.

Kaufman, J.-M., Lapauw, B., Mahmoud, A., T'Sjoen, G., & Huhtaniemi, I. T. (2019). Aging and the male reproductive system. *Endocrine Reviews*, **40**, 906–972.

Kauppila, J. H., & Stewart, J. B. (2015). Mitochondrial DNA: Radically free of free-radical driven mutations. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*, **1847**, 1354–1361.

Kenyon, C., Chang, J., Gensch, E., Rudner, A., & Tabtiang, R. (1993). A *C. elegans* mutant that lives twice as long as wild type. *Nature*, **366**, 461–464.

Kern, C. C., Townsend, S., Salzmann, A., Rendell, N. B., Taylor, G. W., Comisel, R. M., Foukas, L. C., Bähler, J., & Gems, D. (2021). *C. elegans* feed yolk to their young in a form of primitive lactation. *Nature Communications*, **12**, 5801.

Kim, P. S., Coxworth, J. E., & Hawkes, K. (2012). Increased longevity evolves from grandmothering. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4880–4884.

Kim, P. S., McQueen, J. S., Coxworth, J. E., & Hawkes, K. (2014). Grandmothering drives the evolution of longevity in a probabilistic model. *Journal of Theoretical Biology*, **353**, 84–94.

Kleiman, D. G., & Malcolm, J. R. (1981). The evolution of male parental investment in mammals. In D. J. Gubernick & P. H. Klopfer (Eds.), *Parental care in mammals* (pp. 347–387). Springer.

Klepsatel, P., Gáliková, M., De Maio, N., Ricci, S., Schlötterer, C., & Flatt, T. (2013). Reproductive and post-reproductive life history of wild-caught *Drosophila melanogaster* under laboratory conditions. *Journal of Evolutionary Biology*, **26**, 1508–1520.

Kong, A., Frigge, M. L., Masson, G., Besenbacher, S., Sulem, P., Magnusson, G., Gudjonsson, S. A., Sigurdsson, A., Jonasdottir, A., Jonasdottir, A., Wong, W. S. W., Sigurdsson, G., Walters, G. B., Steinberg, S., Helgason, H., Thorleifsson, G., Gudbjartsson, D. F., Helgason, A., Magnusson, O. T., . . . Stefansson, K. (2012). Rate of de novo mutations and the importance of father's age to disease risk. *Nature*, **488**, 471–475.

Kroeger, S. B., Blumstein, D. T., Armitage, K. B., Reid, J. M., & Martin, J. G. (2020). Older mothers produce more successful daughters. *Proceedings of the National Academy of Sciences of the United States of America*, **117**, 4809–4814.

Kuhle, B. X. (2007). An evolutionary perspective on the origin and ontogeny of menopause. *Maturitas*, **57**, 329–337.

Kuo, T.-H., Yew, J. Y., Fedina, T. Y., Dreisewerd, K., Dierick, H. A., & Pletcher, S. D. (2012). Aging modulates cuticular hydrocarbons and sexual attractiveness in *Drosophila melanogaster*. *Journal of Experimental Biology*, **215**, 814–821.

Lahdenperä, M., Gillespie, D. O. S., Lummaa, V., & Russell, A. F. (2012). Severe intergenerational reproductive conflict and the evolution of menopause. *Ecology Letters*, **15**, 1283–1290.

Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M., & Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature*, **428**, 178–181.

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Lahdenperä, M., Mar, K. U., & Lummaa, V. (2014). Reproductive cessation and post-reproductive lifespan in Asian elephants and pre-industrial humans. *Frontiers in Zoology*, **11**, 54.

Lahdenperä, M., Mar, K. U., & Lummaa, V. (2016a). Nearby grandmother enhances calf survival and reproduction in Asian elephants. *Scientific Reports*, **6**, 27213.

Lahdenperä, M., Mar, K. U., & Lummaa, V. (2016b). Short-term and delayed effects of mother death on calf mortality in Asian elephants. *Behavioral Ecology*, **27**, 166–174.

Lahdenperä, M., Russell, A. F., Tremblay, M., & Lummaa, V. (2011). Selection on menopause in two premodern human populations: No evidence for the mother hypothesis. *Evolution*, **65**, 476–489.

Lane, N. (2006). *Power, sex, suicide: Mitochondria and the meaning of life*. Oxford University Press.

Lane, N. (2018). Hot mitochondria? *PLoS Biology*, **16**, e2005113.

Lansing, A. I. (1947). A transmissible, cumulative, and reversible factor in aging. *Journal of Gerontology*, **2**, 228–239.

Lemaître, J.-F., & Gaillard, J.-M. (2017). Reproductive senescence: New perspectives in the wild: Reproductive senescence in the wild. *Biological Reviews*, **92**, 2182–2199.

Lemaître, J.-F., Ronget, V., & Gaillard, J.-M. (2020). Female reproductive senescence across mammals: A high diversity of patterns modulated by life history and mating traits. *Mechanisms of Ageing and Development*, **192**, 111377.

Lemaître, J.-F., Ronget, V., Tidière, M., Allainé, D., Berger, V., Cohas, A., Colchero, F., Conde, D. A., Garratt, M., Liker, A., Marais, G. A. B., Scheuerlein, A., Székely, T., & Gaillard, J. M. (2020). Sex differences in adult lifespan and aging rates of mortality across wild mammals. *PNAS*, **117**, 8546–8553.

Levine, M. E., Lu, A. T., Chen, B. H., Hernandez, D. G., Singleton, A. B., Ferrucci, L., Bandinelli, S., Salfati, E., Manson, J. A. E., Quach, A., Kusters, C. D. J., Kuh, D., Wong, A., Teschendorff, A. E., Widschwendter, M., Ritz, B. R., Absher, D., Assimes, T. L., & Horvath, S. (2016). Menopause accelerates biological aging. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 9327–9332.

Levitis, D. A., Burger, O., & Lackey, L. B. (2013). The human post-fertile lifespan in comparative evolutionary context: The human post-fertile lifespan. *Evolutionary Anthropology*, **22**, 66–79.

Levitis, D. A., & Lackey, L. B. (2011). A measure for describing and comparing postreproductive life span as a population trait: Measuring postreproductive life span. *Methods in Ecology and Evolution*, **2**, 446–453.

Lim, A. S. T., & Tsakok, M. F. H. (1997). Age-related decline in fertility: A link to degenerative oocytes? *Fertility and Sterility*, **68**, 265–271.

Marais, G. A. B., Gaillard, J.-M., Vieira, C., Plotton, I., Sanlaville, D., Gueyffier, F., & Lemaitre, J. F. (2018). Sex gap in aging and longevity: Can sex chromosomes play a role? *Biology of Sex Differences*, **9**, 33.

Marlowe, F. (2000). The patriarch hypothesis: An alternative explanation of menopause. *Human Nature*, **11**, 27–42.

Maures, T. J., Booth, L. N., Benayoun, B. A., Izrayelit, Y., Schroeder, F. C., & Brunet, A. (2014). Males shorten the lifespan of *C. elegans* hermaphrodites via secreted compounds. *Science*, **343**, 541–544.

May-Panloup, P., Boucret, L., Chao de la Barca, J.-M., Desquiret-Dumas, V., Ferré-L'Hotellier, V., Morinière, C., Descamps, P., Procaccio, V., & Reynier, P. (2016). Ovarian ageing: The role of mitochondria in oocytes and follicles. *Human Reproduction Update*, **22**, 725–743.

Medawar, P. B. (1952). *An unsolved problem of biology*. H.K. Lewis and Company.

Melvin, R. G., & Ballard, J. W. O. (2017). Cellular and population level processes influence the rate, accumulation and observed frequency of inherited and somatic mtDNA mutations. *Mutagenesis*, **32**, 323–334.

Mendenhall, A. R., Wu, D., Park, S. K., Cypser, J. R., Tedesco, P. M., Link, C. D., Phillips, P. C., & Johnson, T. E. (2011). Genetic dissection of late-life fertility in Caenorhabditis elegans. *Journals of Gerontology Series A: Biomedical Sciences and Medical Sciences*, **66**(8), 842–854.

Monaghan, P., Maklakov, A. A., & Metcalfe, N. B. (2020). Intergenerational transfer of ageing: Parental age and offspring lifespan. *Trends in Ecology & Evolution*, **35**, 927–937.

Monaghan, P., & Metcalfe, N. B. (2019). The deteriorating soma and the indispensable germline: Gamete senescence and offspring fitness. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 20192187.

Monteleone, P., Mascagni, G., Giannini, A., Genazzani, A. R., & Simoncini, T. (2018). Symptoms of menopause—Global prevalence, physiology and implications. *Nature Reviews Endocrinology*, **14**, 199–215.

Montgomery, S. H., Geisler, J. H., McGowen, M. R., Fox, C., Marino, L., & Gatesy, J. (2013). The evolutionary history of cetacean brain and body size. *Evolution*, **67**, 3339–3353.

Moorad, J. A., & Walling, C. A. (2017). Measuring selection for genes that promote long life in a historical human population. *Nature Ecology and Evolution*, **1**, 1773–1781.

Morton, R. A., Stone, J. R., & Singh, R. S. (2013). Mate choice and the origin of menopause. *PLoS Computational Biology*, **9**, e1003092.

Nattrass, S., Croft, D. P., Ellis, S., Cant, M. A., Weiss, M. N., Wright, B. M., Stredulinsky, E., Doniol-Valcroze, T., Ford, J. K. B., Balcomb, K. C., & Franks, D. W. (2019). Postreproductive killer whale grandmothers improve the survival of their grandoffspring. *Proceedings of the National Academy of Sciences of the United States of America*, **116**, 26669–26673.

Needham, J. (1930). On incubation-time and gestation-time. *Science Progress in the Twentieth Century (1919-1933)*, **25**, 251–263.

Nichols, H. J., Arbuckle, K., Fullard, K., & Amos, W. (2020). Why don't long-finned pilot whales have a widespread postreproductive lifespan? Insights from genetic data. *Behavioral Ecology*, **31**, 508–518.

Nichols, H. J., Zecherle, L., & Arbuckle, K. (2016). Patterns of philopatry and longevity contribute to the evolution of post-

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

reproductive lifespan in mammals. *Biology Letters*, **12**, 20150992.

Olejarz, J. W., Allen, B., Veller, C., & Nowak, M. A. (2015). The evolution of non-reproductive workers in insect colonies with haplodiploid genetics. *eLife*, **4**, e08918.

Otten, A. B. C., & Smeets, H. J. M. (2015). Evolutionary defined role of the mitochondrial DNA in fertility, disease and ageing. *Human Reproduction Update*, **21**, 671–689.

Packer, C., Tatar, M., & Collins, A. (1998). Reproductive cessation in female mammals. *Nature*, **392**, 807–811.

Papageorgiou, D., Christensen, C., Gall, G. E., Klarevas-Irby, J. A., Nyaguthii, B., Couzin, I. D., & Farine, D. R. (2019). The multilevel society of a small-brained bird. *Current Biology*, **29** (21), R1120–R1121.

Pavard, S., E Metcalf, C. J., & Heyer, E. (2008). Senescence of reproduction may explain adaptive menopause in humans: A test of the "mother" hypothesis. *American Journal of Physical Anthropology*, **136**, 194–203.

Peccei, J. S. (2001a). A critique of the grandmother hypotheses: Old and new. *American Journal of Human Biology*, **13**, 434–452.

Peccei, J. S. (2001b). Menopause: Adaptation or epiphenomenon? *Evolutionary Anthropology: Issues, News, and Reviews*, **10**, 43–57.

Péron, G., Bonenfant, C., Lemaitre, J.-F., Ronget, V., Tidiere, M., & Gaillard, J.-M. (2019). Does grandparental care select for a longer lifespan in non-human mammals? *Biological Journal of the Linnean Society*, **128**, blz078.

Photopoulou, T., Ferreira, I. M., Best, P. B., Kasuya, T., & Marsh, H. (2017). Evidence for a postreproductive phase in female false killer whales *Pseudorca crassidens*. *Frontiers in Zoology*, **14**, 30.

Pick, J. L., Nakagawa, S., & Noble, D. W. (2019). Reproducible, flexible and high-throughput data extraction from primary literature: The metaDigitise r package. *Methods in Ecology and Evolution*, **10**(3), 426–431.

Rauset, G. R., Low, M., & Persson, J. (2015). Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology*, **96**, 3153–3164.

Rebolledo-Jaramillo, B., Su, M. S.-W., Stoler, N., McElhoe, J. A., Dickins, B., Blankenberg, D., Korneliussen, T. S., Chiaromonte, F., Nielsen, R., Holland, M. M., Paul, I. M., Nekrutenko, A., & Makova, K. D. (2014). Maternal age effect and severe germ-line bottleneck in the inheritance of human mitochondrial DNA. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 15474–15479.

Reiber, C. (2010). Female gamete competition: A new evolutionary perspective on menopause. *Journal of Social, Evolutionary, and Cultural Psychology*, **4**, 215.

Restrepo-Méndez, M. C., & Victora, C. G. (2014). Maternal mortality by age: Who is most at risk? *The Lancet Global Health*, **2**, e120–e121.

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

Richardson, D. S., Burke, T., & Komdeur, J. (2007). Grandparent helpers: The adaptive significance of older, postdominant helpers in the Seychelles warbler. *Evolution*, **61**, 2790–2800.

Ricklefs, R. E., Scheuerlein, A., & Cohen, A. (2003). Age-related patterns of fertility in captive populations of birds and mammals. *Experimental Gerontology*, **38**, 741–745.

Ridgway, S. H., Carlin, K. P., Van Alstyne, K. R., Hanson, A. C., & Tarpley, R. J. (2017). Comparison of dolphins' body and brain measurements with four other groups of cetaceans reveals great diversity. *Brain, Behavior and Evolution*, **88**, 235–257.

Riehl, C. (2013). Evolutionary routes to non-kin cooperative breeding in birds. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20132245.

Rogers, A. R. (1993). Why menopause? *Evolutionary Ecology*, **7**, 406–420.

Saccone, G., Gragnano, E., Ilardi, B., Marrone, V., Strina, I., Venturella, R., Berghella, V., & Zullo, F. (2022). Maternal and perinatal complications according to maternal age: A systematic review and meta-analysis. *International Journal of Gynecology & Obstetrics*, **159**, 43–55.

Scharf, A., Pohl, F., Egan, B. M., Kocsisova, Z., & Kornfeld, K. (2021). Reproductive aging in *Caenorhabditis elegans*: From molecules to ecology. *Frontiers in Cell and Development Biology*, **9**, 718522.

Schmidt, B. C., & Freina, J. J. D. (2011). Generic placement of the neotropical species of "Phragmatobia" (Erebidae, Arctiinae), with a remarkable matrivorous species from the Peruvian Andes. *ZooKeys*, **149**, 69–88.

Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, **29**, 1–18.

Shanley, D. P., & Kirkwood, T. B. L. (2001). Evolution of the human menopause. *BioEssays*, **23**, 282–287.

Shanley, D. P., Sear, R., Mace, R., & Kirkwood, T. B. L. (2007). Testing evolutionary theories of menopause. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2943–2949.

Sikes, R. S., & Ylönen, H. (1998). Considerations of optimal litter size in mammals. *Oikos*, **83**, 452–465.

Smaers, J. B., Rothman, R. S., Hudson, D. R., Balanoff, A. M., Beatty, B., Dechmann, D. K. N., de Vries, D., Dunn, J. C., Fleagle, J. G., Gilbert, C. C., Goswami, A., Iwaniuk, A. N., Jungers, W. L., Kerney, M., Ksepka, D. T., Manger, P. R., Mongle, C. S., Rohlf, F. J., Smith, N. A., … Safi, K. (2021). The evolution of mammalian brain size. *Science Advances*, **7**, eabe2101.

Smith, R. J., & Cheverud, J. M. (2002). Scaling of sexual dimorphism in body mass: A phylogenetic analysis of Rensch's rule in primates. *International Journal of Primatology*, **23**, 1095–1135.

Stockley, P., & Hobson, L. (2016). Paternal care and litter size coevolution in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20160140.

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Thomas, F., Giraudeau, M., Renaud, F., Ujvari, B., Roche, B., Pujol, P., Raymond, M., Lemaitre, J. F., & Alvergne, A. (2019). Can postfertile life stages evolve as an anticancer mechanism? *PLoS Biology*, **17**, e3000565.

Thompson, M. E., Jones, J. H., Pusey, A. E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa, T., Nishida, T., Reynolds, V., Sugiyama, Y., & Wrangham, R. W. (2007). Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Current Biology*, **17**, 2150–2156.

Thompson, S. D. (1987). Body size, duration of parental care, and the intrinsic rate of natural increase in eutherian and metatherian mammals. *Oecologia*, **71**, 201–209.

Tidière, M., Gaillard, J.-M., Berger, V., Müller, D. W. H., Bingaman Lackey, L., Gimenez, O., Clauss, M., & Lemaître, J. F. (2016). Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. *Scientific Reports*, **6**, 36361.

Tilly, J. L. (2001). Commuting the death sentence: How oocytes strive to survive. *Nature Reviews Molecular Cell Biology*, **2**, 838–848.

Tuljapurkar, S. D., Puleston, C. O., & Gurven, M. D. (2007). Why men matter: Mating patterns drive evolution of human lifespan. *PLoS One*, **2**, e785.

Tuomi, J. (1980). Mammalian reproductive strategies: A generalized relation of litter size to body size. *Oecologia*, **45**, 39–44.

Uematsu, K., Kutsukake, M., Fukatsu, T., Shimada, M., & Shibao, H. (2010). Altruistic colony defense by menopausal female insects. *Current Biology*, **20**, 1182–1186.

Uematsu, K., & Shibao, H. (2018). Extended lifespan and overlapping of generations in a gall-forming social aphid, *Quadrartus yoshinomiyai*. *Insectes Sociaux*, **65**, 241–249.

Verborgh, P., Gauffier, P., Esteban, R., & de Stephanis, R. (2021). Demographic parameters of a free-ranging deep-diving cetacean, the long-finned pilot whale. *Marine Mammal Science*, **37**, 463–481.

Vinicius, L., Mace, R., & Migliano, A. (2014). Variation in male reproductive longevity across traditional societies. *PLoS One*, **9**, e112236.

Vinicius, L., & Migliano, A. B. (2016). Reproductive market values explain post-reproductive lifespans in men. *Trends in Ecology & Evolution*, **31**, 172–175.

von Eugen, K., Endepols, H., Drzezga, A., Neumaier, B., Güntürkün, O., Backes, H., & Ströckens, F. (2022). Avian neurons consume three times less glucose than mammalian neurons. *Current Biology*, **32**, 4306–4313.e4.

Vuarin, P., Lesobre, L., Levêque, G., Saint Jalme, M., Lacroix, F., Hingrat, Y., & Sorci, G. (2021). Paternal age negatively affects sperm production of the progeny. *Ecology Letters*, **24**, 719–727.

Walker, M. L., & Herndon, J. G. (2008). Menopause in nonhuman primates? *Biology of Reproduction*, **79**, 398–406.

Weadick, C. J., & Sommer, R. J. (2016). Unexpected sex-specific post-reproductive lifespan in the free-living nematode *Pristionchus exspectatus*. *Evolution & Development*, **18**, 297–307.

Werner, J., & Griebeler, E. M. (2011). Reproductive biology and its impact on body size: Comparative analysis of mammalian, avian and dinosaurian reproduction. *PLoS One*, **6**, e28442.

Whiteley, J., DiBonaventura, M., Wagner, J. S., Alvir, J., & Shah, S. (2013). The impact of menopausal symptoms on quality of life, productivity, and economic outcomes. *Journal of Women's Health*, **22**, 983–990.

Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, **11**, 398.

Williams, G. C., & Williams, D. C. (1957). Natural selection of individually harmful social adaptations among sibs with special reference to social insects. *Evolution*, **11**, 32–39.

Woodroffe, R., & Vincent, A. (1994). Mother's little helpers: Patterns of male care in mammals. *Trends in Ecology & Evolution*, **9**, 294–297.

Zhang, X., Liu, L., Song, F., Song, Y., & Dai, H. (2019). Ages at menarche and menopause, and mortality among postmenopausal women. *Maturitas*, **130**, 50–56.

Zipple, M. N., Altmann, J., Campos, F. A., Cords, M., Fedigan, L. M., Lawler, R. R., Lonsdorf, E. V., Perry, S., Pusey, A. E., Stoinski, T. S., Strier, K. B., & Alberts, S. C. (2021). Maternal death and offspring fitness in multiple wild primates. *Proceedings of the National Academy of Sciences of the United States of America*, **118**, e2015317118.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. A phylogenetic tree of all species that were said to possess some form of post-reproductive lifespan (however small).

Appendix S1. Supplementary methods.

14697998, 2023, 1, Downloaded from https://zslpublications.onlinelibrary.wiley.com/doi/10.1111/jzo.13096 by University Of Glasgow, Wiley Online Library on [02/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License