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Primate Life Histories, Sex Roles, and Adaptability

Essays in Honour of Linda M. Fedigan

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Chapter 3

Post-Fertile Lifespan in Female Primates and Cetaceans

Mary S. M. Pavelka, Lauren J. N. Brent, D. P. Croft, and Linda M. Fedigan

Abstract Popular and scientific interest in menopause in humans has led to an increased interest in the extent of post-fertile life in other animals, particularly in long-lived social species such as other primates and cetaceans. Information on maximum lifespan achieved and age at last birth are available from long-term observations of known individuals from 11 primate species in the wild. Comparable information from wild cetaceans are more difficult to obtain; however there are relevant fisheries data, as well as a small number of long-term individual-based studies. Using post-reproductive representation (PrR) as a population measure of post-fertile lifespan that allows comparisons across populations and species, this review confirms that among primates, only humans have a maximum lifespan significantly longer than 50 years, and only human female life history includes a significant post-fertile stage of life. We conclude that although a prolonged post-fertile stage of life is very rare in mammals, it does occur in some exceptionally long-lived taxa, such as humans and resident killer and short-finned pilot whales. Thus menopause evolved independently at least three times in mammals, and the reasons for its evolution may differ in different lineages.

Keywords Evolution of menopause · Whale menopause · Post-fertile lifespan primates

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3.1 Introduction

Popular and scientific interest in menopause in humans has led to increased interest in the extent of post-fertile life in other animals, particularly other primates and whales, as whales are another group for whom menopause has been reported (Croft et al. 2015). The focus on these taxonomic groups has arisen, in part, because both contain species in which females are long lived and because of the increasing availability of robust life history data from a range of wild populations. From an evolutionary life history perspective, the important features of menopause are its universality (e.g. all women who live into their late 50s will experience it) and its timing relative to the maximum lifespan of the species (Pavelka and Fedigan 1991; Croft et al. 2015). Regardless of local average life expectancy values, which is highly variable depending on local conditions, *Homo sapiens* are known to be able to live to past 100 years, and thus the longest-lived women will live 50% of their lives in a post-fertile state, and many will live two to four decades in this "sterile" state. Menopause is sometimes erroneously assumed to be an artefact of modernization; however this is based on confusing average lifespan (aka life expectancy), which is highly variable at the population level, with maximum lifespan, which is a species-level ability to maintain life and set by the genome (Pavelka and Fedigan 1991).

At first glance, menopause in captive nonhuman primates appears to be widespread; however on closer examination, these studies simply describe reproductive senescence (a variable decline in reproduction found mostly in very old individuals), not menopause (a species-wide cessation of ovarian cycling that occurs well before somatic senescence). Studies of captive primates, most commonly of macaques (*Macaca*) and chimpanzees (*Pan*), have indicated a decline in ovarian function in individuals who have lived to close to the maximum known lifespan for their species. While there may be important differences in ovarian ageing between Neotropical and Old World primates (Tardif and Ziegler 1992; Tardif et al. 2008), most studies suggest physiological parallels between the hormonal events associated with menopause in women and the reproductive function of older captive primates: failure to ovulate, low oestrogen levels, prolonged follicular phases, and high plasma LH concentrations, for example (e.g. Tardif and Ziegler 1992; Nozaki et al. 1995; Gilardi et al. 1997; Bellino and Wise 2003; Atsalis et al. 2008). However, these laboratory studies generally feature a very small number of very old individuals that may live far longer than individuals in the wild and cannot be considered to describe population-wide traits of evolutionary relevance. Data from wild populations of nonhuman primates reveal the distinctiveness of human female reproductive ageing, with the vast majority of females in wild populations of nonhuman primates dying before they reach the point of reproductive senescence (see below).

Based on research on wild populations to date, two species of toothed whale exhibit a prolonged period of post-reproductive life comparable to humans – the resident ecotype of the killer whale (*Orcinus orca*) and short-finned pilot whale (*Globicephala macrorhynchus*). In the wild, resident killer whale females breed between the ages of 10 and 40 but can live past 90, while short-finned pilot whales breed from 7 to 35 years of age and can live for over 60 years (Marsh and Kasuya 1986; Olesiuk et al. 1990; Croft et al. 2015). Resident killer whales are just one of a number of killer whale ecotypes that differ in their prey specializations, morphology, and behaviour and represent genetically and phenotypically distinct populations. Short- and long-finned pilots are more closely related to each other than either are to killer whales, with the three last sharing a common ancestor in the Miocene.

The current absence of detailed life history information on the other killer whale ecotypes precludes our ability to determine whether menopause is a species-wide trait or one that is confined to the resident killer whales.

In this chapter, we review what is known about reproductive senescence in female primates and cetaceans, focusing on field studies of reproductive history to explore the proportion of the lifespan that is lived after the production of the final infant. Individual cases of old female animals that have ceased to produce infants close to the end of their lifespans are not evidence of a species-wide life history characteristic – for the latter, population-level data are needed. Unfortunately, only a small number of studies on long-lived species with indivdiuals of known age and reproductive history are available for wild animal populations. Life history data for nonhuman primates and cetaceans are especially difficult to obtain given their longevity relative to the age of most research projects. Hormonal profiles, ovarian histology, and direct measures of menstrual activity are not available for most free-ranging primates and cetaceans, although this might well be expected to change as noninvasive methods for sampling are further developed and enhanced. But even so, to address the question of reproductive senescence, these physiological data need to be collected from populations (not just individuals) of known age. Additionally, the very reason that these animals are of particular interest – their long lifespans – means that aged animals followed by researchers from birth are rare. Fortunately, the number of field-based studies that have endured for enough time to be classified as "long term" has increased in recent years (Alberts et al. 2013). Here, we harness information from these studies and ask: just how prevalent is a post-fertile stage of life in primates and cetaceans?

3.2 Reproductive Data from Free-Ranging Individuals

3.2.1 Nonhuman Primates

Preliminary assessments of the life history patterns in free-ranging primates and cetaceans have tended to focus on descriptive values regarding the maximum lifespan achieved, as well as age at last birth. These data allow researchers to describe how close to the end of the *maximum* lifespan final births occur in a species – keeping in mind that the oldest known individuals are almost certainly outliers and that most females die well before this age. Below we describe some of the data that are available for wild primates and cetaceans.

Information on maximum lifespan achieved, as well as age at last birth, are available from individual-based observations of wild populations from at least 11 primate species spanning the taxonomic range (summarized in Fedigan and Pavelka 2011). Although not much has been published on the age at last birth and maximum lifespan for prosimian species, we do have data from the Beza Mahafaly Sifaka Research Consortium indicating that in a population of 219 wild *Propithecus verreauxi*, the oldest known female died at an estimated age of 31 (Bronikowski et al. 2011) and the maximum age at which a female gave birth was 28 years (Alberts et al. 2013). Thus female sifakas can continue to be reproductive up until the age at which time they have completed 90% of their lifespan. As an example from New World monkeys, LMF's 30-year life history study of Costa Rican capuchins (*Cebus capucinus*) also provides evidence of continued reproduction throughout the lifespan. In a sample of 45 females, the oldest individual lived to be 27 years of age, and the maximum age at which a female gave birth was 25, indicating these monkeys can produce infants up until they have completed 93% of their lifespans. And a study sample of 69 Brazilian muriquis revealed that females can live to an estimated 41 years and produce infants until they are 38 (thus up to 93% of their lifespans) (Bronikowski et al. 2011; Alberts et al. 2013; Stier 2018, this volume).

For Old World monkeys, Sommer et al. (1992), Borries et al. (1991), and Koenig et al. (1997) report that in a wild langur group (*Presbytis entellus*) at Jodhpur, India, the oldest female is estimated to have lived to 34 years and the oldest birth occurred in a female aged 32, suggesting that some females can produce infants until they have completed 94% of the species lifespan. These langur researchers also describe a small number of females who lived between 3 and 9 years before death without producing a new infant, suggesting that some idiosyncratic, as opposed to population-wide, termination of reproductive ability may be occurring in this population.

Other Old World monkeys for whom such data are available are baboons and macaques. Alberts and Altmann's data on the Amboseli baboons show that the oldest female in their sample of 211 *Papio cynocephalus* lived to be 28 years and the oldest recorded birth was to a female 24 years of age. Thus, female yellow baboons can continue to produce infants up to the point at which they have completed 86% of their lifespan (Alberts et al. 2013). A population of 207 semi-free-ranging provisioned Barbary macaques (*Macaca sylvanus*), studied over an 11-year period, also showed idiosyncratic variation in the age at which individuals appeared to stop reproducing, but from a species life history perspective, the oldest birth was to a 28-year-old female, and the maximum lifespan in this colony was age 30, thus up to 93% of the lifespan (Paul et al. 1993; Paul 2005).

Japanese monkeys (*Macaca fuscata*) are perhaps the most studied with respect to old age reproduction. Based on demographic data collected since 1954 on the Arashiyama population near Kyoto, the oldest birth was in a 25-year-old female, and the longest-lived female was 33 (Takahata et al. 1995). Pavelka and Fedigan (1999) conducted an extensive analysis of the reproductive histories of 95 females from the Arashiyama West population that had been documented from birth to death. Using Caro et al.'s (1995) interbirth interval criterion for reproductive termination (when the time lag between the last parturition and the death of the mother exceeds two standard deviations of the female's own mean lifetime interbirth interval), they identified that 20 of 70 females eligible for the criterion test were reproductively terminated. While these results could be interpreted as evidence of a phenomenon analogous to human menopause occurring in Japanese monkeys, closer examination of the data revealed that continued reproduction to death is characteristic of the vast majority of females of all ages. This is because a few females of all ages "tested positive" for being post-fertile according to Caro et al.'s (1995) criterion, but these cases were rare at every age. Even between the ages of 20 and 25 (an age category uniformly regarded as old for Japanese macaques), 81% of females were still reproductive. There are no records of any female Japanese macaque ever giving birth after the age of 25. These findings parallel those of Takahata et al. (1995) for Japanese macaques and Walker (1995), Walker and Herndon (2008), and Johnson and Kapsalis (1998, 2008) for the closely related rhesus macaque (*Macaca mulatta*). It is important to note that most macaque females are dead long before they have an opportunity to reach the population-wide cessation of infant production at age 25. Even though they live with almost no predation, less than 3% of the Arashiyama population of provisioned females that survived to reproductive age went on to live to age 25. Using the equation SpeciesA Age X SpeciesA Maximum Lifespan/SpeciesB Age X SpeciesB Maximum Lifespan, a 25-year-old monkey is between 83 and 95 years of age in human terms, depending on whether the human maximum lifespan used is 122 years (https://en.wikipedia.org/wiki/Jeanne_Calment) or the more conservative and commonly used round number of 100 years (Pavelka and Fedigan 1999). As one would expect, those female macaques that did survive to 25 years were visibly aged and showed clear outward signs of advanced age deterioration (somatic senescence).

Great apes are the longest lived of the primates, and here too the evidence strongly suggests that reproductive lifespan is very close to maximum lifespan, especially given the long interbirth intervals in apes. Wich et al. (2004) reported life history data for a wild Sumatran orangutan (*Pongo abelii*) population studied for a 32-year period and found no evidence for reproductive termination and a post-fertile life stage. Maximum lifespan for females was estimated to be 53 years of age, and the maximum age at which a birth was recorded was 50, meaning that almost 95% of the lifespan was completed before the time of last birth. Given that the interbirth interval in this population is greater than 9 years, a female would need to live significantly longer than 9 years after her last offspring before she could be assumed to be post-fertile.

Mountain gorillas (*Gorilla beringei beringei*) have a shorter lifespan, with the maximum lifespan of 43.7 years based on a sample of 66 females from the Virunga Volcano region studied from 1967 to 2004 (Robbins et al. 2006). The oldest female to give birth did so at 40.6 years of age, 93% of the way through the maximum lifespan. The average interbirth interval for these females was 4 years. Using a refinement of the Caro criterion, Robbins et al. identified five females who may have been reproductively terminated; however the post-reproductive lifespan represented only 1–3% of the total lifespan.

Chimpanzees (*Pan troglodytes*) are one of the most common laboratory primates for whom a post-fertile life stage has been reported in a small number of individuals (e.g. Graham 1979; Gould et al. 1981; Jones et al. 2007; Videan et al. 2006). However, none of the reported cases meet the criterion for a population-level cessation of reproductive function that exceeds the pace of general ageing. Thompson et al. (2007) analysed long-term fertility and mortality data in six wild chimpanzee populations and reported that chimpanzees are estimated to be able to live into their early 60s (64 years at Kanyawara and 66 at Ngogo; Wood et al. 2017) and reproduce until approximately 55 years of age. They reported that chimpanzee fertility decline with age is related to overall decline in survivorship and that healthy females maintain high birth rates late into life. Thus, they concluded that, in contrast to other claims, there was no evidence that a post-fertile phase is characteristic of chimpanzee female life history. Included in this data set was Jane Goodall's favourite, the long-lived and very famous female chimpanzee, Flo, from the Gombe Stream National Park in Tanzania. Flo died as an elderly matriarch at an estimated 53 years of age, having given birth to infant Flame at age 49.

3.2.2 Cetaceans

Compared to primates, life history data are arguably even more difficult to obtain from cetaceans due not only to their very long lifespans but also because they live in vast oceanic habitats that make them difficult to track and observe. As a result, and although there are some exceptions that we discuss in greater detail below, much of what we know about cetacean life history unfortunately come from fisheries-based sources or mass stranding events, rather than long-term observations of known individuals. These are not ideal sources of data for a number of reasons, including that maximum lifespans are probably underestimates because many of the oldest/largest animals will have been killed during the years of intensive whaling and because the ages of the animals are not based on longitudinal recordings of known individuals but are estimated from features such as body length or annual growth layers in dentine or cementum (Hamilton et al. 1998). Nevertheless, we can draw useful information regarding the broad patterns of reproduction in whales from these reports. The infraorder Cetacea is divided into two parvorders: the baleen whales (Mysticeti), best known for their baleen filter-feeding system, and the carnivorous toothed whales (Odontoceti). Below we describe the life history parameters for some species from both of these groups, starting with baleen whales and focusing on populations with some of the best described data.

In baleen whales, fin whales are known to survive into their 90s (Lockyer et al. 1979) with 1 female estimated to be as old as 111 (Mizroch 1981). Although the mean age at reproduction of fin whale mothers ranges between 23 and 37 years (Arrigoni et al. 2011), the oldest pregnant female observed to date was 76 years old (Mizroch 1981) or between 68% and 84% of the range of maximum lifespans. Bowhead whales are very long lived, with female maximum lifespan estimated to be over 100 years (George et al. 2004). Moreover, there is physiological evidence (corpora number) that females continue to ovulate in these very late years (George et al. 2004), suggesting that bowhead females are reproductively viable throughout their long lives. The North Atlantic right whale (*Eubalaena glacialis*) is one of the few species of baleen whale for which there is individual-based data, which has been generated using photo identification of known individuals. Seven known females were observed for over 30 years (Hamilton et al. 1998). The oldest of these females was first sighted in 1935 with a calf, and because the mean age at reproductive maturity in this species is 9.6 years, her age in 1995 was estimated as 69. This particular female did not have a calf in any follow-up sightings, which is probably because the sporadic timing of her sightings missed calving events, not because she was reproductively senescent (Hamilton et al. 1998). Of the other six individuals tracked in this population, the oldest female to give birth to a calf was 34 years old, or 52% of the maximum lifespan of this species.

Finer-grained details are known about the life history of toothed whales, including a greater number of individual-based studies and occasional data on the cessation of ovulation from necropsy reports. For example, fisheries data from the long-finned pilot whale, *Globicephala melaena*, demonstrate that females can live upwards of 59 years (Foote 2008; Bloch et al. 1993) with the oldest documented pregnancy occurring in a 55-year-old female (Foote 2008; Martin and Rothery 1993). Thus females of this species can give birth 93% of the way through their maximum lifespan. Necropsy data from fisheries show that less than 4% of mature females had ceased ovulation (Foote 2008; Martin and Rothery 1993), suggesting that somatic and reproductive senescence may be closely aligned in this species. These findings are in stark contrast to those from the closely related short-finned pilot whale, *Globicephala macrorhynchus. Females from this species cease* breeding at a maximum of 36 years of age but can live for over 60 years (Kasuya and Marsh 1984; Marsh and Kasuya 1986). The oldest female to give birth to a calf therefore lived 57.1% of the maximum lifespan of this species. Inspection of corpses from Japanese drive fisheries revealed that 25% of mature females had ceased ovulation, suggesting that short-finned pilot whales undergo physiological changes that preclude reproduction, similar to that which occurs in humans (Kasuya and Marsh 1984).

Evidence for a prolonged post-fertile lifespan in wild killer whales comes from long-term individual-based studies of two populations of resident killer whales in the Pacific waters off North America. These studies started in 1974 and consist of individual demographic data for more than 600 individuals (Olesiuk et al. 1990; Towers et al. 2015). The ages of individuals already alive in 1974 were necessarily estimated, with dates of birth for adult females estimated by subtracting 15 years (the mean age at first reproduction) from the estimated year of birth of her oldest offspring (offspring determined based on a behavioural association and, in some cases, genetic parentage assignment), which was assumed to be her first viable calf (Bigg et al. 1990). Using this method, many females estimated to live between 70 and 80 years (Franks et al. 2016). In these populations, the maximum documented age at parturition is 43 years old. As such, there are currently two mature females in the study populations who are believed to be over 70 years old, and to have last given birth prior to the start of the study in 1974, but who had not been observed to be pregnant or to give birth in the intervening 42 years. It is unknown if there are physiological changes that preclude reproduction in older female resident killer whales (Whitehead and Rendell 2014).

Although the life histories of killer and pilot whales have been documented in the greatest detail, information from a broader range of toothed whales exists. For example, female bottlenose dolphins (*Tursiops truncatus*) can live past 35 years, and pregnancies in these later years have been documented (Stolen and Barlow 2003; Kasuya et al. 1997). In sperm whales, the best data currently available on pregnancy come from fisheries data, where 22 females aged 40–61 years were examined. Of these, only one was pregnant (aged 41) and six were lactating. None of the remaining females were pregnant or ovulating (Best et al. 1984). Age estimates for sperm whales come from tooth layering techniques, and estimated maximum lifespan at between 60 and 70 years (Rice 1989), which has led to the suggestion that the sperm whale may exhibit menopause (Whitehead 2003).

3.3 Measuring Menopause as a Population-Wide Trait

Data on maximum lifespan and age of last birth presented above demonstrate that in most of the species for which information is available, the ability to reproduce is maintained until very late in the lifespan of the species. Thus, these field reports support what has long been asserted by a number of researchers, such as Gosden (1985), who described the "postmenopausal" phase of life in other primates as being short and confined to a few individuals of exceptional longevity, and Small (1982, 1984) who argued that most macaque females continue to cycle until death and that there is great variability in the age of those females that cease to cycle. Also, in 1991, after a careful analysis of all available field and captive data, Pavelka and Fedigan concluded that while a small number of individual monkeys and apes had indeed ceased reproducing or lost reproductive capacity, often in extreme old age, nothing comparable to the universal termination of female fertility halfway through the human lifespan had yet been found in other primates. Menopause in humans, resident killer whales, and short-finned pilot whales occurs in healthy middle age and is distinct from the overall senescence of the organism, and all females who live into the second half of their lifespan will experience it. Women beyond their late 50s (Hill and Hurtado 1991) and female resident killer whales beyond their early 40s are *all* post-fertile (Franks et al. 2016); there are no individuals continuing to reproduce for 70, 80, or 90% of the maximum lifespan, which, as we saw above, is true for virtually all other primates and cetaceans for whom such data exist. Reproductive cessation in nonhuman primates and in many cetaceans, when it occurs, is idiosyncratic, is not population-wide, and mostly occurs in aged individuals such that it is not distinct from the overall somatic senescence of the organism.

There is a tendency among some animal researchers to conclude that they have demonstrated something comparable to menopause when in fact they have demonstrated quite the opposite, from a species life history point of view. For example, Graham (1979:299) concluded that "chimpanzees aged 35 years of age and more show evidence of. .. reproductive senescence closely comparable to that seen during the human climacteric." However, most of the animals he reported upon were very old and in a state of advanced biological senescence, yet *most* of them continued to have primary follicles and to ovulate and cycle until death in old age. The interpretation of physiological changes in individual old females as evidence of menopause, despite continued reproduction until death in the majority of the study subjects, may be driven by the search for a biomedical laboratory model for studying menopause and the treatment of its symptoms in humans. A number of researchers have pointed out that the conflicting claims regarding menopause often rest on the significance attached to individual animals who appear to have ceased producing infants early enough to spend some portion of their lives in a post-fertile state (e.g. Pavelka and Fedigan 1991; Caro et al. 1995).

In an attempt to move beyond the confusion in the literature and to provide an independent assessment of age-related changes in reproductive function across species, Caro et al. (1995) introduced the interbirth interval criterion for identifying post-fertile females. Using demographic data, this method considers a female to be post-reproductive only when she has lived significantly longer (more than two standard deviations longer) than her own average lifetime interbirth interval without giving birth again. It helps to avoid considering females to be post-reproductive simply because they died in a normal interbirth interval. Caro et al. (1995) applied their method to the reproductive records of 14 nonhuman primates from captive breeding colonies in the USA and Europe. They argued that captive colonies were, like most contemporary humans, buffered to some extent from disease and from predation-induced mortality and thus may be more appropriate than comparison with wild primate populations. Additionally, appropriate longitudinal reproductive data on wild female primates were available for few, if any, primate species at the time. Caro et al. (1995) also examined human data from an eighteenth and nineteenth century rural peasant population in Northern Germany. The comparison of age-specific survivorship, fertility, and changes in interbirth intervals in these 15 primates (including humans) showed that in most species, individual females continue to reproduce throughout their lives, while other individuals terminate reproduction well before death. Humans were the exception. The average time between last birth and death values for nonhuman primates ranged from 2 to 6 years in the lemurs and monkeys, 4.5 years for gorillas, 7.1 years for orangutans, and 9.3 years for chimpanzees. However, these may be overestimates as the authors did not subtract the normal interbirth interval from the time period between the last parturition and death, meaning that these values include time during which a female was nursing a new infant, a time in which she would be better considered reproductive than post-reproductive.

Of course, from an evolutionary perspective, we need to know not just whether post-reproductive females are observed in a population but also with what frequency they occur. Measuring post-fertile periods as the time between the end of fertility and the end of life is inherently biased because it includes only individuals that survive after their last reproductive event and does not allow for generalizations to be made regarding the importance of post-fertile lifespan for the population/species (Croft et al. 2015; Levitis and Lackey 2011). Moreover, many measures of the length of post-fertile life tend to be correlated with longevity, making comparisons across species problematic. Recently, Levitis and Lackey (2011) proposed a new measure: post-reproductive representation (PrR) as a population measure of post-fertile lifespan that allows comparisons across populations and species. PrR is an unbiased population measure of reproductive lifespan and quantifies the proportion of females that are post-reproductive under idealized demographic conditions. PrR is calculated from life tables using data from two ages: Age B, the beginning of adulthood, defined as the point at which 5% of lifetime fecundity has been realized, on average, independent of mortality, and Age M, the end of the fecund lifespan, defined as the point at which 95% of lifetime fecundity has been realized, on average, independent of mortality. PrR represents the number of years an average newborn can expect to live as a post-reproductive adult divided by the number of years an average newborn can expect to live as an adult (Levitis and Lackey 2011).

In recent years, a group of ten researchers has collaborated to synthesize their long-term life history data on populations of wild primates that have been studied continuously for decades (e.g. Strier et al. 2010; Morris et al. 2011; Bronikowski et al. 2011). As a result, Alberts et al. (2013) were able to carry out a uniquely extensive comparative study of reproductive senescence in seven natural primate populations, including calculating PrR values (Table 3.1). They compiled individual mortality and reproduction data for 700 individually recognized adult female nonhuman primates that had been studied for more than 250 combined observation years. Human data from the! Kung population of the Kalahari Desert, who at the time of study practised no agriculture and had little contact with agricultural communities, were used to compare the rate of increase in the probability of death with the rate of increase in the probability of reproductive senescence. Thus they were able to test whether reproductive senescence occurs at the same or at a different pace than does general senescence in all seven species. Their results provided strong evidence that reproductive ageing in women is quite distinct from the pattern of human somatic senescence and that it is also distinct from the patterns of reproductive senescence found in a wide range of other primate species. In the nonhuman primates, PrR values ranged from 1% in baboons to 8% in muriquis (Table 3.1). Gorillas and chimpanzees were at 4% and 2%, respectively. In contrast, in the natural human population of Kalahari! Kung, 43% of adult female years are lived by post-fertile individuals. This cross-species analysis stands as the largest and longest-term study to date reporting on reproductive senescence and post-fertile lifespan in humans and other primates.

PrR values in cetaceans are more difficult to calculate due to a general absence of life tables based on observed individuals. However, the PrR is 28% in both short-finned pilot whales (Levitis et al. 2011) and in resident killer whales (Franks

Table 3.1 Published values of female post-reproductive representations (PrRs)

Species	Population	PrR	Reference
Homo sapiens	!Kung	0.425	Levitis et al. (2013)
Homo sapiens	Ache	0.439	Levitis et al. (2013)
Homo sapiens	Haiti 2002	0.460	Levitis et al. (2013)
Homo sapiens	Sweden 1751	0.477	Levitis et al. (2013)
Homo sapiens	Hadza	0.481	Levitis et al. (2013)
Blue monkey (*Cercopithecus mitis*)	Wild	0.02	Alberts et al. (2013)
Blue monkey (*Cercopithecus mitis*)	Wild	0.041	Levitis et al. (2013)
Chimpanzee (*Pan troglodyte*)	Wild	0.018	Levitis et al. (2013)
Chimpanzee (*Pan troglodyte*)	Wild	0.02	Alberts et al. (2013)
Gorilla (*Gorilla beringei*)	Wild	0.04	Alberts et al. (2013)
Hamadryas baboon (*Papio hamadryas*)	Wild	0.005	Levitis et al. (2013)
Muriquis (*Brachyteles hypoxanthus*)	Wild	0.06	Alberts et al. (2013)
Rhesus macaque (*Macaca mulatta*)	Wild	0.007	Levitis et al. (2013)
Sifaka (*Propithecus verreauxii*)	Wild	0.02	Alberts et al. (2013)
White-faced capuchin (*Cebus capucinus*)	Wild	0.04	Alberts et al. (2013)
Yellow baboon (*Papio cynocephalus*)	Wild	0.01	Alberts et al. (2013)
Short-finned pilot whale (*Globicephala macrorhynchus*)	Wild	0.28	Levitis and Lackey (2011)
Resident killer whales (*Orcinus orca*; *based on current age estimates*)	Wild	0.282, $P = 0.001$	

Also shown are the PrRs for the resident killer whales (*Orcinus orca*) calculated using unpublished data (Foster et al. 2012)
The table is adapted from Croft et al. (2015)

et al. 2016) (Table 3.1). These values are well above those reported for any wild nonhuman primate population (Alberts et al. 2013) and indicate that prolonged period of post-reproductive life is a population-level trait in these species.

3.4 The Evolution of Menopause

Menopause is a feature of the life history of all modern humans (*Homo sapiens*) and is not an artefact of modernization (Pavelka and Fedigan 1991; Caro et al. 1995; Fedigan and Pavelka 2011). This population-wide termination of female reproduction decades earlier than the maximum lifespan for a species is, at first pass, very difficult to explain from an evolutionary perspective. Quite simply it should be inherently disadvantageous for individuals to stop reproducing at midlife. Both theoretically and empirically, lifespan and reproductive lifespan are highly correlated in living organisms. It should be no surprise that outside of humans and the two species of toothed whales, no other animals are known to experience early cessation of fertility; instead they do what is predicted by evolutionary theory – they reproduce until close to the end of their lifespans. In the vast majority of species, natural selection clearly favours continued reproduction to the end of the lifespan. Why then has a substantial post-reproductive lifespan evolved in humans and two species of toothed whales?

One possibility is that menopause is a byproduct of the evolution of increasing lifespan in taxa in which the reproductive system could not “keep up” (Pavelka and Fedigan 1991; Fedigan and Pavelka 2011). Over the course of human evolution, the development of a postmenopausal stage of life in humans may be a byproduct of increases in our lifespan beyond the age of 50. Fifty is approximately the same age at which great ape females (chimpanzees, gorillas, orangutans) in the wild cease to give birth (e.g. Nishida et al. 2003; Wich et al. 2004; Robbins et al. 2006; Thompson et al. 2007) and is also close to the maximum lifespan of chimpanzees, our closest living relative. Cutler (1975) looked at the genetic complexity governing rate of ageing and showed that the “maximum lifespan potential” of humans doubled sometime over the past 3 million years. The evolution of the much longer lifespan of human is most likely tied to parallel increases in brain size in our lineage (Rose and Mueller 1998; Kaplan et al. 2000); however, other explanations have been offered. For example, Hawkes (2003) suggested that a novel helping role for post-reproductive grandmothers may explain the increased human lifespan, and Tuljapurkar et al. (2007) suggested that continued old-age male fertility provides a selective force increasing the human lifespan beyond the theoretically expected “wall of death”. More recently, drawing from neuroscience, anthropology, and brain imaging research, Raichlen and Alexander (2014) proposed that the evolution of increased physical activity approximately 2 million years ago served to relax genetic constraints on ageing in human ancestors.

The failure of the reproductive system to maintain functionality along with this increased lifespan may be due to a phylogenetic constraint. As female mammals, women have a reproductive pattern referred to as semelgametogenesis: they are born with approximately 1 million oocytes and primordial follicles, which is all they will ever possess. The number of potential egg cells is fixed at birth and steadily declines thereafter, many to degeneration (von Saal et al. 1994), some spent in ovulation. Unlike male mammals who continue to produce new gametes throughout life, females do not. Oocytes and follicles are depleted throughout a woman’s life until they reach a minimum threshold below which hormonal signals, and then cycling, begin to fail (Armstrong 2001). Oocyte depletion is widely regarded to be the starting point for a series of changes that underlie the menopausal transition in women (Pavelka and Fedigan 1991; Fedigan and Pavelka 2011). The reason for the semelgametogenesis pattern in female mammals may be antagonistic pleiotropy (e.g. Williams 1957; Rose 1991; Gosden and Faddy 1998): it may have high adaptive value early in the life course (intense reproductive output) and was selected for even if it results in reduced fitness (follicular depletion) later in the life course. In the wider research on somatic ageing, it is commonly accepted that antagonistic pleiotropy is a good explanation for the evolution of senescence in general (Wood et al. 2001). Additionally, in the case of oocyte depletion later in life, this effect would only have been experienced in the very longest-lived mammals. However, new data suggest that the number of gametes and/or the rate of their depletion is not fixed across all mammals. For example, female bowhead whales breed throughout their 100-year lifespan, and fin whale females have been observed breeding past the age of 70. It is also reported that African elephant females continue to reproduce until the end of their natural lifespans, which can be upwards of 65 years (Lee et al. 2016). These data support the suggestion by Gosden and Telfer (1987) that oocyte stocks may be variable, and if they are, we must again consider the possibility that rather than not "keeping up" with the extended somatic lifespan, direct opposing selection may have held back the female reproductive lifespan in some taxa (Cant et al. 2009).

The other possibility then is that menopause evolved because direct selection favoured females who stopped reproducing over those who continued, in the absence of a phylogenetic constraint on continued reproduction. The most common adaptive explanation is that menopause evolved due to the increase in inclusive fitness benefits accruing to those who did not produce any new offspring but instead invested in the care and provisioning of the close relatives they already had: existing offspring and grandoffspring. While some studies have found no evidence of inclusive fitness benefits for post-fertile mothers and grandmothers (Hill and Hurtado 1996; Rogers 1993), a number of others do show that females can positively impact the survival of offspring or grandoffspring (Shanley et al. 2007; Hawkes 2003; Hawkes and Coxworth 2013; Lahdenpera et al. 2004; Foster et al. 2012). However, inclusive fitness models have generated conflicting results with respect to whether the benefits older females gain by helping their relatives can outweigh the costs they incur by ceasing to reproduce (summarized in Croft et al. 2015). Moreover, while "helping" can select for longer lifespans, it cannot explain the cessation of reproduction, unless helping necessarily precludes females from reproducing (Croft et al. 2015). Additionally, evidence that post-fertile individuals currently provide benefits to their descendants is not automatically evidence for the origins of menopause (see Gould and Lewontin 1979). Being post-fertile in conjunction with living in societies that afford them the opportunity to direct fitness-enhancing behaviours to their descendants, human females may have been able to take advantage of their post-menopausal stage of life and create secondarily adaptive benefits from the phenomenon of midlife reproductive senescence.

This uncertainty in the literature has led some researchers to suggest that, in addition to the benefits of helping, the costs of continued reproduction must also be considered in adaptive scenarios for the evolution of menopause. Pavelka and Fedigan (2012) investigated the costs of continued reproduction in old Japanese monkey females and found no difference in body weight between females who ceased to reproduce and those who continued, and older females were no more likely to die in the 12 months after giving birth than were younger females. Additionally, a regression of interbirth interval on age at death revealed no tendency for females who produce infants in closer succession to die any earlier. However, of particular relevance to the evolution of menopause in both humans and whales, Cant and Johnstone (2008) and Johnstone and Cant (2010) have suggested that conflict over resources between breeding females is a critical missing term in previous models and that, together, the inclusive fitness benefits older females gain by helping their relatives combined with the costs of reproducing at the same time as younger female group members (the “reproductive conflict hypothesis”) can explain the evolution of menopause. These costs are dependent on the kinship dynamics that are displayed by a species. In resident killer whales, for example, neither males nor females disperse from their natal group. As a result, mean level of relatedness to other group members increases as females age, driven by the fact that females start out with few related males in their groups but start to add closely related males as they produce sons (new related females are added as well but these simply replace older generations of females as they die). With relatedness to the group increasing with age, theoretical models show that older females not only benefit more from helping their group mates but also suffer greater costs from competing against them. That is, once you reach a certain age, continued reproduction leads to costly competition between your new offspring, your daughters, and your grandoffspring. This pattern is in direct contrast to most mammals, where males disperse away from their natal group and females’ mean relatedness to the group remains constant, but is similar to what is predicted to occur in populations of humans with female-biased dispersal (which is arguably the human ancestral state): mothers are related to the offspring of their daughter-in-laws, and thus local relatedness increases with age for these females (summarized in Croft et al. 2015). Indeed, recent empirical results support this reproductive conflict hypothesis in humans and resident killers whales. Older females have been shown to have reduced fitness when they reproduce in conflict, i.e. the new offspring of older females are less likely to survive when they are born at the same time as the new offspring of younger (related) females (Croft et al. 2017; Lahdenpera et al. 2012; Strassman et al. 2011).

3.5 Summary

In this paper, investigating the evidence for post-fertile lifespans in primates and cetaceans, we have highlighted a number of important developments in our efforts to understand the evolution of menopause. First it is clear from the available data on, for example, the baleen fin and Bowhead whales, that reproduction well past the age of 50 is possible in some mammals and that there must be a more variable oocyte supply in different mammalian taxa than previously argued. The second important realization from our review is that although a post-fertile stage of life is very rare in mammals, it does occur in some exceptionally long-lived taxa, such as humans and two species of toothed whales. Short- and long-finned pilots are more closely related to each other than either are to killer whales, with the three last sharing a common ancestor in the Miocene, suggesting that menopause arose independently in killer and short-finned pilot whales. This means that menopause likely evolved independently at least three times in mammals. With this recognition, we must consider that the reasons for the evolution of it may differ in different lineages. It may be a byproduct of increased longevity or the result of direct selection in humans.

However, the evidence for continued reproduction into very old age in a number of whales, combined with mathematical models taking both costs and benefits into account, are showing that direct selection to cease reproduction is a strong possibility in species such as the resident killer whales.

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