

# The evolution of prolonged life after reproduction

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**Why females of some species cease ovulation before the end of their natural lifespan is a longstanding evolutionary puzzle. For many species in captivity, post-reproductive life is simply an epiphenomenon of lengthened lifespan. Yet in natural populations of humans as well as some cetaceans and insects, reproductive senescence occurs much faster than somatic aging and females exhibit prolonged post-reproductive lifespans (PRLSs). Determining the mechanisms and functions that underpin PRLSs has proved a significant challenge. Here we bring together both classic and modern hypotheses proposed to explain PRLSs and discuss their application to both human and nonhuman animals. By taking an integrative and broad taxonomic approach we highlight the need to consider multiple interacting explanations for the evolution of PRLSs.**

## PRLSs: a longstanding evolutionary puzzle

Why females of some species cease ovulation before the end of their natural lifespan is a longstanding evolutionary puzzle [1–3]. Any decline in reproductive function is detrimental to Darwinian fitness and thus classical evolutionary theory predicts the early termination of reproduction should be selected against [2,3]. Reproductive decline long before the end of life in humans has generated tremendous medical and evolutionary interest [1,4–8]. PRLSs are by no means restricted to humans and have been documented in mammals [9,10] fish [11], birds [12,13], and invertebrates [12]. For most of these species, PRLSs are short, are detectable in only a few individuals [10,14,15], and occur only in captivity [11,12]. The notable exceptions to this pattern are some insects and two species of toothed whale that exhibit substantial PRLSs in natural populations [16–20].

Theoretical research over the past 50 years provides a coherent framework to understand senescence in general [1,2], but decoupling somatic and reproductive senescence has proved a major theoretical challenge [4]. Moreover, life-history evolution is difficult to study in long-lived animals because it requires individual-based, long-term studies, which are challenging to maintain and need time

to mature [21], particularly for species whose lifespan can approach 50 or even 100 years (Figure 1). However, for several long-lived nonhuman mammals, detailed demographic data sets have matured sufficiently to allow life-history evolution to be studied in natural populations [14,22–27].

In this review we bring together the evidence for PRLSs across taxonomic groups. We outline the main hypotheses for why PRLSs has evolved and review the evidence in support of these hypotheses in both human and nonhuman animals. Finally we outline the major challenges and priorities for future research.

## Reproductive and somatic senescence in natural populations

Why ageing occurs has been a central question in ecology and evolution for much of the past century [1,2,28,29]. There is general agreement that the evolution of senescence is unavoidably linked to the fact that under natural conditions organisms die from extrinsic hazards [29,30]. Since there are always fewer older individuals in a population than younger ones, the strength of selection on alleles with age-specific fitness effects is expected to weaken with increasing age [2,3] and alleles that confer advantages early in life, by increasing early-life fecundity, can spread to fixation even if they have deleterious effects later [1,31]. The declining strength of selection with age sets the stage for the evolution of physiological mechanisms leading to both reproductive and somatic senescence [28,32].

Somatic and reproductive senescence are inherently linked: there is no benefit to an organism in maintaining a viable germline if somatic senescence has progressed to the point that prevents successful reproduction [4]. Most vertebrate species typically show a gradual decline in reproduction with age [12]. However, in some circumstances reproductive senescence is accelerated relative to somatic senescence leading to a PRLS.

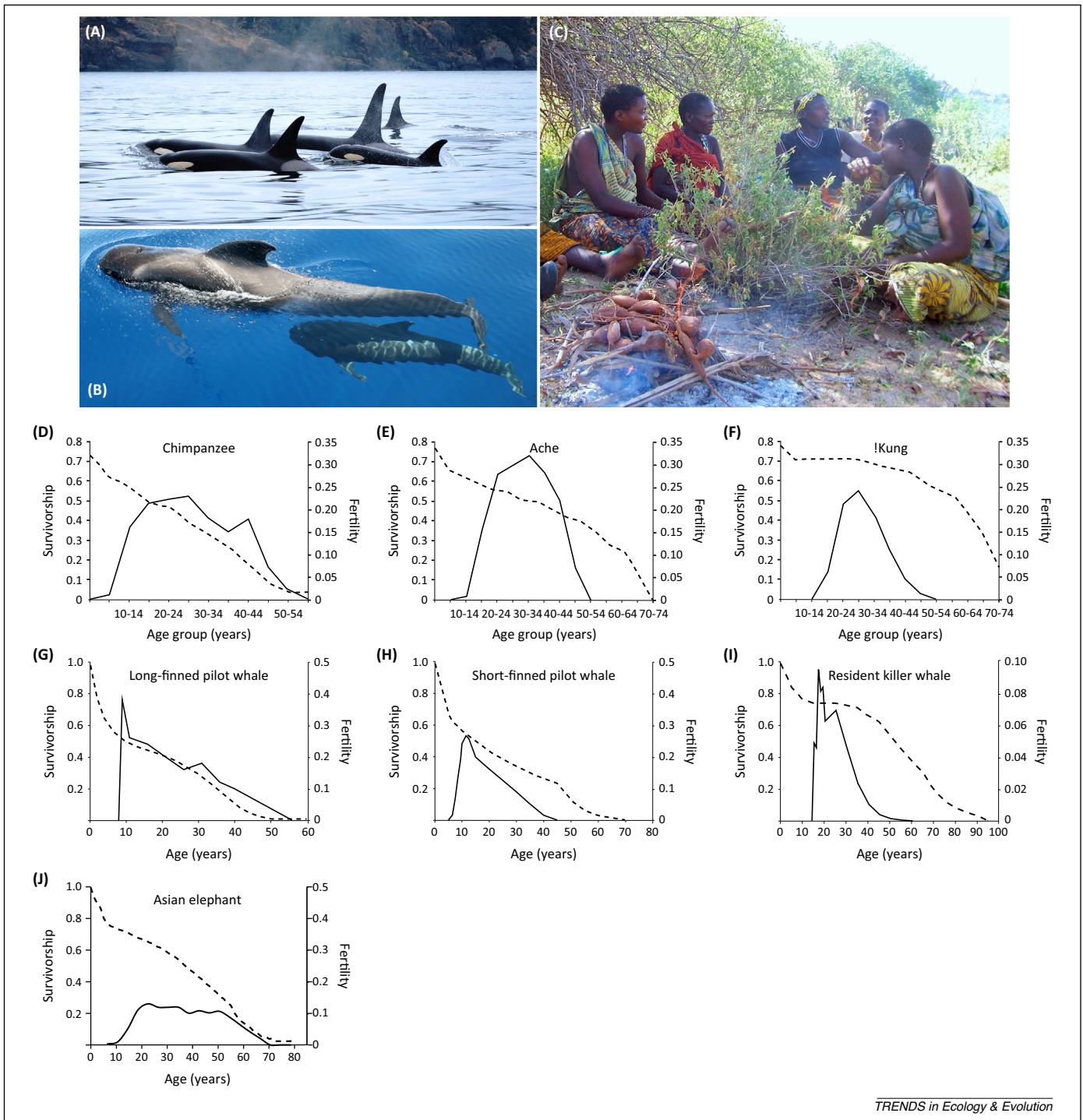
At first glance, PRLSs appear to be widespread and have been documented across a wide range of taxonomic groups [11,13,33,34] and in both males and females [35,36]. These patterns have led some authors to suggest that PRLSs are not an evolutionary oddity [9,12] and do not require special adaptive explanations [8,37]. However, from an evolutionary perspective it is essential to consider both the context in which reproductive senescence occurs and how this trait is distributed within a population. Even if reproductive

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**Figure 1.** (A–C) Vertebrate species that exhibit prolonged post-reproductive lifespans (PRLs). (A) Resident killer whale (*Orcinus orca*). Females generally reproduce between the ages of 12 and 40 years but can survive into their 90s [17,27] (credit Darren Croft). (B) Short-finned pilot whale (*Globicephala macrorhynchus*). Females breed between the ages of 7 and 35 years with a maximum lifespan reaching over 60 years [16] (credit Frants Jensen). (C) *Homo sapiens*. Image showing Hadza women roasting tubers (credit Alyssa Crittenden). (D–J) Survivorship and fecundity plots for vertebrate species that do and do not have prolonged PRLs: (D) chimpanzee; (E,F) *H. sapiens*; (G) long-finned pilot whale; (H) short-finned pilot whale; (I) resident killer whale; and (J) Asian elephant. (D–F) redrawn from [26], (G–I) from [85], and (J) from [14].

and somatic senescence generally occur at similar rates, variation in the relative timing of these processes will result in some individuals becoming post-reproductive before mortality [4]. Many examples of PRLs come from captive populations where individuals are released from extrinsic drivers of mortality (e.g., predators, disease) [8,11,12] or are subject to breeding programmes that can accelerate reproductive senescence [38,39]. Thus PRLs observed in

captivity are most likely an artefact of delayed somatic senescence and/or accelerated reproductive senescence.

Social and cultural factors can also result in a PRL for some individuals. For example, PRLs are common in men from some traditional societies [35]. However, unlike the women in these populations [36], male PRLs are the result of sociocultural constraints on opportunities for late-life reproduction rather than the physiological loss

### Box 1. Defining and measuring PRLSs

There are discrepancies in how the cessation of reproduction and PRLSs are defined, leading to confusion and misunderstandings. In humans reproductive cessation is generally defined operationally as the permanent cessation of menstruation (menopause) resulting from the loss of ovarian follicular activity [86]. In nonhuman animals in the wild, determining ovulation cycles presents a significant challenge and reproductive cessation is often measured as the age at last birth [87]. From an evolutionary perspective, it is the period of life after reproductive cessation that is of key interest. PRLSs are traditionally measured as the time between the end of fertility and the end of life (see [41] for a review) and is expressed as a population/species mean. Yet this measure is inherently biased because it includes only individuals that survive for a certain time after the last reproductive event and does not capture the importance of PRLSs for the population/species. This is elegantly illustrated in an example provided by Levitis *et al.* [36]: in a semi-wild population of *Macaca fuscata* the mean PRLS measured at the end of fertility (22 years) is 3.1 years, suggesting that PRLS may be an important life-history period. However, fewer than 5% of adult females survive to a post-fertile age, clearly demonstrating that post-reproductive life is rare in this population. Moreover, measures of PRLS tend to be correlated with longevity, making comparisons across species problematic (Figure 1). Recently a new measure – PrR [41] – has been proposed to quantify the significance of PRLSs and allow comparisons across populations/species. PrR is an unbiased population measure of reproductive lifespan. Under idealised demographic conditions, PrR equals the proportion of females that are post-reproductive. It 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 realised, 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 realised, on average, independent of mortality. PrR represents the number of years an average newborn can expect to live as a post-reproductive adult (beyond Age M) divided by the number of years an average newborn can expect to live as an adult (beyond Age B). Significance can be calculated using demographic simulations [41].



**Figure 1.** The relationship between PRLS (measured as the remaining life expectancy for individuals who survive beyond reproductive cessation) and life expectancy at birth for 63 species of captive primate [41]. Longevity clearly explains a significant proportion of the variation in PRLS among species (adjusted  $R^2 = 0.67$ ) and highlights difficulties in comparing PRLS between species with different overall longevities. Redrawn from [41].

of fertility [40]. Such patterns are not driven by the decoupling of reproductive and somatic senescence and thus do not generate an evolutionary paradox. Here we focus our attention on PRLSs that are driven by the permanent cessation of fertility.

What then is the evidence for PRLSs in nonhuman animals? Confusion has resulted from inconsistency in the definitions of menopause and PRLSs (Box 1). From an evolutionary perspective we want to know whether the rates of reproductive and somatic senescence have been decoupled in natural populations. We need to know not just whether post-reproductive females are observed in a population but also with what frequency and in what context they occur (Box 1). Recently, Levitis and Bingaman Lackey [41] proposed a new measure: post-reproductive representation (PrR) (Box 1) as a population measure of PRLS that allows comparisons across populations and species. We have collated female PrRs for published studies in Table 1. PrR is variable both within and among species and depends on population-specific mortality rates [41]. In humans, for example, PrR ranges from 0.31 in Trinidad plantation slaves to 0.76 in modern day Japan. In nonhuman primates, significant PrR values are observed only in captivity (Table 1), with healthy females living in the wild under natural mortality rates maintaining high birth rates late into life [26,42,43]. While elephants have a long lifespan, data on Asian elephants (*Elephas maximus*)

suggest that reproductive function is maintained into late life in semi-natural populations [14]. In insects, reproductive cessation has been reported in the gall-forming social aphid *Quadartus yoshinomiya* (Nipponaphidini), where post-reproductive females gain indirect fitness benefits through colony defence against predators (Figure 2) [18,19]. Among vertebrates, humans, resident killer whales (*Orcinus orca*), and short-finned pilot whales (*Globicephala macrorhynchus*) are distinct in their patterns of reproductive and somatic senescence (Figure 1) and a significant proportion of females in populations of these species are post-reproductive (Table 1).

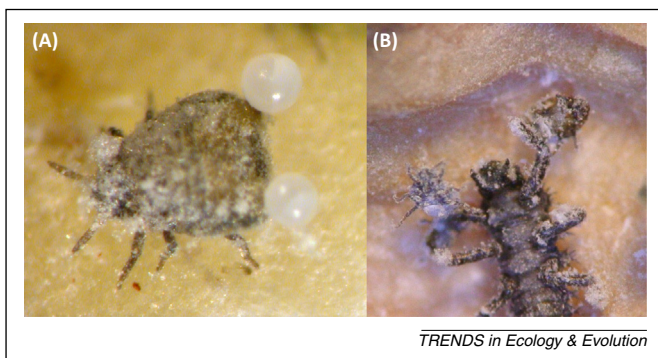
### Nonadaptive hypotheses for the evolution of prolonged life after reproduction

PRLSs in modern humans are often dismissed as an artefact: medicine and the protected environments of the contemporary world allow women to live beyond the supply of primary oocytes [44,45]. There is, however, considerable evidence that humans living with high rates of mortality and without access to modern medicine exhibit PRLSs (Box 2). Others have argued that post-reproductive longevity is an epiphenomenon of antagonistic pleiotropy favouring early-life fertility at the expense of fertility later in life [46] or that PRLSs have evolved as an insurance against the risk of dying by chance before the cessation of reproductive activity [47]. Recently it has been suggested that



**Table 1. Published values of female PrRr together with PrR for the resident killer whale calculated using published data [27] (see Box 1 for a further description of PrR)**

	Species	Population	PrR	Refs reporting PrR
Humans	<i>Homo sapiens</i>	Trinidad plantation slaves 1783–1816	0.315	[36]
	<i>H. sapiens</i>	!Kung	0.425	[36]
	<i>H. sapiens</i>	Ache	0.439	[36]
	<i>H. sapiens</i>	Haiti 2002	0.460	[36]
	<i>H. sapiens</i>	Sweden 1751	0.477	[36]
	<i>H. sapiens</i>	Hadza	0.481	[36]
	<i>H. sapiens</i>	Afghanistan 2002	0.486	[36]
	<i>H. sapiens</i>	Papua New Guinea 2002	0.489	[36]
	<i>H. sapiens</i>	Niger 2002	0.490	[36]
	<i>H. sapiens</i>	Somalia 2002	0.497	[36]
	<i>H. sapiens</i>	Pre-industrial Finns	0.512	[14]
	<i>H. sapiens</i>	UN Less Developed Regions 2002	0.607	[36]
	<i>H. sapiens</i>	UN Less Developed Countries 2002	0.643	[36]
	<i>H. sapiens</i>	USA 2002	0.668	[36]
	<i>H. sapiens</i>	Sweden 2002	0.707	[36]
<i>H. sapiens</i>	Japan 2002	0.760	[36]	
Nonhuman primates	Blue monkey ( <i>Cercopithecus mitis</i> )	Wild	0.02	[23]
	Blue monkey ( <i>C. mitis</i> )	Wild	0.041	[36]
	Chimpanzee ( <i>Pan troglodytes</i> )	Wild	0.018	[36]
	Chimpanzee ( <i>P. troglodytes</i> )	Wild	0.02	[23]
	Chimpanzee ( <i>P. troglodytes</i> )	Zoo	0.224	[36]
	Gorilla ( <i>Gorilla beringei</i> )	Wild	0.04	[23]
	Hamadryas baboon ( <i>Papio hamadryas</i> )	Wild	0.005	[36]
	Hamadryas baboon ( <i>P. hamadryas</i> )	Zoo	0.084	[36]
	Japanese macaque ( <i>Macaca fuscata</i> )	Semi-free ranging	0.054	[36]
	Japanese macaque ( <i>M. fuscata</i> )	Zoo	0.247	[36]
	Muriquis ( <i>Brachyteles hypoxanthus</i> )	Wild	0.06	[23]
	Rhesus macaque ( <i>Macaca mulatta</i> )	Wild	0.007	[36]
	Rhesus macaque ( <i>M. mulatta</i> )	Zoo	0.178	[36]
	Sifaka ( <i>Propithecus verreauxi</i> )	Wild	0.02	[23]
	White-faced capuchin ( <i>Cebus capucinus</i> )	Wild	0.04	[23]
Yellow baboon ( <i>Papio cynocephalus</i> )	Wild	0.01	[23]	
Others	Asian elephant ( <i>Elephas maximus</i> )	Semi-free ranging	0.128	[14]
	Short-finned pilot whale ( <i>Globicephala macrorhynchus</i> )	Wild	0.28	[41]
	Resident killer whale ( <i>Orcinus orca</i> )	Wild	0.22	



**Figure 2.** Post-reproductive females defend the colony in the gall-forming social aphid *Quadartus yoshinomiya* (Nipponaphidini). Colonies are founded when a female gives birth to a generation of wingless aphids. This wingless generation matures inside the gall and gives birth to a generation of winged daughters. Around the time that the gall opens, the wingless generation irreversibly switch from reproduction to defence (A) (credit Keigo Uematsu). These post-reproductive females move to the entrance of the gall to defend the colony from predators. Should a predator approach, post-reproductive females discharge a waxy secretion that solidifies around the predator, to which she becomes attached (B) (credit Keigo Uematsu). Post-reproductive females gain indirect fitness benefits through protecting their offspring from predation [18,19].

males have played a role in the evolution of female longevity: extended lifespan in females has been suggested to be a byproduct of selection on longevity in males [48,49] or due to a mating preference of older males for younger females [50]. Neither of these hypotheses, however, can explain why long-lived females cease reproduction. For solitary species or those that do not interact with kin, PRLSs are most likely a byproduct of selection on other traits. There is, however, mounting evidence that in humans, resident killer whales, and social aphids post-reproductive females increase the survival or reproductive success of their kin [18,19,27,51].

### Adaptive hypotheses

Adaptive hypotheses to explain the evolution of PRLSs are based on the impact that this trait might have on inclusive fitness. For species that live in kin groups, the magnitude of inclusive fitness effects depends on kinship dynamics (Box 3). Adaptive hypotheses have generally been tested using human historical demographic or ethnographic data on contemporary populations that have little or no access to modern health care or contraception [51–54]. However, adaptive hypotheses can and should be applied more

## Box 2. Human longevity: an artefact of modern environments?

Humans' exceptionally long lifespan following reproductive cessation has been suggested to be an artefact of modern medicine and the benign living conditions of the contemporary world [44,45,88]. This idea stems from estimated age distributions of skeletal remains from archaeological sites [8,89] and from studies showing that mean life expectancy at birth is close to 40 years in pre-industrial and hunter-gatherer societies [88]. However, the strength of the inferences made from these data has been questioned. Older individuals are less likely to be represented in the fossil record and adult ages can be underestimated using paleodemographic techniques [90]. Moreover, life expectancy at birth is greatly influenced by high infant and juvenile mortality rates [8,83,90]. A more informative measure of life expectancy and PRLSs is therefore one that considers only individuals that survive to adulthood (Box 1). Approximately three-quarters of girls that survive into adulthood in hunter-gatherer societies live past 45 years [91] and these girls can expect to live into their mid-60s on average (Figure 1). Overall, the ratio of females that live beyond the cessation of reproduction compared with those that do not is large in humans. This includes populations living in high-mortality environments, such as Trinidad plantation slaves. These slaves lived with mortality rates so high they would have led to rapid extinction if not for artificial replacement [36] and yet still a significant proportion of women in this population were post-reproductive (Table 1). The existence of prolonged PRLSs in nonhuman animals living in the wild (Figure 1) also clearly demonstrates that this unusual life-history trait can evolve in the absence of health care and under natural rates of mortality. Considerable inroads into our understanding of human longevity can be expected from future comparative research on the physiological and genomic markers of reproductive senescence and longevity as a powerful means to trace the life-history trajectories of our ancient ancestors.

widely to explain patterns of variation in PRLSs in other species (e.g., [55]).

### Hypotheses for helping kin in late life

Despite the obvious fitness costs associated with reproductive termination, post-reproductive females can continue to gain inclusive fitness benefits by helping their kin. Williams [1] suggested that females that terminate reproduction in mid-life gain fitness advantages by investing in previously born children (the 'mother hypothesis'). By stopping reproduction, females escape the increased risk of mortality associated with late-life pregnancy [56]. Similarly, Hawkes [5], suggests that post-reproductive females increase their inclusive fitness by supporting weaned grand-offspring that are dependent on provisioned food for some time following weaning (the 'grandmother hypothesis') [5].

In humans, there is considerable evidence that the death of a mother compromises her child's survival [57]. However, the impact of maternal death on offspring survival declines over time and might disappear entirely after weaning [57]. By contrast, resident killer whales mothers contribute to their offspring's survival well into adulthood [27]; in the year after their mother's death, mortality risk increases by 2.7 times in adult daughters and 8.3 times in adult sons (aged > 30 years). One potential explanation for the sensitivity of killer whales to maternal death is that post-reproductive mothers act as

repositories for ecological knowledge that is crucial to the survival of their adult offspring, particularly in times of hardship (Box 4). While substantial PRLSs have been reported in short-finned pilot whales, to the best of our knowledge no work has quantified whether PRLSs are adaptive in this species. This is clearly an exciting area for future work. Among invertebrates, some of the best evidence that post-reproductive mothers contribute to the survival of their adult offspring comes from work on the social aphid *Q. yoshinomiyai*, where wingless females switch from reproduction to colony defence (Figure 2).

Tests of the grandmother hypothesis in humans have generally reported that grand-offspring benefit from the presence of grandmothers (see [57] for a recent review). Both paternal and maternal grandmothers can act as helpers; Sear and Mace [57] reported that the presence of a maternal grandmother was associated with an increase in survival of grand-offspring in nine of 13 studies, compared with nine of 17 studies in the case of paternal grandmothers (Fisher exact test:  $P = 0.2$ ). By contrast, there is currently no evidence that the presence of a post-reproductive female benefits grand-offspring survival in resident killer whales [22].

However, evidence that post-reproductive females increase the survival of kin is not sufficient to demonstrate that PRLSs are adaptive. It is also necessary to show that PRLSs results in a net inclusive fitness benefit. Modelling of the mother hypothesis suggests that the costs of diverting resources from reproduction to alloparental care (along with the benefits of escaping the increased risk of mortality associated with reproducing later in life) are not sufficient to outweigh the benefits of continuing reproduction in humans [7,58]. By contrast, a recent model by Pavard *et al.* [59] suggests that PRLSs can evolve via the mother hypothesis. This is dependent on the assumption that the mortality risk of child birth makes late-life reproduction lethal for mothers [59]. Given that even in populations lacking access to modern medical care deaths during child birth are generally less than 3% [60,61], this assumption seems somewhat improbable.

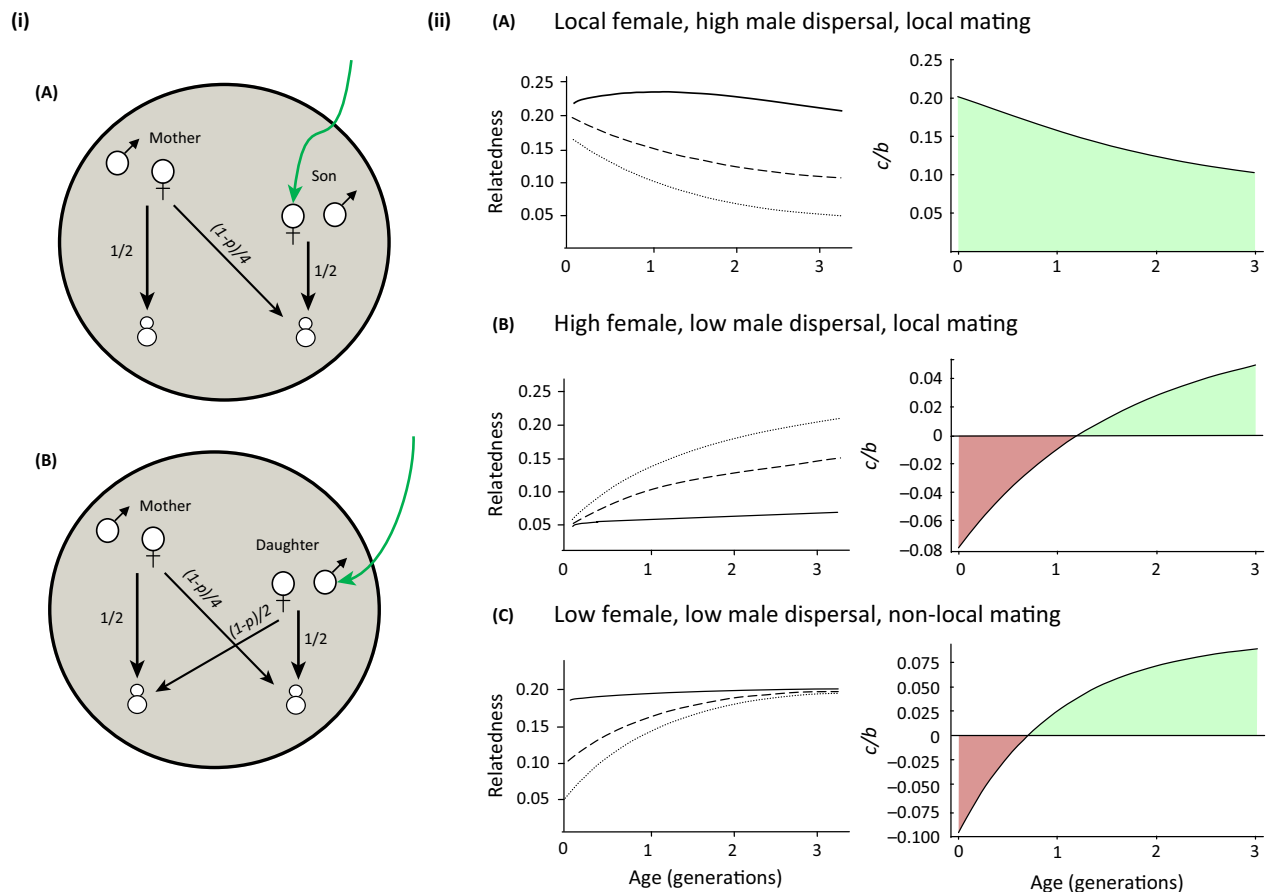
There is also mixed support for the grandmother hypothesis from studies that have modelled the inclusive fitness benefits of grandmothers in humans [7,54,58,62–64]. Models that support the grandmother hypothesis have tended to use the intrinsic rate of population increase as a measure of fitness and hence implicitly assume the PRLS to be a population-level adaptation [62,64]. Some of these models overestimate the benefits of grandmothers because they do not differentiate between the inclusive fitness benefits of rearing one's own offspring (to whom relatedness  $R = 0.5$ ) versus grand-offspring ( $R = 0.25$ ) [62]. Other models have fixed the age of last reproduction at 45 years [63,64]. Why the age at last reproduction should remain fixed in the face of selection for increased longevity is unclear, particularly given heritable variation in the timing of menopause in humans [65]. The assumptions of these models might explain why their results differ from the findings of earlier models that suggest the fitness benefits of a PRLS are not sufficient to fully explain its evolution [7,58].

**Box 3. Kinship dynamics**

The term kinship dynamics refers to the age-related changes in relatedness to local group members that occur over an individual's lifespan, as some individuals disperse away from the group and others die and are replaced [55]. In social mammals, dispersal is typically male biased [92], but several lines of evidence suggest that humans may have evolved in groups in which dispersal was female biased [55,60,69] (Figure 1). In these circumstances, theory predicts that older females should stop breeding when females of the next generation start to breed, which closely matches data from hunter-gatherers [69]. The model's predictions do not rely on strict patrilocality in ancestral humans, which remains a matter of debate [60,93,94]. Even a slight female bias in dispersal (a form of 'bilocality' [95]) favours younger females in reproductive competition with older females [69].

Cant and Johnstone's [69] model based on female-biased dispersal at first appears inapplicable to cetaceans that exhibit prolonged PRLSs, in which neither sex disperses and mating occurs between groups. To understand how alternative demographics influence selection on social traits, Johnstone and Cant [55] extended structured population genetic models [96,97] to derive general

formulae to predict the strength and direction of selection for helping and harming across the lifespan. The typical mammalian pattern of male-biased dispersal leads to females becoming less closely related to local offspring as they grow older (Figure 1iiA), but two unusual demographic patterns – female-biased dispersal (characteristic of Old World apes) and natal philopatry with extra-group mating (characteristic of cetaceans that show a PRLS) – both lead to an increase in local relatedness of female breeders to other group members with age. Hominins and cetaceans that exhibit prolonged PRLSs are, by virtue of their unusual demography, predisposed to evolve PRLSs and late-life helping (Figure 1iiB,C). Finally, Ubeda *et al.* [98] showed that the differing kinship dynamics of paternally inherited and maternally inherited alleles under ape-like demography may explain why menopause is preceded by a long period of endocrinological turbulence leading to unpleasant vasomotor symptoms such as hot flushes and night sweats. Societies with more extreme female bias in dispersal are predicted to exhibit a shorter perimenopause, less severe hormonal fluctuations, later menopause, and a reduced incidence of premature ovarian failure. This model has potentially important medical implications, but its predictions remain untested.



**Figure 1.** Kinship dynamics and their consequences for selection on social traits. Modified from [55,60]. (i) Schematics showing relatedness asymmetries within family groups given sex differences in dispersal. Male and female symbols represent parents. (A) Where females disperse and males are philopatric, a mother is related to the offspring of her daughter-in-law by  $(1 - p)/4$ , where  $p$  is the probability of extra-pair paternity. The daughter-in-law, by contrast, is unrelated to the mother's offspring and is predicted to outcompete the older female in reproductive competition. (B) Where females are the philopatric sex, relatedness asymmetries favour mothers in competition with their daughters. (ii) Effect of demography on patterns of age-specific relatedness and selection for social acts across the lifespan. Graphs on the left show age-specific relatedness to a breeding female of other females (unbroken lines) and of males (broken lines) in her group as a function of her age. The broken curves show mean relatedness to a female of other breeders, averaged across both sexes. Age is scaled in mean generation lengths. Results are plotted for three different demographic systems: (A) a low rate of female dispersal, a high rate of male dispersal, and mating occurring within the local group; (B) high female dispersal, low male dispersal, and local mating; and (C) low dispersal by both sexes with mating occurring outside the group. Graphs on the right show corresponding selection for helping (boosting the fecundity of other local breeders) and harming (reducing the fecundity of other local breeders) across the lifespan. A focal female can perform social acts that result in an immediate gain of  $b$  offspring for other breeders at an immediate cost  $c$  to herself. Red areas indicate selection for harming; green areas indicate selection for helping. See [55] for further details.



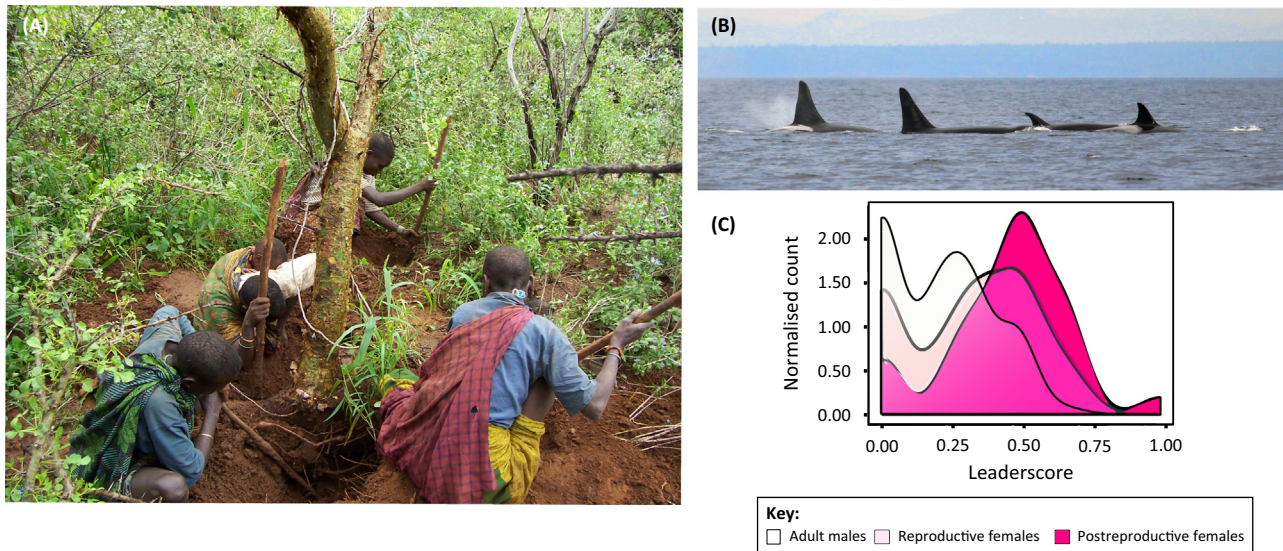
#### Box 4. Post-reproductive helpers

Understanding precisely how post-reproductive females help their relatives is critical to our understanding of the evolution of PRLSs. Post-reproductive females can help by capitalising on their two distinct characteristics: (i) they are typically the older members of a population; and (ii) they are no longer burdened with reproduction.

(i) With increased age comes increased experience of the social and physical environment. By sharing the information they have gathered over time, post-reproductive females can help their relatives to find food, detect predators, solve problems, navigate, and avoid social conflicts. For example, in wild resident killer whales post-reproductively aged females are more likely, compared with males and younger females, to lead groups as they travel around foraging grounds [82] (Figure 1B,C). Intriguingly, these females act as leaders especially in years with low resource abundance when their relatives have the most to gain from information on the location of food. However, the wisdom benefits of age are not limited to females that have ceased reproducing, and older females from other long-lived species also share information with their relatives. For example, groups of African elephants (*Loxodonta africana*) that contain an

older female respond more quickly to the calls of predators and rivals [68,99]. Menopause will only evolve when inclusive fitness benefits outweigh the costs of terminating reproduction and recent theoretical research suggests that kinship dynamics (Box 3) plays a key role in determining the costs and benefits of the PRLS.

(ii) Other forms of helping can be performed only by females who have stopped reproducing. For these females, post-reproductive helping can take the form of offspring care and predatory defence. Post-reproductive gall-forming aphids (Figure 2) break down their reproductive organs and develop glue glands, which they use to defend their relatives by fatally attaching themselves to predators [18,19]. In other species, helping can depend on a female's lack of reproduction as well as her age. Weight gain in weaned Hadza children is positively related to the amount of time their post-reproductive grandmother spends foraging for tubers [100] (Figure 1A). Only adults are strong enough to dig tubers from the earth [100] and elderly females may have expertise in obtaining this important resource. Post-reproductive Hadza women are probably also able to share food with their relatives because they do not have dependent offspring of their own.



**Figure 1.** (A) Hadza women digging for tubers (credit Alyssa Crittenden). (B) Leadership in resident killer whales. Post-reproductive mother (K14) leading adult daughter (K42), adult son (K26), and another adult male (J27) (credit David Ellifrit, Center for Whale Research). (C) Distribution of leaderscore for resident killer whales normalised to have the same area and smoothed using kernel density estimates, redrawn from [82]. Leaderscore was calculated as the number of times an individual led group movement in a year/the total number of times they were seen. Figure shows adult males (>12 years of age), reproductively aged females (12–34 years), and post-reproductively aged females ( $\geq 35$  years).

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The observation that age at last reproduction is very similar in humans and nonhuman primates [26,66] has also been taken as support for the grandmother hypothesis and as evidence that the extension of lifespan in humans is a derived trait. However, other long-lived mammals continue to reproduce until they die [14] and oocyte stocks are known to be variable among mammals [67]. Indeed, old female African elephants boost the reproductive success of their kin [68] while continuing to reproduce until the end of their natural lifespan [15]. Thus it seems that opposing selection has held back the female reproductive lifespan in humans (see [60] for a detailed discussion). The difficulty in demonstrating inclusive fitness benefits of PRLSs via mother and grandmother effects [7,58], combined with the hypothesised existence of opposing selection on

reproductive lifespan, has prompted a search for new adaptive explanations.

#### The reproductive conflict hypothesis

Recent theoretical work by Cant and Johnstone [55,69] suggests that conflict over resources for reproduction might be a critical missing term in previous inclusive fitness calculations [7,54,58,62]; that together, the inclusive fitness costs of reproductive conflict and the inclusive fitness benefits of late-life helping can explain the evolution of the PRLS (the ‘reproductive conflict hypothesis’). According to this hypothesis, two unusual patterns of demography are predicted to lead to an increase in the relatedness of breeding females to the local group as they age: female-biased dispersal and local mating (thought to

characterise ancestral humans [69]) and natal philopatry combined with nonlocal mating (characteristic of cetacean species that experience PRLSs [70]). Asymmetry in the relatedness of old and young females to local offspring could predispose humans and cetaceans to evolve reproductive cessation (Box 3). This model predicts that reproductive overlap between generations should involve substantial fitness costs, favouring early reproductive cessation and separation of reproductive generations [55,69]. The potential for intergenerational reproductive conflict in ancestral humans can explain the timing of reproductive cessation and why humans exhibit a very low degree of reproductive overlap compared with most other primate species [60].

Recent tests of the reproductive conflict hypothesis in humans have yielded mixed results [71–74]. Two studies have found evidence of the costs of reproductive conflict (also see [53]). First, in a study on pre-industrial Finns, Lahdenperä *et al.* [71] reported that simultaneous intergenerational reproduction resulted in a reduction in offspring survival of up to 66%, which, when combined with the risks of dying during child birth, were sufficient to generate selection against late-life reproduction. Similarly, Mace and Alvergne [72] found that when mothers were in competition with their own daughters they exhibited a slowed reproductive rate and an increased risk of infant death. The opposite effect, however, was found for unrelated females living in close proximity, with older women benefiting and younger women suffering costs of reproductive competition [72]. Work on historical Norwegian women found no evidence of costs of reproductive overlap [74]. In this study, however, the period of overlap was set to 15 years and thus the effects of reproductive competition early in life were diluted. In a study comparing age at menopause across ethnic groups with different patterns of post-marital residence, Snopkowski *et al.* [73] found no evidence that female-biased dispersal resulted in a quicker progression to menopause. It is possible that the evolutionary effects of reproductive conflict on the timing of menopause occurred in ancestral patrilocal societies and that modern humans share a similar age at menopause due to common descent. To date there have been no tests of the role of demography and reproductive conflict on the evolution of PRLSs in any nonhuman and there is clearly great potential for future work in this area.

### Why are PRLSs rare in natural populations?

Given that the capacity for post-fertility survival appears to be widespread, why are prolonged PRLSs restricted to just three vertebrate species? Significant benefits of females on offspring and grand-offspring survival post-weaning have been reported in nonhuman animals that do not exhibit a PRLS under natural conditions, such as red deer (*Cervus elaphus*) [75], chimpanzees (*Pan troglodytes*) [76], and Japanese macaques (*Macaca fuscata*) [77]. It appears that longevity alone does not necessarily lead to a PRLS [14] and that the unusual patterns of kinship dynamics in humans and some cetaceans might have predisposed them to the evolution of a PRLS (Box 3).

Kinship dynamics alone, however, are insufficient to explain the taxonomic distribution of PRLSs. Male

philopatry and female-biased dispersal occur in other primates such as the hamadryas baboon (*Papio hamadryas*) [78], which does not show a PRLS under natural conditions (Table 1). Moreover, as is the case for most cooperative-breeding birds [79], dispersal in the Seychelles warbler (*Acrocephalus sechellensis*), which shows grandmothering while maintaining reproductive capability [80], is female biased [81]. In carpenter bees (*Xylocopa pubescens*), old females displaced from the dominant breeding position guard the offspring of younger females (often their daughters [20]). In contrast to the social aphid *Q. yoshinomiya*, these old females appear to maintain reproductive capability [20].

Why, then, has a post-fertile lifespan not evolved in more species? We suggest that understanding how females compete for reproduction and help their kin, and how the magnitude of these costs and benefits change across the lifespan, is fundamental to understanding variation across species in the evolution of PRLSs (Box 4). We should expect females to forgo late-life reproduction only where doing so boosts the fitness of their kin and where helping is more effective if females are no longer reproducing themselves (Box 4). A broad inclusive fitness approach can be used to better understand life-history evolution in nonhuman animals [27] and give new insight into the evolutionary pressures that are likely to have shaped human life-history evolution [82].

### Concluding remarks

The question of why prolonged life after the cessation of fertility has evolved in some species has not been fully answered. There is substantial evidence that mothers and grandmothers provide significant survival and reproductive benefits to their children and grandchildren and that intergenerational reproductive conflict is detrimental in some societies. Yet there remains a great debate in the literature regarding which hypothesis explains the evolution of PRLSs. We believe that much of this debate is misguided. As with the study of any social trait, evolutionary explanations for PRLSs require an integrated approach that considers cooperation and competition in the same framework (Box 3). Determining what combination of positive and negative social effects has driven this unusual life-history trait presents a significant challenge and the results are likely to differ among populations and species. It is not a useful dichotomy to divide adaptive explanations into those based on ‘stopping early’ versus ‘living longer’ [83], because a prolonged post-fertile lifespan is the consequence of rapid reproductive senescence relative to somatic senescence; that is, the stopping of reproduction earlier than expected from lifespan. For toothed whales and humans, the challenge is to explain why reproductive lifespan has not extended commensurate with lifespan as it has in other long-lived social mammals such as elephants and blue whales [69]. We advocate that understanding patterns of reproductive conflict among kin and how this changes across the lifespan is fundamental to answering this question.

A major challenge for this research field is that empirical studies tend to be correlational, which make it difficult to infer causality. The recent finding of an adaptive



post-fertile lifespan in aphids [19] is an exciting development as it provides a tractable model system where experimental manipulation is possible. Studies on nonhuman animals provide an ideal opportunity to test the generality of the theoretical framework proposed to underpin the PRLS in humans. Hypotheses based on features that are common to social organisms can be adapted and extended to include nonhuman primates [69], cetaceans [53], and phylogenetically more distant species [18–20].

We report that significant PRLSs occur in only three vertebrate species living under natural conditions (Figure 1). It is likely that this conclusion is subject to type II error. For many cetaceans we simply lack sufficient data to determine whether they have a PRLS. With the limited data available, it seems that numerous other species of toothed whale might show accelerated rates of reproductive senescence [16]. Further research is needed to confirm whether PRLSs are common in other toothed whales. Moreover, resident killer whales are one of several killer whale ecotypes that differ in their prey specialisations, morphology, and kinship dynamics – female dispersal has been suggested in other ecotypes [84]. It is thus likely that different life-history patterns have evolved in the different killer whale ecotypes and we eagerly anticipate future work in this area. Widening the taxonomic testbed for the evolutionary theories of PRLSs certainly provides exciting opportunities for future research and will further our understanding of our own life-history evolution.

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