would have become firm friends and collaborators like I have with so many of the other people I met during this time.

Steven Pinker has a great paean to stereopsis in Chapter 4 of his book *How the Mind Works* that begins, "stereo vision is one of the glories of nature and a paradigm of how other parts of the mind might work". I saw first-hand how true this is during the four years that I spent in Bruce Cumming's lab at the National Eye Institute. More recently, it's been fascinating to turn my attention to stereopsis in praying mantids. These are the only invertebrates known to see in stereo, and I'm very excited about exploring this completely different form of stereopsis.

Do you have a scientific hero? That would probably be a nineteenth-century Prussian with an impressive moustache: Hermann von Helmholtz. I first knew him to be a physicist so was amazed to discover that he had made even greater contributions in 'physiological optics'. I haven't read all of his magnum opus, but I've always enjoyed the parts I have, complete with snarky asides about Ewald Hering. He was astonishingly ahead of his time, e.g. in developing the theory of perception as unconscious inference. Sometimes I think much of vision science is just filling in the details of Helmholtz…

Do you feel a push towards more applied science? How does that affect your own work? Yes, in the UK there certainly is such pressure. I'm not sure whether it's a good thing for science overall. However, personally, I have been gradually developing the applications of my own work. I'm working with industry to apply vision science to the development of next-generation visual displays, and I am using such displays myself to develop better clinical vision tests for children. I'm also exploring any possible applications of the stereo vision of the praying mantis for robotics. I find such applications really interesting and rewarding — though sometimes it's embarrassing when vision science can't answer apparently basic questions. And it's definitely motivating to think that your research might make a difference in the near term. So I consciously try to make sure that my research includes basic, clinical and industry-relevant strands.

What would you tell a young person are the pros and cons of a scientific career? The great pro is the science. Neuroscience is such an exciting and rapidly developing area within which to work — I try never to forget how lucky I am to be paid to think about such cool ideas. I love the fact that I'm always learning, adding skills and trying to master new material and new literature — it never stops! I also love scientific culture — its truly international nature, the openness to ideas, the 'holy obligation to strive for truth' discussed by Ione Fine and Horace Barlow in previous Q & As. There are considerable cons though, so I can't be too surprised at how many talented young people leave academia. The lack of job stability — being on short-term contracts until one is well into one's 30s or beyond and often needing to move nationally or internationally between jobs — is a barrier to family life. The constant rejection, of grants and papers, is a challenge to resilience. I worry about the high rates of mental illness that have been reported amongst PhD students and early career researchers, and I wonder how much this reflects structural problems in science.

Given these issues, how easy is it to combine science with family life? It has been relatively straightforward for me, but I'm very aware of how lucky I've been, most of all because I'm married to a wonderful man, Marc, who is an amazing father. He's never complained about being left to look after the kids at home while I go off to attend a conference or pursue a collaboration; he was even happy to move to the States for my career. Luckily, he's a teacher, which is a career that complements that of an academic very well — he can do the school holidays and I can do the last-minute 'sick child' days. Parental leave for young scientists is getting better in the UK, but it still needs work to minimise the career hit I think, and more could be done to help with flexible and affordable childcare. Being a parent is the joy of my life and certainly puts everything else into perspective — so long as the kids are all right, scientific failures are no big deal.

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Evolution of menopause

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Women experience menopause — the cessation of reproductive function — at around 50 years of age and typically live for decades after the end of fertility. Among mammals, only four species of toothed whales seem to show a similar pattern of early reproductive cessation followed by prolonged post-reproductive life. In this primer, we discuss the possible reasons for the evolution of this unusual life history trait, and why it is restricted to humans and to whales.

Menopause is one of the most striking and curious features of human life history. Women across the globe experience menopause at a similar age, with some geographical variation. But even in 'natural fertility' populations that lack access to modern medicine and technology, this is usually followed by many years of active life. Among the Hadza hunter gatherers of Tanzania, for example, 40% of newborn girls survive to 50 years, and those that reach this age can expect to live into their seventies (Figure 1). The ubiquity of menopause, despite vast differences in ecology and technology, suggests that it is an evolved feature of human reproductive physiology, not an artefact of modern living. How did this unusual life-history trait evolve, and is it related to other peculiar features of *Homo sapiens*?

These questions have attracted interest because classic life-history theory predicts that there should be no selection for survival past the end of reproduction. Physiological systems required for survival are predicted to senesce at similar rates to those required for reproduction, so organisms are expected to continue to reproduce, albeit with declining efficiency, across their lifespan. In women, one manifestation of reproductive senescence is the process of follicular atresia, the progressive depletion over time of the initial reserve stock of follicles in the

ovaries. Girls are born with several hundred thousand of these, each of which has the potential to mature and release its egg into the oviduct for fertilisation. For reasons that are still poorly understood, the initial follicle stock dies off rapidly through infancy and adulthood until, by around 50 years, too few follicles remain to sustain the hormonal feedbacks underlying monthly ovulation. By contrast, other bodily functions, such as nerve conduction velocity, lung and kidney function, decline more slowly into old age. Menopause is the result of disproportionately rapid reproductive senescence compared to somatic senescence in the human female (Figure 1).

The human pattern of reproductive cessation followed by prolonged post-reproductive life is rare among mammals, but not unique. Recent evidence suggests that four other mammals exhibit a similar life-history pattern in the wild, all of them toothed whales: killer whales, short-finned pilot whales, narwhals and beluga whales. A convenient metric to compare life histories across species is 'post-reproductive representation' (PrR), defined as the proportion of adult female years being lived by post-reproductive females. In most wild mammals, PrR is very close to zero, because females spend only a tiny fraction of their adult lives in a post-reproductive state. To illustrate, PrR values for chimpanzees and elephants are 0.01 and 0.04, respectively; whereas the PrR value for killer whales is 0.31, and is 0.44 in Hadza women (Figure 2). Killer-whale mothers typically cease reproduction in their late thirties or early forties, but can live into their seventies or eighties — a life history that is remarkably similar to that of human females living in natural fertility conditions.

The evolution of menopause

To explain the unusual duration of post-reproductive life in humans (and potentially in whales too), biologists have turned to what is now known as the 'grandmother hypothesis'. First proposed by Peter Medawar in his 1952 essay "An unsolved problem of biology", the hypothesis suggests that post-reproductive females who can no longer produce more children

of their own may nevertheless continue to promote their genetic contribution to future generations. Older females can do so by helping their existing offspring to survive and raise grandchildren (who will carry some of their grandmother's genes). In this way, genes that promote post-reproductive survival might be favoured by natural selection, driving the evolution of longer post-reproductive lifespans. If the grandmother hypothesis is right, then menopause is an outcome of kin selection, in which genes for post-reproductive helping behaviour spread because of the benefits their bearers confer on other, related beneficiaries, who are likely (due to their relatedness) to carry those same genes.

Medawar's suggestion was elaborated by George C. Williams in 1957 and William D. Hamilton in 1966, but became well known more recently thanks to pioneering research by Kristen Hawkes and colleagues, and emerging data on grandmother effects in natural fertility human populations. For example, maternal grandmothers were found to boost the survival of their grandoffspring in a rural Gambian population, and a remarkable dataset from 18th and 19th century Finland revealed that the presence of either a maternal or paternal post-reproductive grandmother was associated with a substantial increase in the lifetime reproductive success of her offspring. More recently still, studies of killer whales have shown that post-reproductive females may play a similar role in this species. The grandmother hypothesis thus seems to provide a plausible Darwinian explanation for prolonged post-reproductive survival

Empirical support for the helpful role of grandmothers, however, leaves some important questions unanswered. Although women who survive past the age of last reproduction can gain indirect fitness benefits by helping to raise grandchildren, it is not clear that these outweigh the potential benefits to be gained by continuing to bear more children of their own. Why then should women stop reproducing in the first place? A mother is related to
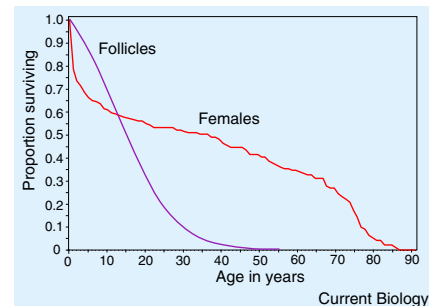

Figure 1. Menopause and senescence.
Menopause is the result of a mismatch between the rates of reproductive and somatic senescence. The red line shows survivorship data for Hadza women living without access to modern medicine or technology. Purple line shows predicted proportion of remaining ovarian follicles as a function of age, based on histological analyses from populations in Europe and Canada. Girls are born with an initial ovarian reserve of several hundred thousand primordial follicles. By age 40 around 3% of the maximum reserve remains. Hadza data from Blurton-Jones (2016), follicular attrition data from Wallace and Kelsey (2010; reproduced with permission).

her own offspring by a coefficient of one half, but to her grand-offspring only by a coefficient of one quarter. In Darwinian terms, therefore, it pays to give up having more children only if one can expect to help raise twice as many additional grandchildren by doing so. Proponents of the grandmother hypothesis point out that childbirth becomes increasingly dangerous with maternal age, and that children born later in their mother's life will enjoy her support for a shorter time. But even taking these factors into account, quantitative analyses of costs and benefits suggest that reproductive cessation occurs earlier than is optimal.

One possible explanation for the timing of menopause invokes the kin-selected costs of continued reproduction. While a helpful, post-reproductive grandmother can confer a fitness benefit on her existing children, a reproductively active grandmother who continues to reproduce alongside them may impose fitness costs. Human offspring are expensive to raise, and often rely on support from adults other than their parents, especially relatives. Hence, an older female who continues to bear children may deplete the supply of help available to her existing offspring. Recent evidence
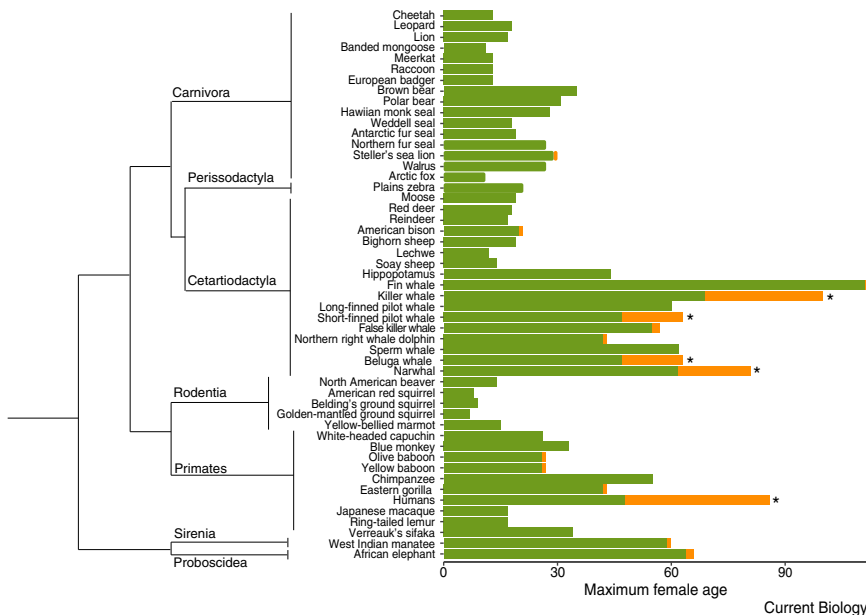
Figure 2. Menopause is rare in mammals.
Bars show the proportion of female years in the population being lived by reproductive (green) and postreproductive (orange) females, for 51 species of mammal (Ellis *et al.* 2018a, b; reproduced with permission). For five species, humans, killer whales, short-finned pilot whales, narwhals, and beluga whales, this proportion is significantly different from zero (Ellis *et al.* 2018a, b).

suggests that co-reproduction across generations can indeed reduce the fitness of the younger generation. Moreover, similar results have also been obtained for killer whales. So, just as kin-selected benefits offer a plausible, adaptive explanation for post-reproductive survival, kin-selected costs seem to help account for early reproductive cessation. The efficacy of this strategy in minimizing reproductive competition between generations is highlighted by the strikingly low degree of reproductive overlap between generations in humans and killer whales compared to non-menopausal mammal species.

The role of kin dynamics
One puzzle, however, still remains. Kin selection can favour individuals who forego the chance of reproducing themselves in order to help their relatives. But why, in humans and menopausal whales, is it older females who give up having young of their own, in order to assist younger beneficiaries? Biologists have identified and studied many examples of reproductive altruism in other species, but the great majority of these involve younger females

foregoing reproduction in order to assist older, established breeders. In some cases, such as birds who assist older females (often their mother or a close relative) as 'helpers at the nest', this may represent only a temporary strategy, with helpers eventually taking on the role of breeders later in life. In other organisms, such as eusocial ants and bees or the naked mole rat (the only eusocial mammal), some individuals may give up the chance for reproduction entirely and become sterile workers. But in all cases, it is younger helpers who assist older breeders. What makes menopause unusual is that it involves older, post-reproductive females helping younger breeders. Can this reversed pattern of help be understood in terms of kin selection?

A possible explanation is that due to patterns of dispersal and mating, females of menopausal species tend to become more closely related to other members of their social group as they age (Figure 3). This would favour kin-selected helping by older rather than younger females. For example, if younger females commonly leave their own natal social group to join that of their mate, they face potential

competition with their mothers-in-law. In this scenario, the inclusive fitness benefit of giving up direct reproduction to act as a helper is greater for the older female, because she is related to her daughter-in-law's children via her son (while the younger female is unrelated to her mother-in-law's children). By contrast, if daughters more often remain at home, and so face competition with their mothers, both relatedness and the potential benefits of helping are greater for the younger rather than the older female.

What was the typical pattern of dispersal in ancestral human populations? If it was on average female-biased, then the above argument could help to explain the evolution of menopause in our species. Dispersal is female-biased in other great apes (by contrast with most other primates), which might suggest that the same was true of our ancestors. However, the issue is controversial; genetic evidence for ancestral patterns of human dispersal is contradictory, and surveys of contemporary hunter-gatherer populations suggest that dispersal is rarely confined exclusively to one sex. Nevertheless, the argument requires only a female bias in dispersal, and studies of historical populations have shown that the kin-selected costs of reproductive overlap between generations are greater when the overlap involves mother-in-law and daughter-in-law rather than mother and daughter. These findings suggest that relatedness asymmetries between older and younger females do matter.

The strongest evidence that relatedness asymmetries have played a role in the evolution of menopause comes from a recent study of killer whales, the only other menopausal mammal for which long-term data are available to test these ideas. These whales exhibit very little dispersal by either sex, coupled with non-local mating. Theory predicts that this unusual pattern of dispersal should result in similar age-specific changes in relatedness to those observed in humans (Figure 3). Over 40 years of killer whale data showed that patterns of relatedness in killer whale groups are strikingly similar to those predicted by theory. Moreover, older females suffer more from reproductive overlap
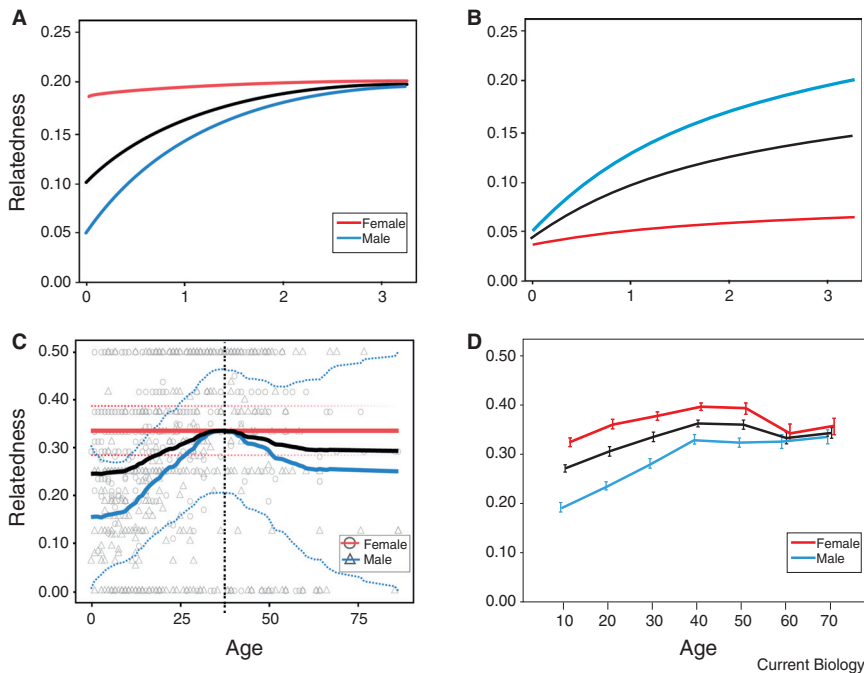
Figure 3. Demography influences patterns of kinship across the lifespan.
In most mammals dispersal is male-biased with the consequence that females are predicted to become less closely related to other group members as they age (Johnstone and Cant 2010; reproduced with permission). However, two unusual demographic systems, low dispersal of both sexes coupled with non-local mating, illustrated in panel (A), and female-biased dispersal coupled with local mating, illustrated in panel (B), result in females becoming more closely related to other group members as they get older. Red line, blue line, black line: relatedness to females, males, average group members, respectively. (C) Age-specific relatedness of females to other group members in resident killer whales matches the theoretical predictions, up to the end of reproduction (shown by vertical dashed line; Croft *et al*. 2017; reproduced with permission). In this population neither sex disperses and females mate with non-local males, corresponding to case (A) of the model. (D) Age-specific relatedness of females to other members of the household in 'duolocal' Mosuo in Sichuan province, China (with permission from Wu, J. J., He, Q. Q., Deng, L. L., Wang, S. C., Mace, R., Ji, T., and Tao, Y. (2013). Communal breeding promotes a matrilineal social system where husband and wife live apart. Proc. R. Soc. B. 280(1758), 20130010.; reproduced with permission). In the duolocal marital residence system females remain in their natal households but marry men who remain outside the group, again matching case (A) of the model.

between generations than younger females, again as theory predicts. In this species leadership by older, post-reproductive females is important for the survival of the group, particularly when food is scarce. These benefits conferred by post-reproductive females, together with the costs of intergenerational reproductive conflict, can explain why killer whales have evolved a menopausal life history so similar to that of humans.

In this article, we have focused on the ways in which patterns of kinship within a social group may shape female life histories. The same principles, however, apply to male life histories too. There is enormous sex-specific variation in mammalian life histories that remains very poorly understood.

Why, for instance, do males live substantially longer than females in bow-headed whales and Baird's beaked whales? Hopefully, studies of menopause will encourage biologists to investigate the impact of kinship dynamics on life history evolution more generally. In addition, evidence that somatic and reproductive senescence may be driven by rather different selective pressures suggests that there is more to learn about the ageing process, and the symptoms we experience when different physiological systems deteriorate independently over time. Lastly, while we have been chiefly concerned to understand the evolutionary causes of menopause, many of its evolutionary consequences remain to be explored. The dramatic

disparity between male and female life histories in menopausal species, for instance, gives rise to a marked skew in the sex-ratio of reproductively active adults, which is likely to influence the evolution of mating systems and the process of sexual selection. Understanding the causes and consequences of menopause may thus prove key to understanding the evolution of human life history as a whole.

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