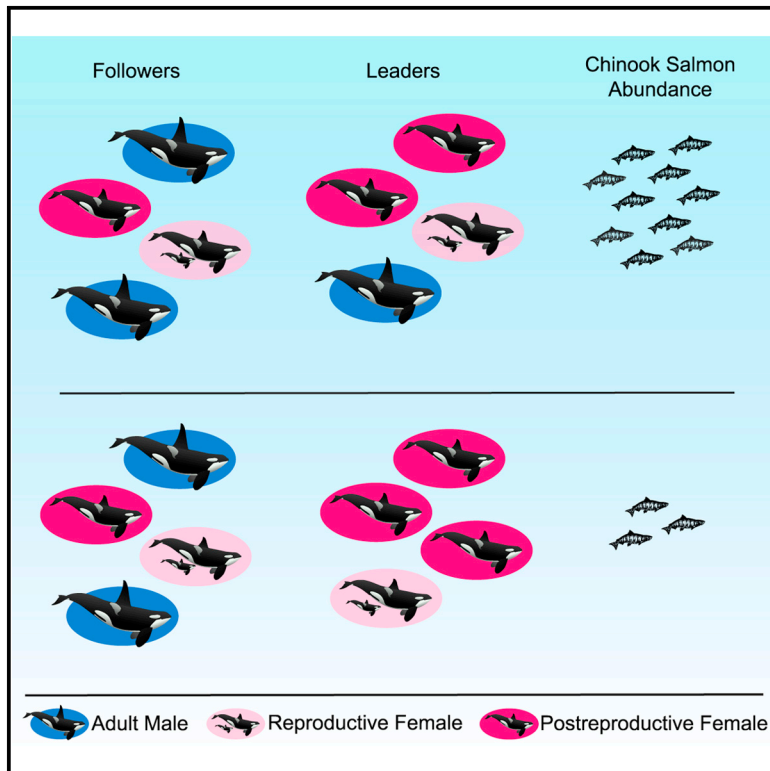


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Ecological Knowledge, Leadership, and the Evolution of Menopause in Killer Whales

Graphical Abstract



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In Brief

Brent et al. show that postreproductively aged female resident killer whales are more likely to lead collective movement. Leadership by these females is especially prominent in difficult years when salmon abundance is low. This is the first evidence that the wisdom of elders can drive selection on survival following the termination of reproduction.

Highlights

- Postreproductively aged female resident killer whales lead collective movement
- Leadership by postreproductive females is most prominent when food abundance is low
- Sons are more likely than daughters to follow their mothers

Ecological Knowledge, Leadership, and the Evolution of Menopause in Killer Whales

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Summary

Classic life-history theory predicts that menopause should not occur because there should be no selection for survival after the cessation of reproduction [1]. Yet, human females routinely live 30 years after they have stopped reproducing [2]. Only two other species—killer whales (*Orcinus orca*) and short-finned pilot whales (*Globicephala macrorhynchus*) [3, 4]—have comparable postreproductive lifespans. In theory, menopause can evolve via inclusive fitness benefits [5, 6], but the mechanisms by which postreproductive females help their kin remain enigmatic. One hypothesis is that postreproductive females act as repositories of ecological knowledge and thereby buffer kin against environmental hardships [7, 8]. We provide the first test of this hypothesis using a unique long-term dataset on wild resident killer whales. We show three key results. First, postreproductively aged females lead groups during collective movement in salmon foraging grounds. Second, leadership by postreproductively aged females is especially prominent in difficult years when salmon abundance is low. This finding is critical because salmon abundance drives both mortality and reproductive success in resident killer whales [9, 10]. Third, females are more likely to lead their sons than they are to lead their daughters, supporting predictions of recent models [5] of the evolution of menopause based on kinship dynamics. Our results show that postreproductive females may boost the fitness of kin through the transfer of ecological knowledge. The value gained from the wisdom of elders can help explain why female resident killer whales and humans continue to live long after they have stopped reproducing.

Results

There is mounting evidence that menopause evolved via inclusive fitness benefits gained by helping kin; both postreproductive humans [11–14] and killer whales [15] increase the reproductive success and/or survival of their relatives.

But how postreproductive females help their kin remains enigmatic. Individual animals gain knowledge about their environments as they age [16–18] and can transfer this information to group mates [19]. Like early humans, killer whales and pilot whales rely on food whose availability varies widely in space and time [20, 21]. One hypothesis for the evolution of menopause via inclusive fitness is, therefore, that postreproductive females buffer their kin against environmental hardships by storing and providing ecological information on the location and timing of resources [7, 8]. But this hypothesis remains untested.

To test the hypothesis that postreproductive females act as repositories of ecological knowledge, we determined whether postreproductively aged female killer whales occupy leadership positions during group movement in and around salmon foraging grounds. Female resident killer whales generally breed between the ages of 12 and 40 but can survive into their 90s [4]. Males, on the other hand, rarely survive beyond 50 [4]. In resident killer whales, neither sex disperses from the maternal group, and both adult males and females remain with their mothers [22]. Resident killer whales forage in groups and feed predominantly on salmon, with Chinook salmon, *Oncorhynchus tshawytscha*, making up more than 90% of their diet during the summer salmon migration [23, 24]. Salmon abundance varies considerably in space and time [25, 26], fluctuating annually due to anthropogenic impacts and El Niño events [25, 26], and is an important driver of both reproductive success and mortality in resident killer whales [9, 10]. As such, individual killer whales with information on where and when to find salmon could provide other group members with considerable benefits.

We predicted that, compared to other adults (i.e., adult males and reproductively aged females), postreproductively aged females would be more likely to lead group movement in and around salmon foraging grounds. We also predicted that postreproductively aged females would be especially likely to lead group movement in years when their primary food source was in low supply and therefore potentially more difficult to locate. To quantify leadership, we analyzed 751 hr of video footage of Southern resident killer whales in the coastal waters of British Columbia and Washington engaged in directional travel (Figure 1A; Movie S1), collected during nine summer salmon migrations (2001–2009). Multigenerational demographic records have been recorded for the Southern population of resident killer whales since 1976, allowing us to determine relatedness among subjects. Observations were made on a total of 102 individuals (N = 58 females, 44 males) ranging from 0 to 91 years of age (Table S3). We classified the individual at the front of a traveling group as the leader [27, 28] and all other individuals as followers (Figure 1B; Table S3).

Who Leads?

We found that adult females were more likely to lead group movement compared to adult males (permutation-based binomial regression on the number of times an adult whale was a leader in a given year relative to the number of times they were a follower, regression coefficient = -0.93 , $p < 0.0001$; Table S2; Figure 1C). Among adult females, postreproductively

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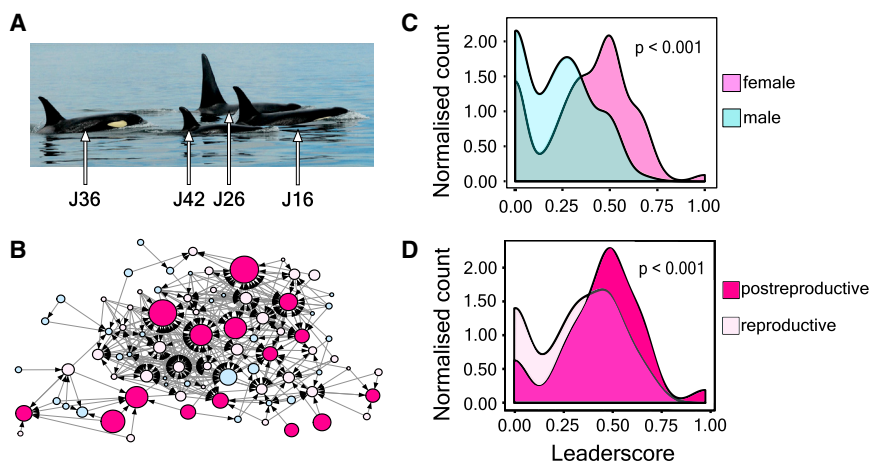


Figure 1. Postreproductively Aged Female Killer Whales Lead Group Movement

(A) A postreproductively aged female, J16, leads her adult son and two adult daughters. (Photo credit: Dave Ellifrit, Center for Whale Research.) (B) In this example leadership network (year 2003), arrows point toward leaders. Age increases with node size. Dark pink nodes represent postreproductively aged females, light pink nodes represent reproductively aged and juvenile females, and blue nodes represent males. (C) Distribution of “leader score” values by sex, normalized to have the same area and smoothed using kernel density estimates. Leader score values are used for visualization only and were calculated as number of times an individual led a group movement in a year/the total number of times they were seen. Statistical results are based on permutation-based binomial regression models in which the dependent variable was the number of times a whale was a leader

in a given year relative to the number of times they were a follower. Adult females were significantly more likely to lead compared to adult males ($N = 48$ females, 24 males, 419 whale years), controlling for the impact of age on leadership. (See also [Figure S2](#).) (D) Distribution of leader scores in adult females. Postreproductively aged females (35+ years of age) were significantly more likely to lead compared to reproductively aged females (12–34 years of age) ($N = 23$ postreproductive females, 32 reproductive females, 307 whale years).

aged whales (≥ 35 years old, which is the mean age at last reproduction for Southern resident females that lived past the age of peak adult female mortality) were more likely to lead group movement compared to reproductively aged females (regression coefficient = 0.50, $p < 0.001$; [Table S2](#); [Figure 1D](#)).

Leading in Times of Environmental Hardship

We next asked whether postreproductively aged females were more likely to lead groups during years with low availability of their primary food resource. We used test-fisheries data [[29](#)] to quantify Chinook salmon abundance in our study area ([Figure S1](#)). We found a significant relationship between leadership and the interaction between salmon abundance and female reproductive state (permutation-based binomial regression on the number of times an adult female was a leader in a given year relative to the number of times they were a follower, regression coefficient = -0.67 , $p = 0.048$; [Table S2](#)). While leadership in reproductively aged adult females was constant, leadership by postreproductively aged females was negatively related to salmon abundance: postreproductively aged females were more likely to lead group movement in years when salmon abundance was low ([Figure 2](#)). These results demonstrate that in times of food scarcity, postreproductive female killer whales play a prominent role in leading group movement.

Who Follows?

Because neither sex disperses from the maternal group in resident killer whales, theory based on kinship dynamics [[5](#)] predicts that a female’s relatedness to her group increases with age and that old mothers maximize their fitness by ensuring their offspring’s survival and reproductive success. A previous study of this population showed that adult whales benefit from their mother’s presence: in the year after their mother’s death, mortality risk increases up to 2.7-fold in adult daughters and 8.7-fold in adult sons [[15](#)]. Observed differential benefits accrued by sons and daughters accord with recent theory [[5](#)] that predicts that resident killer whale mothers should direct more help toward sons than daughters because sons offer greater potential inclusive fitness benefits. Sons have higher

reproductive potential and mate outside the group; thus, their offspring do not compete for resources within the matriline. If postreproductive mothers support sons disproportionately over daughters, we should therefore expect differential patterns of following by male and female offspring. Females also live longer than males and have greater opportunities to obtain information about the environment. Males may therefore rely more on the ecological knowledge of older females. We therefore also examined patterns of following and predicted that (1) compared to females, males would be more likely to follow their mother, and (2) all whales would prefer to follow postreproductively aged females, but this preference would be particularly strong in males. We determined the likelihood with which males and females followed their mothers while controlling for their tendency to follow postreproductively aged females and vice versa ([Table S1](#)). Other potentially important factors, such as age of the follower, were also accounted for.

Males were more likely than females to follow their mother (permutation-based binomial model on data recording the number of times individual A followed individual B relative to the number of times A did not follow B, regression coefficient = 0.39, $p < 0.001$; [Table S2](#); [Figure 3A](#)). There was no overall difference in the rate at which whales followed their mothers compared to non-mothers (regression coefficient = 0.86, $p = 0.059$; [Table S2](#); [Figure 3A](#)), which may be because non-mothers included adult sisters and grandmothers, whom individuals are also likely to follow. Whales were also more likely to follow postreproductively aged females compared to reproductively aged females (regression coefficient = 0.62, $p = 0.002$; [Table S2](#); [Figure 3B](#)), but there were no differences between the sexes: males and females followed postreproductive leaders the same amount (regression coefficient = 0.33, $p = 0.111$; [Table S2](#); [Figure 3B](#)). We explored whether this relationship differed over time, i.e., in relation to salmon abundance, but again found no difference between the sexes: both males and females were more likely to follow postreproductively aged leaders compared to reproductively aged leaders in years with low salmon abundance (regression coefficient = 0.20, $p = 0.366$; [Table S2](#)). Thus, while males were significantly

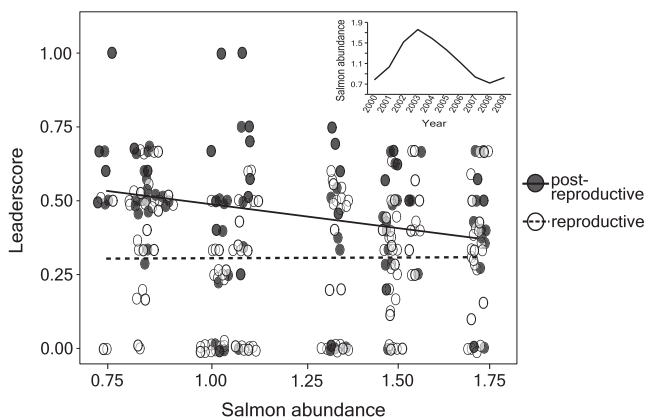


Figure 2. Postreproductively Aged Female Killer Whales Are More Likely to Lead Group Movement Compared to Reproductively Aged Females in Times of Low Salmon Abundance

As in [Figure 1](#), leader score is used for visualization (N = 48 females, 307 whale years). Analyses were based on permutation-based binomial regression models that account for repeated measures on individuals, sampling biases, and the impact of group size (see [Figure S3](#)). Inset: abundance of Chinook salmon in the study area per year of study, measured as the number of fish caught divided by the total catch for the reference period from 1979 to 1982.

more likely to follow their mother than females were, both males and females preferred to follow postreproductive females and did so particularly in years with low resource abundance.

Discussion

Our results provide the first evidence that a benefit of prolonged life after reproduction is that postreproductive individuals act as repositories of ecological knowledge. Postreproductively aged female killer whales lead group movement in and around salmon foraging grounds, and this is exaggerated when salmon are in low supply and the selective pressure to locate food is at its highest.

It has been suggested that menopause in humans is simply an artifact of modern medicine and improved living conditions [30]. However, mounting evidence suggests that menopause in humans is adaptive. Living beyond 60 in hunter-gatherer populations is more common than previously believed [31], and women with a prolonged postreproductive lifespan have greater inclusive fitness because their offspring breed earlier and more frequently [13]. In hunter-gatherers, one way that menopausal women help their relatives, and thus improve their own inclusive fitness, is by sharing food [32]. Menopausal women may also share another key commodity—information. Humans were preliterate for almost the entirety of our evolutionary history [8], and information was necessarily stored in individuals. The oldest and most experienced individuals were those most likely to know where and when to find food, particularly during dangerous and infrequent conditions such as drought [8, 33]. Wild resident killer whales do not have the benefits of medical care, but, similar to humans, females can live for more than 40 years after they have ceased reproducing [4]. An individual resident killer whale’s ability to find salmon is crucial to their fitness; in years with low salmon abundance, resident killer whales are more likely to die and less likely to reproduce [9, 10]. Our finding that postreproductively aged female killer whales are especially likely to lead group movement

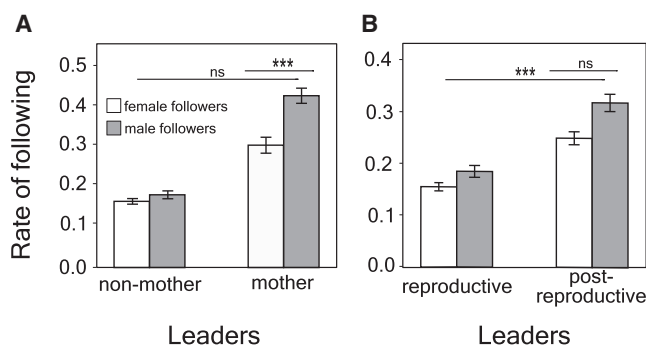


Figure 3. Who Do Killer Whales Follow?

Statistical results are based on a permutation-based binomial regression model in which the dependent variable was the number of times a specific individual A followed a specific leader B in a given year relative to the number of times that those two individuals were observed traveling together when B was not leading A. For ease of visualization, we plot the rate of following (error bars = SEM), calculated as the number of times A followed B, divided by the number of times A and B were observed in a given year, which accounts for differences in encounter frequency and for the fact that individuals cannot follow each other if they do not travel together.

(A) Compared to female followers, males were especially likely to follow their mother (N = 136 mother-offspring pairs, N = 6,821 pairs where the potential leader was an adult female but not the mother of the potential follower).

(B) All whales were more likely to follow postreproductively aged female leaders compared to reproductively aged female leaders, with no differences between male and female followers.

in years with low salmon abundance suggests that the ecological knowledge of elders helps explain why females of this species live long after they have stopped reproducing. Postreproductive female killer whales may provide other knowledge to their relatives. For example, postreproductive members of this socially complex species may have greater social knowledge that could help kin navigate social interactions. Further work is needed to test this hypothesis. As one of the only other menopausal mammals, and as a species that does not transfer information via written communication, killer whales may provide insight into how menopause evolved in preliterate humans.

In accordance with past theoretical predictions based on kinship dynamics [5], we also found that mothers are more likely to lead their sons, the sex through which they can gain the greatest inclusive fitness benefits. This finding may also explain previously observed sex differences in survivorship in relation to the death of mothers in this population: sons have a greater probability of dying compared to daughters following the death of their postreproductively aged mother [15], suggesting that sons have the most to gain from following their mothers. Seminal theoretical models [19, 34] have shown that information can be transferred through moving animal groups without the use of signals and in the absence of group members’ knowing which individuals have information. Therefore, although it is unlikely (and unnecessary) that males know whether their mothers have information [19], their tendency to follow their mothers could be regulated by their bond to her and reinforced by positive interactions, e.g., food sharing.

If Many Animals Share Experience Gained with Age, Why Is Menopause Rare?

Understanding the mechanisms and functions of collective knowledge and collective decision-making has been a major

focus of empirical and theoretical work over the last decade [34]. Although significant progress has been made, the evolutionary consequences of collective cognition remain poorly understood. In the present study, our finding that older, post-reproductively aged female resident killer whales lead group movement clearly demonstrates the potential of collective cognition to shape the evolution of life-history traits, such as menopause. The wisdom benefits of age are likely to be widespread, and recent research has shown that older individuals in a range of taxa can improve the ability of groups to navigate, solve problems, and respond to potential dangers [17, 18, 35, 36]. For instance, the reproductive success of African elephants (*Loxodonta africana*) is enhanced in the presence of older female relatives, who are more capable of assessing social and predatory threats [17, 36]. Given the widespread potential for older individuals living in kin-structured societies to gain inclusive fitness benefits by sharing information, why is menopause restricted to some toothed whales and humans? Menopause will only evolve when inclusive fitness benefits outweigh the costs of terminating reproduction. Recent theoretical research suggests that kinship dynamics play a key role in determining the costs and benefits of menopause [5, 12]. In humans, resident killer whales, and short-finned pilot whales, a female's mean local relatedness to her group, and thus the benefits she can gain through helping her relatives, increases with age [5]. For example, in resident killer whales, where neither sex disperses [22], females are born into groups with their mothers and older siblings. As a female ages, the relatives she has lost due to their death are replaced by her own nondispersing sons and daughters. In ancestral humans, similar age-related increases in relatedness were driven by female-biased dispersal [5]. Both cases contrast with most long-lived mammals, where sons disperse from their natal groups and where a female's mean local relatedness either declines or is relatively constant throughout her lifetime [5]. In humans, resident killer whales, and short-finned pilot whales, the benefits of helping therefore increase with age, which is thought to predispose these three species to menopause.

Resident killer whales are just one of a number of killer whale ecotypes, which differ in their prey specialization, morphology, and behavior, and which in some cases represent genetically distinct populations [37, 38]. Evidence suggests that not all ecotypes are characterized by the same social structure as resident killer whales [39], with female dispersal putatively occurring in some of the other ecotypes. Whether or not menopause occurs in other killer whale ecotypes is therefore an important question for future research.

Identifying the mechanisms by which postreproductive females contribute to the survival and reproductive success of kin is essential to understanding how menopause evolved. Since the benefits conferred through knowledge are likely to grow rather than diminish with age, helping through the transfer of information may be an important driver of the evolution of menopause. Together, our findings clearly point toward postreproductive females' providing important information to their relatives and as such support the hypothesis that helping relatives is one mechanism that led to the evolution of menopause.

Supplemental Information

Supplemental Information includes three figures, three tables, Supplemental Experimental Procedures, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.01.037>.

Author Contributions

D.W.F., E.A.F., and D.P.C. conceived the study. Field data were collected by E.A.F. and K.C.B. Videos were coded by E.A.F. Statistical analyses were performed by L.J.N.B., D.W.F., and D.P.C. L.J.N.B. wrote the first draft of the manuscript with input from D.P.C., D.W.F., and M.A.C. All authors contributed to the final draft of the manuscript.

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