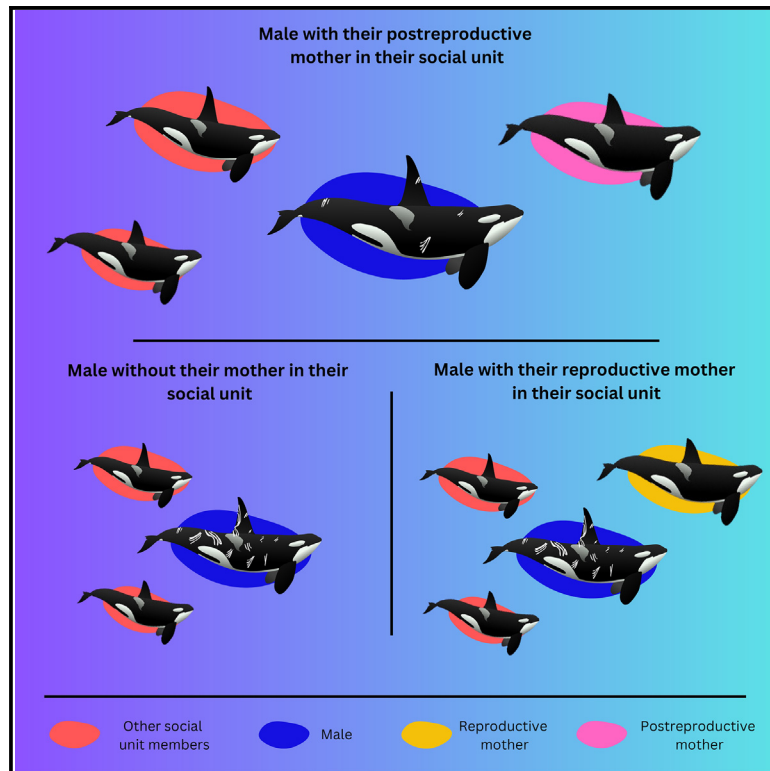


Current Biology

Postreproductive female killer whales reduce socially inflicted injuries in their male offspring

Graphical abstract



Authors

Charli Grimes, Lauren J.N. Brent, Samuel Ellis, Michael N. Weiss, Daniel W. Franks, David K. Ellifrit, Darren P. Croft

Correspondence

cg565@exeter.ac.uk (C.G.),
d.p.croft@exeter.ac.uk (D.P.C.)

In brief

Grimes et al. show that in resident killer whales, socially inflicted injuries are lower for males in the presence of their postreproductive mothers. The same effect is not observed in females, providing evidence that social support is directed toward male offspring, and may be a key pathway by which postreproductive females help their relatives.

Highlights

- Postreproductive females lower the number of injuries their sons receive
- Similar effects are not observed in daughters or grandoffspring of either sex
- Older females direct social care toward male offspring, not the whole social unit



Report

Postreproductive female killer whales reduce socially inflicted injuries in their male offspring

Charli Grimes,^{1,5,*} Lauren J.N. Brent,^{1,4} Samuel Ellis,^{1,4} Michael N. Weiss,^{1,3,4} Daniel W. Franks,² David K. Ellifrit,³ and Darren P. Croft^{1,*}

¹Centre for Research in Animal Behaviour, University of Exeter, EX4 4QG Exeter, UK

²Department of Biology, University of York, YO10 5DD York, UK

³Center for Whale Research, Friday Harbor, WA 98250, USA

⁴These authors contributed equally

⁵Lead contact

*Correspondence: cg565@exeter.ac.uk (C.G.), d.p.croft@exeter.ac.uk (D.P.C.)

<https://doi.org/10.1016/j.cub.2023.06.039>

SUMMARY

Understanding the evolution of menopause presents a long-standing scientific challenge^{1–3}—why should females cease ovulation prior to the end of their natural lifespan? In human societies, intergenerational resource transfers, for example, food sharing and caregiving, are thought to have played a key role in the evolution of menopause, providing a pathway by which postreproductive females can boost the fitness of their kin.^{4–6} To date however, other late-life contributions that postreproductive females may provide their kin have not been well studied. Here, we test the hypothesis that postreproductive female resident killer whales (*Orcinus orca*) provide social support to their offspring by reducing the socially inflicted injuries they experience. We found that socially inflicted injuries, as quantified by tooth rake marks, are lower for male offspring in the presence of their postreproductive mother. In contrast, we find no evidence that postreproductive mothers reduce rake marking in their daughters. Similarly, we find no evidence that either reproductive mothers or grandmothers (reproductive or postreproductive) reduce socially inflicted injuries in their offspring and grandoffspring, respectively. Moreover, we find that postreproductive females have no effect on reducing the rake marks for whales in their social unit who are not their offspring. Taken together, our results highlight that directing late-life support may be a key pathway by which postreproductive females transfer social benefits to their male offspring.

RESULTS

Classic life-history theory predicts there should be no selection for survival following the cessation of reproduction.⁷ In humans and five species of toothed whales, however, females continue to live well beyond their reproductive years.^{3,8,9} In hunter-gatherer societies, for example, females that reach sexual maturity can expect to live for 26 years following menopause,⁸ and in killer whales (*Orcinus orca*), females can expect to live 22 years (southern-resident ecotype;¹⁰). Unraveling the evolutionary origins of menopause is a long-standing interdisciplinary challenge.^{1–3} In human societies there is overwhelming evidence that mothers can provide significant fitness benefits to their offspring and grandoffspring via intergenerational resource transfers in the form of food sharing and caregiving.^{4,11–13} Similarly, in resident killer whale societies, postreproductive females act as repositories for ecological knowledge of when and where to find food¹⁴ and directly share 57% of fish they catch.¹⁵ Furthermore, these females have been shown to provide a survival advantage to not only their offspring (particularly adult males¹⁶) but also their grandoffspring.¹⁷

Resource transfer is not the only way postreproductive females may benefit their kin and they may take on other social roles in family groups. For example, in human societies, women can play an important role in conflict management¹⁸ and older women may have greater social influence.¹⁹ Evidence from some small-scale human societies also suggests that women occupy key leadership roles in the context of within-group conflict resolution.^{20,21} However, the extent to which such social roles have shaped the evolution of menopause remains unknown.

We used tooth rake marks—the thin, white, parallel lines that appear as the result of the teeth of another animal puncturing the skin²²—to quantify socially inflicted injuries (Figure 1). Where direct observations of behavior in marine mammals are difficult to observe, tooth rake markings on the skin's surface provide clear indirect evidence of social interactions.^{22–27} Killer whales are the ocean's apex predator and have no natural predators other than humans. Moreover, resident killer whales are exclusively fish-eating,²⁸ and thus do not prey on species that could inflict rake marks, meaning that all observed rakes are acquired through intraspecific social interactions.²⁹ Killer whales, like many other





Figure 1. Image on left shows tooth rake marks on the dorsal fin and anterior peduncle of a male killer whale and close-up image of the dorsal fin (right) shows damage from rake marks resulting in open wounds

Photograph courtesy of the Center for Whale Research.

cetacean species, exhibit tooth rake marks across all age classes,^{29–34} with male resident killer whales typically displaying a higher average number of these marks than females.²⁹ Biting has been found to be closely associated with aggressive behavior in several species of toothed whales,^{35,36} and rake marks have commonly been used to assess relative rates of intraspecific aggression in a range of cetacean species.^{22,23,25,35} Rake marks also likely occur as the result of rough play in killer whales²⁹ and interactions that start playful can often turn aggressive in toothed whales,²⁵ resulting in physical injury.

We used a unique dataset including nearly 50 years of multi-generational demographic records for 103 wild resident-ecotype (fish-eating) killer whales, 6,934 photos quantifying socially inflicted injuries, and comprehensive resource (salmon) abundance data to test the hypothesis that postreproductive females reduce socially inflicted injuries in their offspring and grandoffspring. Specifically, we analyzed the relationship between the composition of the social unit and socially inflicted injuries in the presence or absence of (1) an individual's postreproductive mother or grandmother or (2) their reproductive mother or grandmother. To determine whether postreproductive females provide general support to all members of their social unit, not just their offspring and grandoffspring, we also examined the rake mark patterns of individuals who did not have their mother in their social unit but had a postreproductive female present who was not their mother or grandmother.

We use “rake density” as our measure of social injury, which was defined as the proportion of pixels of an individual's skin (visible in a photograph) that were raked at a given time.²⁹ This is expressed in all models as a binomial draw of the number of rake pixels, given the number of pixels visible (see STAR Methods).

Do mothers reduce socially inflicted injuries in offspring?

We first examine the direct causal effects of maternal presence on rake marks, observing that males exhibit lower rake density when their postreproductive mother is in their social unit, compared with males with their reproductive mother (post.

mean = -0.55 , 95% CI = $[-0.83, -0.26]$, Figure 2A) or no mother within their social unit (post. mean = -0.76 , 95% CI = $[-1.24, -0.28]$, Figure 2A). This provides strong evidence that postreproductive females lower the rake density their male offspring receive. No difference in rake density was observed between males whose reproductive mother was present in their social unit and males with no mother in their social unit (post. mean = 0.16 , 95% CI = $[-0.20, 0.54]$, Figure 2A). In contrast, no difference in rake density was observed between females with their postreproductive mother in their social unit and females with their reproductive mother (post. mean = 0.016 , 95% CI = $[-0.26, 0.32]$, Figure 2B), or with no mother in their social unit (post. mean = -0.17 , 95% CI = $[-0.56, 0.21]$). Similarly, our results indicate no difference in rake density between females whose reproductive mother was present in their social unit and those whose mother was not present in their social unit (post. mean = -0.21 , 95% CI = $[-0.54, 0.10]$, Figure 2B).

Do grandmothers reduce socially inflicted injuries in grandoffspring?

In contrast to the mother effects, we find no evidence that the presence of grandmothers is associated with a lower rake density for their male or female grandoffspring, regardless of her reproductive status. We observed no difference in rake density between males with their postreproductive grandmother in their social unit and males with their reproductive grandmother (post. mean = -0.25 , 95% CI = $[-0.77, 0.32]$, Figure 3A) or with no grandmother in their social unit (post. mean = -0.18 , 95% CI = $[-0.59, 0.22]$, Figure 3A). Females exhibit the same patterns, with no difference in rake density observed between females with their postreproductive grandmother, reproductive grandmother (post. mean = -0.43 , 95% CI = $[-1.24, 0.44]$), or no grandmother present in their social unit (post. mean = -0.34 , 95% CI = $[-0.78, 0.07]$, Figure 3B).

Is social support directed to offspring or do postreproductive females benefit other social unit members?

To establish if postreproductive females are directing their support to male offspring, or if the presence of a postreproductive female in a social unit provides general benefits to other group members—for example, by mediating social conflict across the social unit as a whole—we examined the effect of the presence of a postreproductive female, who was not the mother or grandmother of the focal individual, on rake density. We found no evidence that the presence of a postreproductive female affects the rake density exhibited by non-offspring or grandoffspring of either sex in the social unit (males: post. mean = -0.01 , 95% CI = $[-0.37, 0.33]$, Figure 2A, and females: post. mean = 0.03 , 95% CI = $[-0.31, 0.34]$, Figure 2B).

DISCUSSION

Here, we show that socially inflicted injuries are lower for male offspring in the presence of their mother, but only when she is postreproductive. We find that this social support does not extend to female offspring, grandoffspring, or non-offspring social unit members, demonstrating that postreproductive mothers direct their support toward male offspring, and there is not a

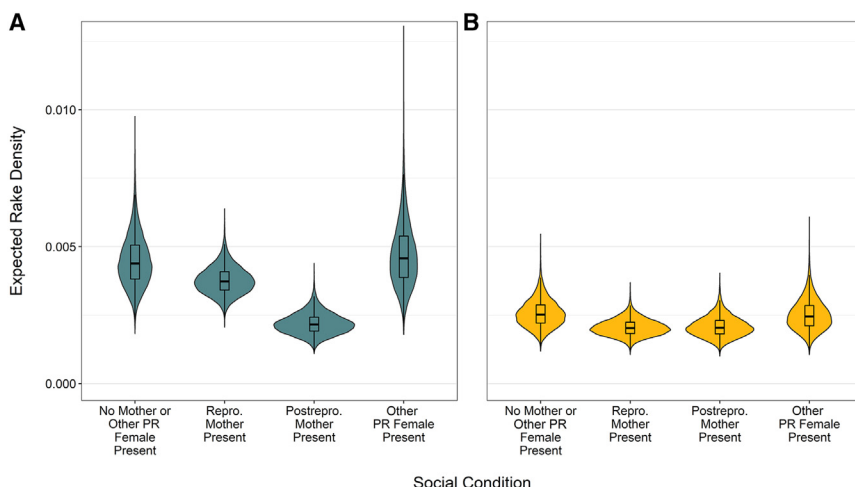


Figure 2. Violin plots derived from posterior distributions of a model examining maternal presence effects on rake density for males and females

Plots show the difference in expected rake density between (A) males and (B) females in different social conditions. Repro. denotes reproductive and Postrepro./PR denotes postreproductive. Distributions show the model-derived predicted rake density of a hypothetical 12-year-old whale, with all other covariates held to their mean. Boxes span the first to third quartiles, the horizontal line inside the boxes represents the median, and the thin vertical lines represent the upper and lower adjacent values.

general effect of postreproductive females modulating the behavior of their social group as a whole.

Menopause is hypothesized to have evolved, in part, through the inclusive fitness benefits associated with ceasing reproduction and assisting offspring to survive and reproduce.¹ In human societies, there is strong evidence that postreproductive females can benefit the reproductive success of their offspring^{4–6} and survival of grandoffspring.³⁷ Like humans, a prominent feature of resident killer whale societies is the indirect fitness contributions females make in late life toward the survival and reproduction of their kin.^{14,16,17} Previous research in resident killer whales has established that resource transfer is a key mechanism by which postreproductive females help their kin—directly via food sharing^{15,38} or indirectly through leadership in group foraging.¹⁴ Here, we provide the first evidence that postreproductive females also benefit their male offspring by reducing their socially inflicted injuries.

An unusual feature of resident killer whale societies is that male killer whales remain in close association with their mothers for the duration of their lives,³⁹ which may enable them to benefit in a number of ways from the social support provided by their postreproductive mothers. First, damage to the skin provides a route of infection for pathogens that could lead to increased mortality.^{40,41} Resident killer whales are regularly exposed to environmental pathogens via the sea surface layer.^{42,43} Infectious diseases have been found to cause mortality across all age classes in wild killer whales,⁴⁰ and necropsies of killer whales from the west coast of the USA and Canada indicate that pathogens introduced through wounds can lead to mortality.⁴⁰ Second, the reduction in injuries of sons with postreproductive mothers maybe due to postreproductive females providing agonistic support to sons during aggressive interactions with other males, which could provide reproductive benefits. In Bigg's (mammal-eating) killer whales, for example, although both sexes disperse from the natal group as they mature, postreproductive females often travel with their adult sons^{44,45} and have been observed to aid their sons in intergroup agonistic interactions.⁴⁶ In bonobos (*Pan paniscus*), mothers support their sons during conflict with other males, which translates to a higher paternity success of their son.^{47,48} Female resident killer whales may be able to provide this support without directly engaging in aggressive

interactions. In human hunter-gatherer societies, for example, women use vocal and behavioral gestures to mediate group conflict,⁴⁹ rather than physically involving themselves as a third party in conflict. In resident killer whales, postreproductive females exhibit the lowest rake density of all age classes,²⁹ potentially reflecting a lack of direct physical involvement in conflict. Though tooth rake marks are an indication of socially inflicted wounds, injuries may be obtained in other ways that are more difficult to quantify. Severe injuries resulting from trauma, such as ramming and blunt force, have been reported in other species of dolphin^{35,36,50} and in Bigg's killer whales.⁴⁶ More direct observations of these behaviors are required in the resident killer whale population in order to determine which behavioral strategies are employed during social interactions. Future work using high-resolution video collected from unoccupied aerial vehicles⁵¹ provides an exciting opportunity to quantify the type of social support postreproductive females provide their offspring and how sons benefit from this support.

Our finding that old (postreproductive) but not young (reproductive) mothers provide social support to their sons raises the question of what role social support has played in the evolution of menopause in killer whales? In resident killer whales neither sons nor daughters disperse, which results in an increase in a female's relatedness to her local group as she ages. Females are initially born into a group without their father, however, as they start to reproduce they recruit male offspring to their group, increasing their local relatedness to males and the group as a whole.^{52–54} These patterns of kinship dynamics will select for increased helping and decreased harming in older females as compared with younger females.^{54,55} Reproduction is a form of generalized harm because it increases within-group resource competition.^{56,57} Kinship dynamics in resident killer whales means that older females are under increased selection not to harm by reproducing than are younger females. This reproductive conflict hypothesis⁵⁵ is supported in resident killer whales where, as predicted by theory, older females lose out in reproductive competition with younger females.⁵³ Intergenerational reproductive conflict provides a mechanism to help explain why females terminate reproduction well before the end of their expected adult lifespan.⁵⁵ However, for a prolonged postreproductive lifespan to evolve there needs to be a pathway by which postreproductive females can help their kin.⁵⁸ Previous evidence, combined with the results presented here, suggests

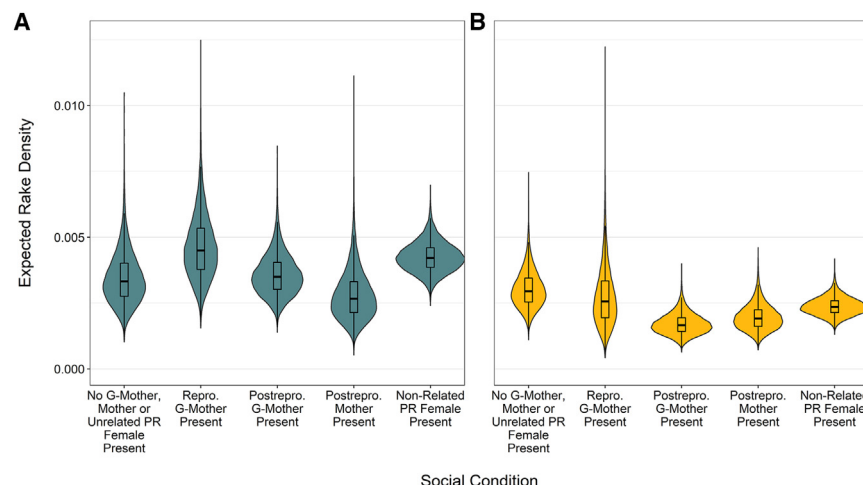


Figure 3. Violin plots derived from posterior distributions of a model examining if grand-mother presence effects rake density for males and females

Plots show the difference in expected rake density between (A) males and (B) females in different social conditions. Repro. denotes reproductive, Postrepro./PR denotes postreproductive and G-mother denotes grandmother. Distributions show the model-derived predicted rake density of a hypothetical 12-year-old whale, with all other covariates held to their mean. Boxes span the first to third quartiles, the horizontal line inside the boxes represents the median, and the thin vertical lines represent the upper and lower adjacent values.

that in resident killer whales this pathway is via increasing the survival (and thus reproductive success) of their adult sons,¹⁶ which carries a significant cost to mothers.⁵⁹ In addition to food sharing, knowledge transfer is likely to have played a key role in the evolution of menopause in both killer whales and humans,⁶⁰ and we have shown previously that postreproductive females act as repositories for ecological knowledge of when and where to find food.¹⁴ It is also likely that knowledge is important in providing social support and that older postreproductive females have knowledge and experience that younger (reproductive) females lack. Killer whales live in a multi-level society where all individuals in the population can interact³⁹ and postreproductive mothers may have knowledge of other social groups that helps navigate and avoid conflict.⁶¹ For example, in African elephants (*Loxodonta africana*) older females in the social group have superior knowledge of other social groups that can reduce intergroup aggression.⁵¹ Future research examining the role that postreproductive females play during intergroup interactions in killer whales would be particularly valuable.

Why is support directed to sons rather than daughters? This pattern of maternal care can be explained by kinship dynamics theory, which predicts that females should preferentially direct helping behavior toward their sons.⁵⁴ Outgroup mating means that when a daughter reproduces, the calf is reared within the social group, which is costly for the local group. In contrast, when a son reproduces another social group carries the cost of rearing the calf and thus mothers can maximize their inclusive fitness benefits by preferentially helping their sons over their daughters.⁵⁴ Consistent with this prediction and our findings presented here, previous work has found that mothers provide a greater survival benefit to their male over their female offspring¹⁶ and that mothers show lifelong investment in their male offspring.⁵⁹

Given the matrilineal, philopatric structure of resident killer whale societies³⁹ and the survival benefits postreproductive grandmothers provide to their grandoffspring,¹⁷ multigenerational influences on patterns of social conflict might be expected in this population. However, we find no evidence that grandmothers provide social support to their grandoffspring, irrespective of their reproductive state. Postreproductive females may provide survival benefits to their grandoffspring in other ways, for example, through sharing ecological knowledge of when

and where to find food.¹⁴ Our results show that directed social support is, however, focused on their sons.

Taken together, our findings provide strong evidence that social support and mediation of participation in risky behavior is likely to be a key pathway by which postreproductive females contribute to the reproductive success and survival of their male offspring and, when taken together with our previous findings,^{14,16,53} can help explain why killer whales have evolved the longest postreproductive lifespan of all non-human animals.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead contact
 - Materials availability
 - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
 - Study population: Southern resident killer whales
 - Tooth rake mark coding
 - Social unit membership and estimated relatedness
 - Social unit composition
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2023.06.039>.

ACKNOWLEDGMENTS

We thank our colleagues who collected the observational data over the past four decades, particularly Erin Heydenrich, Astrid van Ginneken, and the late Ken Balcomb. Our thanks extend to our colleagues at the Centre for Research in Animal Behaviour at the University of Exeter for their valuable input on the project. Support for this research was provided by a Natural Environment Research Council grant (NE/S010327/1). S.E. also acknowledges support from a Leverhulme Early Career Research Fellowship. Data collection was supported in the southern resident population by funding from Earthwatch

Institute and NOAA Fisheries. We would like to dedicate this work to our late colleague Ken Balcomb, whose passion for the whales will continue to inspire our future work.

AUTHOR CONTRIBUTIONS

C.G., L.J.N.B., M.N.W., S.E., D.K.E., and D.P.C. conceived the project. C.G. conducted statistical analysis with input from S.E., M.N.W., D.W.F., and D.P.C. Field work was conducted by D.K.E. and M.N.W. C.G. crafted the initial version of the manuscript with input from D.P.C. and all authors contributed to subsequent drafts. Funding was acquired by D.P.C., D.W.F., and S.E.

DECLARATION OF INTERESTS

The authors declare that they have no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as a gender minority in their field of research. One or more of the authors of this paper self-identifies as living with a disability. We avoided “helicopter science” practices by including the participating local contributors from the region where we conducted the research as authors on the paper. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

Received: May 1, 2023

Revised: June 13, 2023

Accepted: June 13, 2023

Published: July 20, 2023

REFERENCES

- Williams, G.C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11, 398–411.
- Packer, C., Tatar, M., and Collins, A. (1998). Reproductive cessation in female mammals. *Nature* 392, 807–811.
- Croft, D.P., Brent, L.J.N., Franks, D.W., and Cant, M.A. (2015). The evolution of prolonged life after reproduction. *Trends Ecol. Evol.* 30, 407–416. <https://doi.org/10.1016/j.tree.2015.04.011>.
- Mace, R., and Sear, R. (2007). Are humans cooperative breeders? In *Grandmotherhood: The Evolutionary Significance of the Second Half of Female Life*, E. Voland, A. Chasiotis, and W. Schiefelhoevel, eds. (Rutgers University Press), pp. 143–159.
- Sear, R., Mace, R., and McGregor, I.A. (2000). Maternal grandmothers improve nutritional status and survival of children in rural Gambia. *Proc. Biol. Sci.* 267, 1641–1647. <https://doi.org/10.1098/rspb.2000.1190>.
- Voland, E., and Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhörn. *Behav. Ecol. Sociobiol.* 52, 435–443. <https://doi.org/10.1007/s00265-002-0539-2>.
- Hamilton, W.D. (1966). The moulding of senescence by natural selection. *J. Theor. Biol.* 12, 12–45. [https://doi.org/10.1016/0022-5193\(66\)90184-6](https://doi.org/10.1016/0022-5193(66)90184-6).
- Ellis, S., Franks, D.W., Natrass, S., Cant, M.A., Bradley, D.L., Giles, D., Balcomb, K.C., and Croft, D.P. (2018). Postreproductive lifespans are rare in mammals. *Ecol. Evol.* 8, 2482–2494. <https://doi.org/10.1002/ece3.3856>.
- Ellis, S., Franks, D.W., Natrass, S., Currie, T.E., Cant, M.A., Giles, D., Balcomb, K.C., and Croft, D.P. (2018). Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. *Sci. Rep.* 8, 12833. <https://doi.org/10.1038/s41598-018-31047-8>.
- Nielsen, M.L.K., Ellis, S., Towers, J.R., Doniol-Valcroze, T., Franks, D.W., Cant, M.A., Weiss, M.N., Johnstone, R.A., Balcomb, K.C., Ellifrit, D.K., and Croft, D.P. (2021). A long postreproductive life span is a shared trait among genetically distinct killer whale populations. *Ecol. Evol.* 11, 9123–9136. <https://doi.org/10.1002/ece3.7756>.
- Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M., and Russell, A.F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* 428, 178–181. <https://doi.org/10.1038/nature02367>.
- Shanley, D.P., Sear, R., Mace, R., and Kirkwood, T.B.L. (2007). Testing evolutionary theories of menopause. *Proc. Biol. Sci.* 274, 2943–2949. <https://doi.org/10.1098/rspb.2007.1028>.
- Chapman, S.N., Lahdenperä, M., Pettay, J.E., Lynch, R.F., and Lummaa, V. (2021). Offspring fertility and grandchild survival enhanced by maternal grandmothers in a pre-industrial human society. *Sci. Rep.* 11, 1–11. <https://doi.org/10.1038/s41598-021-83353-3>.
- Brent, L.J.N., Franks, D.W., Foster, E.A., Balcomb, K.C., Cant, M.A., and Croft, D.P. (2015). Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr. Biol.* 25, 746–750. <https://doi.org/10.1016/j.cub.2015.01.037>.
- Wright, B.M., Stredulinsky, E.H., Ellis, G.M., and Ford, J.K. (2016). Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*. *Anim. Behav.* 115, 81–95. <https://doi.org/10.1016/j.anbehav.2016.02.025>.
- Foster, E.A., Franks, D.W., Mazzi, S., Darden, S.K., Balcomb, K.C., Ford, J.K.B., and Croft, D.P. (2012). Adaptive prolonged postreproductive life span in killer whales. *Science* 337, 1313. <https://doi.org/10.1126/science.1224198>.
- Natrass, S., Croft, D.P., Ellis, S., Cant, M.A., Weiss, M.N., Wright, B.M., Stredulinsky, E., Doniol-Valcroze, T., Ford, J.K.B., Balcomb, K.C., and Franks, D.W. (2019). Postreproductive killer whale grandmothers improve the survival of their grandoffspring. *Proc. Natl. Acad. Sci. USA* 116, 26669–26673. <https://doi.org/10.1073/pnas.1903844116>.
- Smith, J.E., Ortiz, C.A., Buhbe, M.T., and van Vugt, M. (2020). Obstacles and opportunities for female leadership in mammalian societies: A comparative perspective. *Leadersh. Q.* 31, 101267. <https://doi.org/10.1016/j.leaqua.2018.09.005>.
- Brown, J.K., and Kerns, V. (1985). In *Her Prime: A New View of Middle-Aged Women*, J. Brown, and V. Kerns, eds. (University of Illinois Press). <https://doi.org/10.2307/2069956>.
- Smith, J.E., Gavrillets, S., Mulder, M.B., Hooper, P.L., Mouden, C.E., Nettle, D., Hauert, C., Hill, K., Perry, S., Pusey, A.E., et al. (2016). Leadership in Mammalian Societies : Emergence , Distribution , Power , and Payoff. *Trends Ecol. Evol.* 31, 54–66. <https://doi.org/10.1016/j.tree.2015.09.013>.
- von Rueden, C., Alami, S., Kaplan, H., and Gurven, M. (2018). Sex differences in political leadership in an egalitarian society. *Evol. Hum. Behav.* 39, 402–411. <https://doi.org/10.1016/j.evolhumbehav.2018.03.005>.
- Mccann, C. (1974). Body scarring on cetacea-odontocetes. *Sci. Reports Whales Res. Inst.* 26, 145–155.
- MacLeod, C.D. (1998). Intraspecific scarring in odontocete cetaceans: An indicator of male “quality” in aggressive social interactions? *J. Zool.* 244, 71–77. <https://doi.org/10.1017/S0952836998001083>.
- Heithaus, M.R. (2001). Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): A review. *J. Zool.* 253, 53–68. <https://doi.org/10.1017/S0952836901000061>.
- Connor, R.C., Watson-Capps, J.J., Sargeant, B.L., Scott, E.M., and Mann, J. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Beyond Behav.* 142, 21–44. <https://doi.org/10.1163/1568539053627712>.
- Luksenburg, J.A. (2014). Prevalence of external injuries in small cetaceans in Aruban waters, southern Caribbean. *PLoS One* 9, e88988. <https://doi.org/10.1371/journal.pone.0088988>.
- Robeck, T.R., St. Leger, J.A., Robeck, H.E., Nilson, E., and Dold, C. (2019). Evidence of variable agonistic behavior in killer Whales (*Orcinus orca*) based on age, sex, and ecotype. *Aquat. Mamm.* 45, 430–446. <https://doi.org/10.1578/AM.45.4.2019.430>.

28. Ford, J.K.B., Ellis, G.M., and Balcomb, K.C. (2000). Killer whales: The natural history and genealogy of *Orcinus orca* in British Columbia and Washington State Second (UBC Press).
29. Grimes, C., Brent, L.J.N., Weiss, M.N., Franks, D.W., Balcomb, K.C., Ellifrit, D.K., Ellis, S., and Croft, D.P. (2022). The effect of age, sex, and resource abundance on patterns of rake markings in resident killer whales (*Orcinus orca*). *Mar. Mamm. Sci.* 38, 941–958. <https://doi.org/10.1111/mms.12908>.
30. Olson, P.A., and Gerrodette, T. (2008). Killer Whales of the Eastern Tropical Pacific: A Catalog of Photo-Identified Individuals. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC 428, 126.
31. Tixier, P., Gasco, N., Roche, C., and Guinet, C. (2010). Killer whales of the Crozet Islands Austral and Antarctic French Territories: photo-identification catalogue 2010. *Cent. D'études Biol. DeChize CNRS Villiers En Bois*.
32. Towers, J.R., Ellis, G.M., and Ford, J.K.B. (2015). Photo-identification Catalogue and Status of the Northern Resident Killer Whale Population in 2014. In Canadian Technical Report of Fisheries and Aquatic Sciences, 3139.
33. Mruscok, M.-T. (2017). Killer whales of West Iceland (West Iceland Nature Research Centre (Náttúrustofa Vesturlands)).
34. Towers, J.R., Sutton, G.J., Shaw, T.J.H., Malleon, M., Matkin, D., Gisborne, B., Forde, J., Ellifrit, D., Ellis, G.M., Ford, J.K.B., et al. (2019). Photo-identification catalogue, population status, and distribution of Bigg's killer whales known from coastal waters of British Columbia, Canada. *Can. Tech. Rep. Fish. Aquat. Sci.* 305.
35. Samuels, A., and Gifford, T. (1997). A quantitative assessment of dominance relations among bottlenose dolphins. *Mar. Mamm. Sci.* 13, 70–99.
36. Connor, R.C., Wells, R.S., Mann, J., and Read, A.J. (2000). The bottlenose dolphin: Social Relationships in a Fission-Fusion Society. In *Cetacean Societies: Field Studies of Dolphins and Whales*, J. Mann, R.C. Connor, P.L. Tyack, and H. Whitehead, eds. (University of Chicago Press), pp. 91–126.
37. Ukonaho, S., Chapman, S.N., Briga, M., and Lummaa, V. (2023). Grandmother presence improved grandchild survival against childhood infections but not vaccination coverage in historical Finns. *Proc. Biol. Sci.* 290, 20230690.
38. Ford, J.K.B., and Ellis, G.M. (2006). Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Mar. Ecol. Prog. Ser.* 316, 185–199. <https://doi.org/10.3354/meps316185>.
39. Olesik, P.F., Bigg, M.A., and Ellis, G.M. (1990). Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. - Int. Whal. Comm. Spec. Issue* 12, 209–243.
40. Raverty, S., Leger, J.S., Noren, D.P., Huntington, K.B., Rotstein, D.S., Gulland, F.M.D., Ford, J.K.B., Bradley Hanson, M., Lambourn, D.M., Huggins, J., et al. (2020). Pathology findings and correlation with body condition index in stranded killer whales (*Orcinus orca*) in the northeastern Pacific and Hawaii from 2004 to 2013. *PLoS One* 15, 1–31. <https://doi.org/10.1371/journal.pone.0242505>.
41. Raverty, S. (2016). Final Report AHC Case: 16-1760.. 7pp.
42. Gaydos, J.K., Balcomb, K.C., Osborne, R.W., and Dierauf, L. (2004). Evaluating potential infectious disease threats for southern resident killer whales, *Orcinus orca*: A model for endangered species. *Biol. Conserv.* 117, 253–262. <https://doi.org/10.1016/j.biocon.2003.07.004>.
43. Raverty, S.A., Rhodes, L.D., Zabek, E., Eshghi, A., Cameron, C.E., Hanson, M.B., and Schroeder, J.P. (2017). Respiratory Microbiome of Endangered Southern Resident Killer Whales and Microbiota of Surrounding Sea Surface Microlayer in the Eastern North Pacific. *Sci. Rep.* 7, 394. <https://doi.org/10.1038/s41598-017-00457-5>.
44. Baird, R.W., and Whitehead, H. (2000). Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* 78, 2096–2105. <https://doi.org/10.1139/cjz-78-12-2096>.
45. Nielsen, M.L.K., Ellis, S., Weiss, M.N., Towers, J.R., Doniol-valcroze, T., Franks, D.W., Cant, M.A., Ellis, G.M., Ford, J.K.B., Malleon, M., et al. (2023). Temporal dynamics of mother – offspring relationships in Bigg's killer whales : opportunities for kin-directed help by post-reproductive females. *Proc. R. Soc. A B.* 290.
46. Towers, J.R., Hallé, M.J., Symonds, H.K., Sutton, G.J., Morton, A.B., Spong, P., Borrowman, J.P., and Ford, J.K.B. (2018). Infanticide in a mammal-eating killer whale population. *Sci. Rep.* 8, 1–8. <https://doi.org/10.1038/s41598-018-22714-x>.
47. Surbeck, M., Mundry, R., and Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proc. Biol. Sci.* 278, 590–598. <https://doi.org/10.1098/rspb.2010.1572>.
48. Surbeck, M., Boesch, C., Crockford, C., Thompson, M.E., Furuichi, T., Fruth, B., Hohmann, G., Ishizuka, S., Machanda, Z., Muller, M.N., et al. (2019). Males with a mother living in their group have higher paternity success in bonobos but not chimpanzees. *Curr. Biol.* 29, R354–R355. <https://doi.org/10.1016/j.cub.2019.03.040>.
49. Lewis, J. (2014). Pygmy hunter-gatherer egalitarian social organization: the case of the Mbendjele BaYaka. In *Congo Basin hunter-gatherers*, B. Hewlett, ed. (Transaction Publishers), pp. 219–244.
50. Connor, R.C., Read, A.J., and Wrangham, R.W. (2000). Male reproductive strategies and social bonds. In *Cetacean Societies: Field Studies of Dolphins and Whales*, J. Mann, R.C. Connor, P.L. Tyack, and H. Whitehead, eds. (The University of Chicago Press), pp. 247–269.
51. Weiss, M.N., Franks, D.W., Giles, D.A., Youngstrom, S., Wasser, S.K., Balcomb, K.C., Ellifrit, D.K., Domenici, P., Cant, M.A., Ellis, S., et al. (2021). Age and sex influence social interactions, but not associations, within a killer whale pod. *Proc. Biol. Sci.* 288, 20210617. <https://doi.org/10.1098/rspb.2021.0617>.
52. Ellis, S., Johnstone, R.A., Cant, M.A., Franks, D.W., Weiss, M.N., Alberts, S.C., Balcomb, K.C., Benton, C.H., Brent, L.J.N., Crockford, C., et al. (2022). Patterns and consequences of age-linked change in local relatedness in animal societies. *Nat. Ecol. Evol.* 6, 1766–1776. <https://doi.org/10.1038/s41559-022-01872-2>.
53. Croft, D.P., Johnstone, R.A., Ellis, S., Nattrass, S., Franks, D.W., Brent, L.J.N., Mazzi, S., Balcomb, K.C., Ford, J.K.B., and Cant, M.A. (2017). Reproductive Conflict and the Evolution of Menopause in Killer Whales. *Curr. Biol.* 27, 298–304. <https://doi.org/10.1016/j.cub.2016.12.015>.
54. Johnstone, R.A., and Cant, M.A. (2010). The evolution of menopause in cetaceans and humans: The role of demography. *Proc. Biol. Sci.* 277, 3765–3771. <https://doi.org/10.1098/rspb.2010.0988>.
55. Cant, M.A., and Johnstone, R.A. (2008). Reproductive conflict and the separation of reproductive generations in humans. *Proc. Natl. Acad. Sci. USA* 105, 5332–5336. <https://doi.org/10.1073/pnas.0711911105>.
56. Taylor, P.D. (1992). Altruism in viscous populations - an inclusive fitness model. *Evol. Ecol.* 6, 352–356. <https://doi.org/10.1007/BF02270971>.
57. Taylor, P.D. (1992). Inclusive fitness in a homogeneous environment. *Proc. R. Soc. B Biol. Sci.* 249, 299–302.
58. Thouzeau, V., and Raymond, M. (2017). Emergence and maintenance of menopause in humans: A game theory model. *J. Theor. Biol.* 430, 229–236. <https://doi.org/10.1016/j.jtbi.2017.07.019>.
59. Weiss, M.N., Ellis, S., Franks, D.W., Nielsen, M.L.K., Cant, M.A., Johnstone, R.A., Ellifrit, D.K., Balcomb, K.C., and Croft, D.P. (2023). Costly lifetime maternal investment in killer whales. *Curr. Biol.* 33, 744–748.e3. <https://doi.org/10.1016/j.cub.2022.12.057>.
60. Aimé, C., André, J.B., and Raymond, M. (2017). Grandmothering and cognitive resources are required for the emergence of menopause and extensive post-reproductive lifespan. *PLoS Comput. Biol.* 13, 1–20. <https://doi.org/10.1371/journal.pcbi.1005631>.
61. McComb, K., Moss, C., Durant, S.M., Baker, L., and Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science* 292, 491–494. <https://doi.org/10.1126/science.1057895>.
62. R Core Team. R: A Language and Environment for Statistical Computing. Vienna. <https://www.R-project.org>.

63. Bürkner, P.C. (2017). brms: An R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* 80, <https://doi.org/10.18637/jss.v080.i01>.
64. Stan Development Team (2022). *Stan Modeling Language User's Guide and Reference Manual*.
65. Stan Development Team RStan. the R interface to Stan. R package version 2.26.13.
66. Balcomb, K.C., Boran, J.R., and Heimlich, S.L. (1982). Killer whales in greater Puget Sound. *Reports Int. Whal. Comm.* 32, 681–685.
67. Ford, J.K., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S., and Balcomb III, K.C. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can. J. Zool.* 76, 1456–1471. <https://doi.org/10.1139/cjz-76-8-1456>.
68. Miller, P.J.O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* 192, 449–459. <https://doi.org/10.1007/s00359-005-0085-2>.
69. Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B., and Balcomb, K.C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. - Int. Whal. Comm. Spec. Issue* 12, 383–405.
70. Weiss, M.N., Franks, D.W., Croft, D.P., and Whitehead, H. (2019). Measuring the complexity of social associations using mixture models. *Behav. Ecol. Sociobiol.* 73, 8. <https://doi.org/10.1007/s00265-018-2603-6>.
71. Ellis, S., Franks, D.W., Weiss, M.N., Cant, M.A., Domenici, P., Balcomb, K.C., Ellifrit, D.K., and Croft, D.P. (2021). Mixture models as a method for comparative sociality: social networks and demographic change in resident killer whales. *Behav. Ecol. Sociobiol.* 75, 75. <https://doi.org/10.1007/s00265-021-03006-3>.
72. McNicholas, P.D. (2016). Model-Based Clustering. *J. Classif.* 33, 331–373. <https://doi.org/10.1007/s00357-016-9211-9>.
73. Barrett-Lennard, L. (2000). Population structure and mating patterns of killer whales as revealed by DNA analysis. PhD Thesis (University of British Columbia).
74. Bürkner, P. (2016). Define Custom Response Distributions with brms, pp. 1–10.
75. Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* 1, 103–113. <https://doi.org/10.1111/j.2041-210x.2010.00012.x>.
76. Lenth, R. (2019). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.2. <https://CRAN.R-project.org/package=emmeans>.
77. Wickham, H. (2016). Programming with ggplot2. In *ggplot2. Use R!* (Springer).
78. Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., et al. (2019). Welcome to the Tidyverse. *J. Open Source Softw.* 4, 1686. <https://doi.org/10.21105/joss.01686>.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw data	This paper	https://zenodo.org/deposit/8026912
Software and algorithms		
R	R Core Team ⁶²	https://www.r-project.org
Brms	Bürkner et al. ⁶³	https://cran.r-project.org/web/packages/brms/
RStan	Stan Development Team ⁶⁴	https://cran.r-project.org/web/packages/rstan/
Stan	Stan Development Team ⁶⁵	https://mc-stan.org

RESOURCE AVAILABILITY

Lead contact

Further information and requests for methods and materials should be directed to and will be fulfilled by the lead contact, Charli Grimes (cg565@exeter.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All original data has been deposited at Zenodo and is publicly available as of the date of publication. The DOI is listed in the [key resources table](#).
- All original code has been deposited at Zenodo and is publicly available as of the date of publication (<https://zenodo.org/deposit/8026912>).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

This study is based on demographic and social data collected from the southern resident killer whale population, a genetically distinct ecotype whose core habitat in the summer months are the coastal waters of Washington State, USA and British Columbia, Canada. Permits to conduct photographic surveys of the population were granted by the USA National Oceanic and Atmospheric Administration (NOAA/NMFS33,GA14A,532-1822,15569,21238) and the Department of Fisheries and Oceans Canada (DFOSARA388).

METHOD DETAILS

Study population: Southern resident killer whales

Southern resident killer whales (*Orcinus orca*) are a genetically distinct ecotype whose core habitat in the summer months are the coastal waters of Washington State, USA and British Columbia, Canada. The Center for Whale Research, based on San Juan Island, USA, has been monitoring the southern residents since 1976 via a photographic census using photo-ID techniques.^{39,66,67} There is no natal dispersal and all individuals in the population can be identified based on the natural variability in shape and size of the dorsal fin and their unique saddle patch. Since 1976, all whales in the population have been observed each year, allowing all births and deaths to be reliably inferred from data collected by the census. Female resident killer whales are generally considered to be reproductive between the ages of 12 and 40,³⁹ and beyond this enter their postreproductive lifespan. As such, we consider any female above the age of 40 to be postreproductive.

During census observations, photographs were taken from boats of all individual whales present, when conditions were suitable for photo identification, i.e., sea state of less than Beaufort 4. Photographs of the whales were taken at a position perpendicular to the whales' direction of travel as the whales' surfaced and, where possible, both sides of the whales were photographed.

Tooth rake mark coding

Photographs taken from the Center for Whale Research's annual census were assessed for the presence of new, often white, tooth rake marks (see Grimes et al.²⁹ for detailed methodology). At least one photo of each side of the whale was available for each whale, each year, and where multiple photographs of a whale were available each year, the two highest quality images (one from each side of the whale) were selected for analysis. Photographs were analysed using reference images from the previous year to ensure that the same rake was not coded twice and that all new tooth rakes were captured. All image analysis was carried out in GNU Image Manipulation Programme version 2.8.

Two values from every photograph of each whale were recorded. The first was the number of pixels that the entire visible surface of the whale in the image occupied, and the second was the number of pixels that each new tooth rake occupied which was totaled cumulatively. In each image, rake pixels were considered in relation to the number of pixels occupied by the entire visible surface of the whale in order to standardize for the variation in total exposed surface area in each photograph and for variation in the pixel density of photos, particularly for photos from earlier years compared to later digital years. Rake mark pixels and total surface area pixels were calculated annually for each year and used in our analysis.

Social unit membership and estimated relatedness

Since we are interested in patterns of tooth rake marks, which can only be created by direct contact with other whales, we used observed patterns of social association within the population to define the social units of each whale. For the purpose of this study, social groups are defined as "social units", based on social associations calculated from photographs and videos collected by the Center for Whale Research between 1979 and 2013. There is no dispersal from social groups in this population³⁹ and matrilineal travel together into inshore waters to forage, but when foraging actively, individuals and groups will regularly spread out over a number of kilometers to forage.³⁸ These groups, however, are coordinated and dynamic, with subgroups regularly undergoing fission and fusion. For the current analysis we want to capture the longer time social associations of individuals at the larger social unit, rather than these short-term foraging dynamics, thus we use a broad scale definition of social association as individuals observed within acoustic range (10km⁶⁸) which provides a meaningful measure of long-term stable social units in this population.⁶⁹

Binomial mixture models were then used to classify all social bonds in the population by their association strength^{70,71} and from this, determine the social unit of a given whale in each year, which we consider to be the social partners with whom they share the strongest category of social association in that year.⁵² Binomial mixture models can be used to classify the social bonds present in the population into distinct classes based on their strength,^{70,71} and facilitates accurate examination of how social bonds between individuals respond to demographic and ecological changes over time. For every pair of whales in the population, we calculated the number of times they are observed in association, and the number of times they were observed separately (while both are alive) over all years of the study. A series of k-component mixture models were then fit to these data, where $k = 1-9$, and we used Integrated Completed Likelihood⁷² to select the best fitting model. A four-component mixture model was the most parsimonious fit and therefore used to define each whale's social environment. For each whale in each year, their strongest (k4 component) social partners were calculated, and those partners were considered to be that individual's social unit in that year. This method results in group structures that correspond well to the natural structure of matrilineal, which are often referenced in the southern resident population, with the social unit of each whale directly reflecting the social partners they associate with most commonly in a given year and are therefore most likely to be having close social contacts with.

We define local relatedness — calculated as the average pairwise relatedness from a whale to their social unit — within these previously defined individual social units.⁵² Matrilineal pairwise relatedness was calculated based on the pedigree, which, in this population, is assigned by inferred maternity, based on direct observations of infant swimming behaviour, conducted by the Center for Whale Research³⁹ and population genetic structure.⁷³ This assignment has high confidence certainty, since all females were encountered every year within a 6-month period and consequently, calves born within this time frame are almost always observed when swimming in close association with their mother.

Relatedness was calculated to a depth of two degrees while accounting for error induced by unknown relatedness. This was done by applying the methods developed in Ellis et al.,⁵² implemented through the R package *comparekin* (github.com/samellisq/comparekin). In brief, this method involved classifying all social partners as unrelated ($r = 0$), related within the second degree ($r = 0.5, 0.25$ etc.) or of unknown relatedness. Pairwise relatedness is unknown if, due to gaps in the pedigree, two whales could be related in the second degree but confirmation of this is not possible. For example, if one whale's mother is unknown an older female's social partner could be their mother, sister or a non-relative, we therefore considered their relatedness to be unknown. This known and unknown relatedness was used, along with binomial theorem, to build this into a measure of estimated local relatedness, with error around it.⁵² These values were calculated for every individual in the population in each year and whales were only included in the analysis if their pairwise local relatedness was known to greater than 20% of their group-mates. Individuals whose social unit could not be determined or whose mother could not be identified were removed from the analysis, resulting in observations made on a total of 130 individuals (67 males and 63 females).

Social unit composition

We constructed our first model (Equation 1), to test the hypothesis that postreproductive females direct social support towards their offspring by reducing the conflict their offspring experience. Prior to analysis, we first established if an individual's mother was alive or dead. If alive, we determine her reproductive status (either reproductive or postreproductive) and assigned them to a social condition

based on this: i. individuals with their postreproductive mother present in their social unit, (prm = 1), or ii. individuals with their reproductive mother in their social unit (rm = 1). For individuals whose mother was dead/died during the study period, or those whose mother was alive but not one of their strongest associates during the year the photograph was taken, we then determined if another postreproductive female was in the social unit and assigned them to social conditions based on this: iii. another postreproductive female in the social unit (opr = 1) (Figure S1). We modeled the probability p of a pixel on whale i in year t being a ‘raked pixel’ as:

$$x_{t,i} \sim \text{BetaBinomial}(N_{t,i}, \bar{p}_{t,i}, \theta) \logit(\bar{p}_{t,i}) = \beta_{0,s_i} + \beta_1 \tau r_{t,i} + \beta_{3,s_i} \text{prm}_{t,i} + \beta_{4,s_i} \text{rm}_{t,i} + \beta_{5,s_i} \text{opr}_{t,i} + \beta_6 g_{t,i} + \beta_7 q_{t,i} \beta_8 C_t \\ + \beta_9 t + \beta_{10} a.s_{t,i} + \delta_i + \varrho_t \tau r_{t,i} \\ \sim \text{Normal}(r_{t,i}, e r_{t,i}) \delta \sim \text{Normal}(0, \sigma_\delta) \varrho \sim \text{Normal}(0, \sigma_\varrho) \beta \sim \text{Normal}(0, 1) \theta = \varphi + 2\varphi \sim \text{Exponential}(1) \sigma \sim \text{Studentt}(3, 0, 2.5) \quad (\text{Equation 1})$$

As well as the social terms, in this model we also include terms for: age-sex class ($a.s$), sex (s), social unit size (g), chinook salmon abundance (C), number of photos taken of a whale (g), true local relatedness (τr : modeled as drawn from a normal distribution around observed relatedness r), and random effects for individual (δ) and year (ϱ), (see Table S1 for full list).

To determine whether the social conflict experienced by whales is influenced by the presence of their postreproductive grandmother, we ran a second model (Equation 2), this time using multigenerational data. During our study period, the maternal grandmothers of 94 whales in our population are known and thus included in this analysis (44 males and 51 females). All individuals with no known grandmother were excluded from the analysis, regardless of if their mother was known.

Data processing prior to analysis, including determining the following: first, we established if an individual’s grandmother was alive or dead. If alive, we determined her reproductive status (either reproductive or postreproductive) and assigned the individual to a social condition based on this (1. individuals with their postreproductive grandmother in their social unit, (prgm = 1) or 2. individuals with their reproductive grandmother in their social unit (rgm = 1)). For all individuals in the study whose grandmother and mother were known, we determined whether their postreproductive mother was present in their social unit (regardless of her reproductive age) and if so, assigned them to a third social condition (3. Postreproductive mother present, prm = 1). Finally, those individuals who did not have their mother or grandmother in their social unit, we determined if an another postreproductive female was in their social unit and assigned them to a final social condition (4. another postreproductive female in the social unit, opr = 1) (Equation 2). We modeled the probability p of a pixel on whale i in year t being a ‘raked pixel’ as:

$$x_{t,i} \sim \text{BetaBinomial}(N_{t,i}, \bar{p}_{t,i}, \theta) \logit(\bar{p}_{t,i}) = \beta_{0,s_i} + \beta_1 \tau r_{t,i} + \beta_{3,s_i} \text{prm}_{t,i} + \beta_{4,s_i} \text{prgm}_{t,i} + \beta_{5,s_i} \text{rgm}_{t,i} \\ + \beta_{6,s_i} \text{opr}_{t,i} + \beta_7 g_{t,i} + \beta_8 q_{t,i} + \beta_9 C_t + \beta_{10} t + \beta_{11} a.s_{t,i} + \delta_i + \varrho_t \varrho_i \tau r_{t,i} \\ \sim \text{Normal}(r_{t,i}, e r_{t,i}) \delta \sim \text{Normal}(0, \sigma_\delta) \varrho \sim \text{Normal}(0, \sigma_\varrho) \beta \sim \text{Normal}(0, 1) \theta = \varphi + 2\varphi \sim \text{Exponential}(1) \sigma \sim \text{Studentt}(3, 0, 2.5) \quad (\text{Equation 2})$$

For this model, we include the four social terms listed above, and see Table S1 for full list of additional terms.

Tooth rake mark density has been observed to fluctuate in response to salmon abundance in this population²⁹ and, as such, salmon abundance was included as an exogenous variable in our analysis to improve the estimate of rake density (Figure S2). Annual chinook salmon abundance indices from West Coast Vancouver Island and Northern British Columbia (two areas frequented by the southern residents) were extracted from the technical reports published by the Pacific Salmon Commission test fisheries. These values are calculated based on test fishing results before and after commercial fishing seasons. Mean values from both areas were calculated annually and used in our analysis. Due to the restrictions on available salmon stock data prior to 1979, photographs used in the analysis were limited to between 1979 and 2013.

QUANTIFICATION AND STATISTICAL ANALYSIS

Generalized linear mixed models in a Bayesian framework were used to examine social condition effects on rake density for both offspring and grandoffspring within the population. Exposure variables and covariates were computed annually for each individual whale in the population and rake density was included as the outcome variable, passed as a success|trials (success+failure) syntax, or in this instance “total rake pixels”|trials (“total visible pixels”) in our models (see Equations 1 and 2). The models were fit with a custom beta-binomial distribution (see vignette::beta_binomial2⁷⁴) to account for over dispersion. To control for other factors that are potential confounders on rake density, we included the size of the social unit and the estimated relatedness (and the error surrounding it) of an individual to those in their social unit. Social unit size is included to close non-causal pathways and relatedness is included because it is a mediator and we wish to block the indirect causal effect through relatedness (Figure S2). Given the variation in rake density observed between age-sex classes in southern resident killer whales,²⁹ we include age-sex class as a categorical variable in the model. Age-sex classes were defined as in Grimes et al.,²⁹ where males were categorized as: calves (0–3 years old), juveniles (4–12 years old), subadults (13–20 years old) and adults (21 years old and older) and for females: calves (0–3 years old), juveniles (4–12 years old) and adults (13 years and older). Chinook salmon abundance, year and number of photos were also

included as fixed effects and whale ID and year as random effects to account for within-group variation in behaviour and repeated measures. To allow the interpretation of effect sizes, all non-binary predictor variables were standardized.⁷⁵ We set normal priors with mean 0 and standard deviation 1 for all population level effects. Four chains were run simultaneously, each with 8000 iterations and 2000 warm-up iterations. Convergence was achieved for all four chains ($\hat{r} = 1.00$ for all coefficient estimates) and were checked for and adjusted to ensure: convergence of coefficients; absence of divergent transitions; sufficient tree depths; and effective sample sizes in both the ‘bulk’ and the tails of the distribution.

After the models, contrasts were analysed to determine whether an individual’s social condition influenced rake density using the emmeans package in R.⁷⁶ Three groups of pairwise comparisons were made, for offspring/grandoffspring sex and each of the social conditions. All reported results are contrasts between direct causal effects and for all contrasts of interest, we report posterior mean values and 95% credible intervals around these coefficients for each exposure variable. Since the effects of estimated relatedness and social unit size are not a focus of this manuscript, we report these results in [Tables S2](#) and [S3](#).

All statistical analysis and figure generation was carried out in R (R Development Core Team 2019, version 4.0.4) using the dplyr, ggplot2, tidyr, tidybayes and brms packages^{63,77,78} and we evaluated the models with Hamiltonian Markov Chain Monte Carlo algorithm implemented in Stan via brms.^{63,78}