Integrating spatiotemporal and cultural dimensions of animal behavior can enhance conservation

William K. Oestreich[1]*, Dawn R. Barlow[2]*, Taylor A. Hersh[2]

[1] Monterey Bay Aquarium Research Institute, Moss Landing, California, USA; woestreich.research@gmail.com

[2] Marine Mammal Institute, Oregon State University, Newport, Oregon USA
* Authors contributed equally to this study

Abstract: Behavioral ecology has seen a recent integration of the spatiotemporal and cultural elements of animal behavior. However, similar integration in ecosystem management and wildlife conservation remains an important gap. Here we explore how the intersections among space, time, and culture in animal behavior can inform and enhance conservation practices. Drawing on instructive examples from cetaceans, we examine instances where protection of a location or resource can facilitate the conservation of culture (e.g., place-based, socially learned behaviors), and where focusing on conserving culturally distinct groups can yield protection in space and time (e.g., memory of migratory destinations). These examples highlight the value of examining these intersecting dimensions and their interactions. We propose that the foundations learned from behavioral ecology theory can aid in identifying key research gaps, and can guide conservation actions which consider space, time, and culture in concert. Such integrated efforts can enable more holistic protections for diverse taxa.

Keywords: Animal culture, behavioral ecology, cetaceans, conservation, social learning, migration, foraging, communication, social behavior

Social interactions in space and time shape culture—the inheritance of behavioral traditions through social learning from others (Whiten 2021). In turn, culture influences behavior in space and time. This interplay is evident in human lives and societies, and is increasingly recognized in non-human animals as well (Whiten 2021; Laland & Janik 2006). In theory, behavioral ecologists are now establishing the inherent connections between culture and animal behavior in space and time (Brakes et al. 2019). Yet in conservation application, efforts have focused predominantly on conservation in space (and, to a lesser extent, time) via defining critical habitat while the importance of conserving cultural units remains theoretically attractive but practically nebulous (but see Whitehead et al. 2023). Here, we posit that these spatiotemporal and cultural elements are related and complementary, and considering them in concert will benefit conservation efforts.

Whereas these concepts apply to diverse taxa, we primarily draw from examples of these dynamics in cetaceans (whales, dolphins, and porpoises) for several reasons: (1) cetaceans have provided repeated discoveries of social learning and culture across species and behavioral domains; (2) many populations of cetaceans exhibit long-range movement and communication behaviors which highlight the interactions among space, time, and culture, as well as their combined effect on sociality; and (3) there is widespread investment in cetacean conservation and their ongoing recovery from industrial exploitation. Because of these elements, cetaceans provide relatively well-studied, instructive examples on the intersections among space, time, and culture in animal behavior and conservation that can be extended to inform the conservation of diverse taxa.

Animal sociality: interactions in space, time, and culture

The spatiotemporal and social dimensions of animal behavior are inherently intertwined: social interactions influence behavior in space and time, and spatiotemporal overlap influences social behaviors (Webber et al. 2023). For many animals, social interactions are most apparent in their aggregations. Aggregations may form as a result of many individuals responding to the same environmental cues (e.g., indication of a resource that is clumped in space and time) and/or the persistent, mutual social attraction exhibited by social groups (Ward & Webster 2016). Although aggregating can come at a cost (e.g., increased competition for resources), its widespread evolution underscores the benefits of overlapping with conspecifics in space and time. Among other benefits, social aggregations provide a forum for dense social interactions and acquisition of valuable social information which can be used to track resources, find mates, and socially learn critical behaviors. These social interactions most commonly occur between conspecifics that are proximate in space and time (Figure 1A). However, many animals have also evolved the capacity to transmit and acquire non-local social information. For example, acoustic signals (particularly in aquatic ecosystems) can propagate widely beyond the producing individual's proximate surroundings, enabling long-range and inconspicuous sociality in space (Tyack 2022; Dodson et al. 2024). In other cases, individuals can leave social information about their presence or behavior on a landscape (e.g., scent marks, disturbance of the physical environment) that persists through time.

In some cases, these proximate or distant social interactions give rise to culture, in the form of "group-typical behaviour patterns, shared by members of animal communities, that are to some degree reliant on socially learned and transmitted information" (Laland & Janik 2006). Such socially learned and group-typical patterns are found in a diversity of behaviors, including foraging tactics (Aplin et al. 2015), migration (Aikens et al. 2022), acoustic communication (Garland et al. 2011), mating site preferences (Warner 1988), and more. These cultural elements of animal behavior both influence and are influenced by spatial and temporal patterns of animal behavior (Figure 1B). For example social learning and transmission of behaviors can occur in specific places (e.g., shared roosts) and at particular times (e.g., breeding season). The inverse dynamic also occurs: culture influences behavior in space and time. For example, socially transmitted information in animal groups can lead to the emergence of culture around both spatial (Berdahl et al. 2018) and temporal (Oestreich et al. 2022) patterns of migratory behavior.

While there is an increasing emphasis on integrating spatiotemporal and cultural elements of animal behavior in theoretical behavioral ecology, similar integration in ecosystem management and wildlife conservation remains an important gap. Historically, conservation efforts have strongly emphasized geographic management strategies, focusing on the protection of spaces (e.g., critical breeding habitat). Recent years have seen greater consideration of both spatial and temporal elements of protection, with dynamic management practices implemented to provide protection that shifts in space through time (Maxwell et al. 2015; Oestreich et al. 2020). Largely independently, the importance of animal culture to conservation, particularly in regards to defining units to conserve, has received increasing attention (Brakes et al. 2019; Brakes et al. 2021; Whitehead et al. 2004). Yet integration of spatiotemporal and culture-focused conservation interventions remains elusive, despite the myriad ways in which these elements of behavior influence one another (Figure 1).

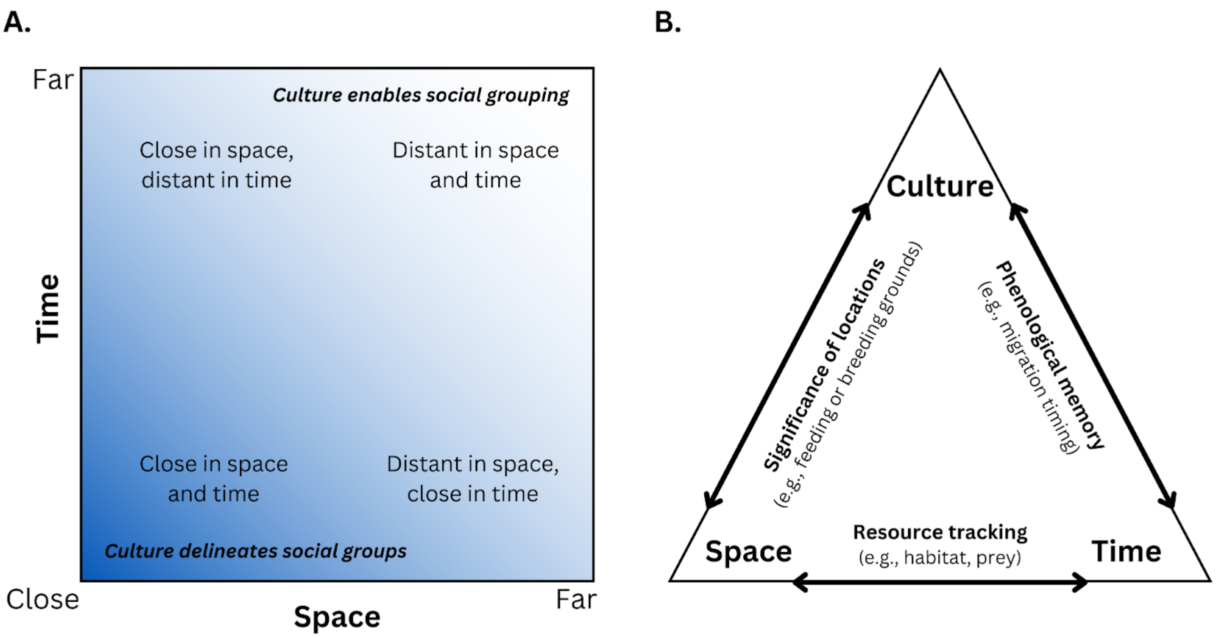

Figure 1. Conceptual schematics illustrating the intersecting dimensions of space, time, and culture in animal behavior. **A.** The interacting spatial and temporal dimensions of animal sociality. Shading indicates the likelihood of social grouping occurring; the presence of a cultural dimension enables delineation of distinct social groups near the origin (i.e., when individuals are close in space and time), but also social grouping at the “far” ends of the axes (i.e., when there is a disconnect in space and/or time). **B.** Depiction of the interactive effects of space, time, and culture, with examples of how the interactions can affect behavior.

Lessons learned from cetaceans

Cetaceans represent a diverse order of highly mobile and often wide-ranging species, inhabiting varied and dynamic habitats throughout the global oceans in which they exhibit many examples of complex social structure. Among cetacean species, there are numerous cases in which social learning of a behavior is tied to a particular space and/or time. Humpback whales (*Megaptera novaeangliae*) exhibit specialized feeding behaviors such as “lobtail” feeding on sand lance (*Ammodytes americanus*) in the Gulf of Maine, United States. This socially learned and culturally transmitted behavior is performed by only a subset of the humpback whales on the foraging grounds (Allen et al. 2013). In Southern Brazil, bottlenose dolphins (*Tursiops truncatus gephyreus*) feed cooperatively on migrating mullet (*Mugil liza*) by coordinating their foraging behavior with human fishers casting nets from shore in a way that is mutually beneficial to both the humans and dolphins (Cantor et al. 2018). Northern resident killer whales (*Orcinus orca*) in

British Columbia, Canada, rely on specific shallow gravel shorelines for “beach rubbing” behavior, a rare and culturally transmitted behavior whereby they rub their bodies on the benthos at high tide (Williams et al. 2009). These cases exemplify the intersection of spatiotemporal and cultural dimensions of behavior, demonstrating how cultural conservation can in some cases be achieved by conserving a location or resource in space and time. For example, Stellwagen Bank National Marine Sanctuary protects a culturally significant location and time (foraging season, especially during years of high sand lance abundance) for humpback whales that perform the socially learned lobtail feeding behavior (Allen et al. 2013). Similarly, smooth pebble beaches in British Columbia that killer whales use for beach rubbing are within the no-entry Robson Bight Ecological Reserve (Williams et al. 2009). In this way, culturally transmitted behaviors are conserved via protection measures in space and time.

In other cases, cultural elements of behavior are not inherently tied to a specific place or time, but instead influence behavior over a broad range of spatiotemporal scales. For example, sperm whales (*Physeter macrocephalus*) produce socially learned vocalizations known as “codas”, and different cultural groups of whales, called “vocal clans”, exhibit preferences for specific coda types. These culture-specific coda preferences can be spread over ocean basins (i.e., certain vocal clans span beyond overlap in space and time) and also delineate distinct social groups even in sympatry (i.e., vocal clans persist when overlapping in space and time) (Hersh et al. 2022). These discoveries have led to proposals for sperm whale vocal clans to be the unit of management (Brakes et al. 2019; Brakes et al. 2021), rather than an exclusive focus on geographically or genetically defined stocks. Cultural memory of migratory routes and destinations in southern right whales (*Eubalaena australis*) represents another case of how culture influences behavior and can influence protection in space and time. This species exhibits cultural traditions in migratory destination fidelity (Carroll et al. 2015), meaning that the loss of culturally distinct population segments (and their associated migratory destinations) has altered the places and times that represent critical habitat for this population (Harcourt et al. 2019). Restoring lost behaviors requires consideration of social learning mechanisms, experienced individuals, and culture in conservation interventions (e.g., translocation), which must also be integrated with geographic protections based on the spatiotemporal influences of culture (Barker et al. 2022).

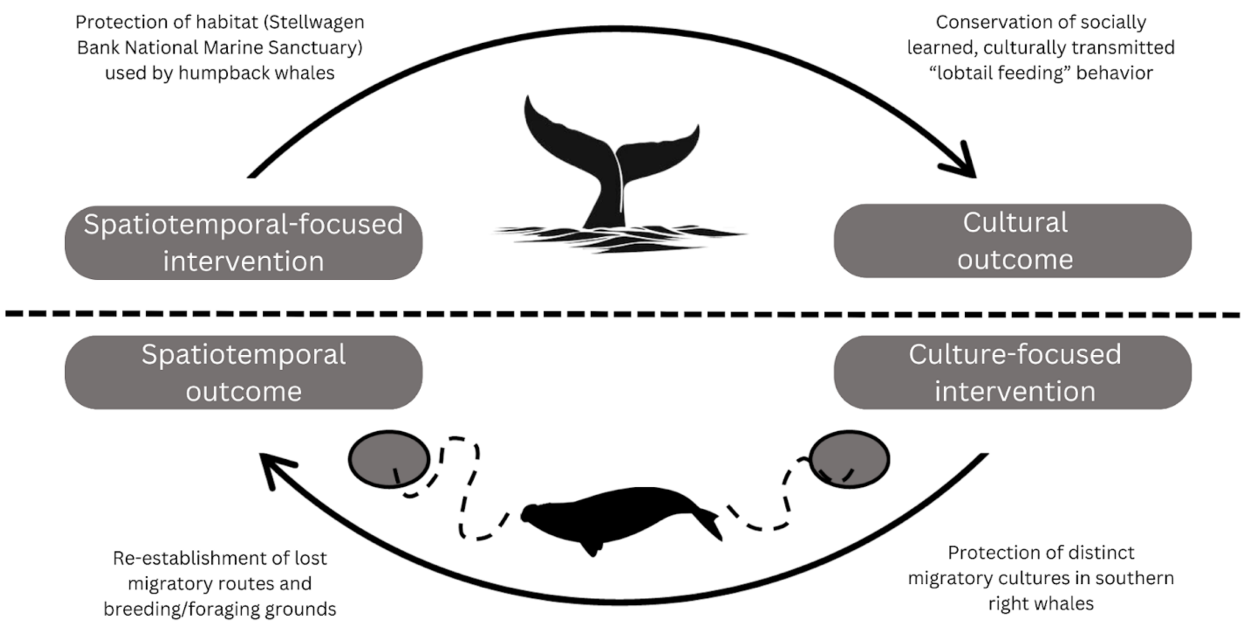

Figure 2. Examples of how culture can be conserved through spatiotemporal interventions, and spatiotemporal conservation can be achieved through culture-focused interventions**.** Right whale credit: Chris Huh CC BY-SA 3.0. Humpback whale: public domain.

Understanding spatial, temporal, and cultural dimensions can direct research and conservation

Conservation efforts for cetaceans have focused predominantly on protection of critical habitat (for feeding, migration, or breeding) in space and time (Tetley et al. 2022). Yet current theory increasingly emphasizes the importance of cultural units (Brakes et al. 2019). We posit that these three axes of behavior are related and complementary. Dimensions of space, time, and culture interact to collectively shape how animals behave, where they go, and with whom they interact (Fig. 1B). This notion is reflected in a recent proposition to use "migratory herds"—groups of whales that are unified by common feeding and wintering grounds, with migratory routes and destinations learned and maintained through cultural memory—as the unit to conserve for humpback and gray (*Eschrichtius robustus*) whales in certain parts of the world (Martien et al. 2023). We readily acknowledge that researchers and conservation practitioners may not have comprehensive knowledge of the spatial, temporal, and cultural dimensions that influence the behavior and demography of an animal population of interest. However, because these dimensions of animal behavior are intertwined—for example, cultural information can be gained from studying spatiotemporal dynamics of socially interacting animals—we propose that the framing of research questions and interpretation of findings can be enhanced when viewed through the lens of how the three interact (Fig. 1B).

Considering dimensions of space, time, and culture in animal behavior can aid in identifying key research gaps and directing strategic conservation. For example, it can be informative to consider the individual and combined effects of loss of specific individuals from a population, degradation of certain key habitat areas, or asynchrony in time (Cantor et al. 2023). Focusing on protecting cultural units or specific individuals may still fall short if they lose access to critical foraging areas due to anthropogenic impacts, whereas focusing on designating protected areas in space and time may fall short if key individuals with knowledge of specialized behaviors adapted to that place are lost. Conversely, considering the intersection of spatiotemporal and cultural dimensions can facilitate decision making about where to concentrate management efforts: there are scenarios in which focusing on a place or a resource can facilitate the conservation of culture (e.g., place-based, socially learned behaviors), or scenarios where focusing on conserving a cultural unit can yield conservation in space and time (e.g., cultural memory of migratory destinations) (Figure 2).

Considering the intersections among space, time, and culture in behavior has already enabled successful conservation interventions for migratory birds (Mueller et al. 2013; Abrahms et al. 2021), fish (Brown & Laland, 2001), and terrestrial mammals (Jesmer et al. 2018). Off the coast of Washington, United States, recent legislation is attempting to do the same for killer whales. Whereas all killer whales are protected under the U.S. Marine Mammal Protection Act, different cultural groups of killer whales in the region are exhibiting vastly different population trajectories (Williams et al. 2024). As of January 2025, vessel operators must stay at least 1,000 yards away from Southern resident killer whales, which are critically endangered; in contrast, the exclusion zone around other sympatric cultural groups with better conservation outlooks, such as transient or northern resident killer whales, is 200 yards (Washington State Legislature 2025). In this way, cultural identity is being used to inform and, hopefully, enhance conservation via mitigation of impacts in space and time.

We increasingly understand the interdependence of spatial, temporal, and cultural components of behavior in theory. Each of these dimensions is also independently considered in applications to ecosystem management and conservation interventions. We propose that this foundation creates the opportunity for conservation actions that consider space, time, and culture in concert, and that such integrated efforts will enable more holistic protections for diverse taxa.

Funding

D.R.B was supported by the Marine Mammal Institute at Oregon State University. T.A.H. was supported by a L'Oréal USA For Women in Science Fellowship.

Data availability

No original data are included in this manuscript.

References

Abrahms, B., Teitelbaum, C. S., Mueller, T., & Converse, S. J. (2021). Ontogenetic shifts from social to experiential learning drive avian migration timing. *Nature Communications*, 12(1), 7326.

Aikens, E. O., Bontekoe, I. D., Blumenstiel, L., Schlicksupp, A., & Flack, A. (2022). Viewing animal migration through a social lens. *Trends in Ecology & Evolution*, 37(11), 985-996.

Allen, J., Weinrich, M., Hoppitt, W., & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, 340(6131), 485-488.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538-541.

Barker, K. J., Xu, W., Van Scoyoc, A., Serota, M. W., Moravek, J. A., Shawler, A. L., ... & Middleton, A. D. (2022). Toward a new framework for restoring lost wildlife migrations. *Conservation Letters*, *15*(2), e12850.

Berdahl, A. M., Kao, A. B., Flack, A., Westley, P. A., Codling, E. A., Couzin, I. D., ... & Biro, D. (2018). Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1746), 20170009.

Brakes, P., Dall, S. R., Aplin, L. M., Bearhop, S., Carroll, E. L., Ciucci, P., ... & Rutz, C. (2019). Animal cultures matter for conservation. *Science*, *363*(6431), 1032-1034.

Brakes, P., Carroll, E. L., Dall, S. R., Keith, S. A., McGregor, P. K., Mesnick, S. L., ... & Garland, E. C. (2021). A deepening understanding of animal culture suggests lessons for conservation. *Proceedings of the Royal Society B*, *288*(1949), 20202718.

Brown, C., & Laland, K. (2001). Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, *59*(3), 471-493.

Cantor, M., Simões-Lopes, P. C., & Daura-Jorge, F. G. (2018). Spatial consequences for dolphins specialized in foraging with fishermen. *Animal Behaviour*, 139, 19-27.

Cantor, M., Farine, D. R., & Daura-Jorge, F. G. (2023). Foraging synchrony drives resilience in human–dolphin mutualism. *Proceedings of the National Academy of Sciences*, 120(6), e2207739120.

Carroll, E. L., Baker, C. S., Watson, M., Alderman, R., Bannister, J., Gaggiotti, O. E., ... & Harcourt, R. (2015). Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. *Scientific Reports*, 5(1), 16182.

Dodson, S., Oestreich, W. K., Savoca, M. S., Hazen, E. L., Bograd, S. J., Ryan, J. P., ... & Abrahms, B. (2024). Long-distance communication can enable collective migration in a dynamic seascape. *Scientific Reports*, 14(1), 14857.

Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., ... & Noad, M. J. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology*, 21(8), 687-691.

Harcourt, R., Van der Hoop, J., Kraus, S., & Carroll, E. L. (2019). Future directions in Eubalaena spp.: comparative research to inform conservation. *Frontiers in Marine Science*, *5*, 530.

Hersh, T. A., Gero, S., Rendell, L., Cantor, M., Weilgart, L., Amano, M., ... & Whitehead, H. (2022). Evidence from sperm whale clans of symbolic marking in non-human cultures. *Proceedings of the National Academy of Sciences*, 119(37), e2201692119.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., ... & Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, *361*(6406), 1023-1025.

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542-547.

Martien, K. K., Taylor, B. L., Lang, A. R., Clapham, P. J., Weller, D. W., Archer, F. I., & Calambokidis, J. (2023). The migratory whale herd concept: A novel unit to conserve under the ecological paradigm. *Marine Mammal Science*, *39*(4), 1267-1292.

Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., ... & Crowder, L. B. (2015). Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. *Marine Policy*, 58, 42-50.

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P., & Fagan, W. F. (2013). Social learning of migratory performance. *Science*, 341(6149), 999-1002.

Oestreich, W. K., Aiu, K. M., Crowder, L. B., McKenna, M. F., Berdahl, A. M., & Abrahms, B. (2022). The influence of social cues on timing of animal migrations. *Nature Ecology & Evolution*, 6(11), 1617-1625.

Oestreich, W. K., Chapman, M. S., & Crowder, L. B. (2020). A comparative analysis of dynamic management in marine and terrestrial systems. *Frontiers in Ecology and the Environment*, 18(9), 496-504.

Tetley, M. J., Braulik, G. T., Lanfredi, C., Minton, G., Panigada, S., Politi, E., ... & Hoyt, E. (2022). The important marine mammal area network: a tool for systematic spatial planning in response to the marine mammal habitat conservation crisis. *Frontiers in Marine Science*, *9*, 841789.

Tyack, P. L. (2022). Social organization of baleen whales. In Ethology and behavioral ecology of mysticetes (pp. 147-175). Cham: Springer International Publishing.

Washington State Legislature. (2025). RCW 77.15.740: Protection of southern resident orca whales—Unlawful activities—Penalty. [accessed 2025 Jan 10]. https://app.leg.wa.gov/rcw/default.aspx?cite=77.15.740

Ward, A., & Webster, M. (2016). Sociality: the behaviour of group-living animals (Vol. 407). Berlin, Germany: Springer.

Warner, R. R. (1988). Traditionality of mating-site preferences in a coral reef fish. *Nature*, 335(6192), 719-721.

Webber, Q. M., Albery, G. F., Farine, D. R., Pinter-Wollman, N., Sharma, N., Spiegel, O., ... & Manlove, K. (2023). Behavioural ecology at the spatial–social interface. *Biological Reviews*, 98(3), 868-886.

Whitehead, H., Rendell, L., Osborne, R. W., & Würsig, B. (2004). Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biological Conservation*, 120(3), 427-437.

Whitehead, H., Ford, J. K., & Horn, A. G. (2023). Using culturally transmitted behavior to help delineate conservation units for species at risk. *Biological Conservation*, 285, 110239.

Whiten, A. (2021). The burgeoning reach of animal culture. *Science*, *372*(6537), eabe6514.

Williams, R., Lusseau, D., & Hammond, P. S. (2009). The role of social aggregations and protected areas in killer whale conservation: the mixed blessing of critical habitat. *Biological Conservation*, 142(4), 709-719.

Williams, R., Lacy, R. C., Ashe, E., Barrett-Lennard, L., Brown, T. M., Gaydos, J. K., … & Paquet, P. (2024). Warning sign of an accelerating decline in critically endangered killer whales (*Orcinus orca*). *Communications Earth & Environment*, *5*(1), 173.