Social ageing varies within a population of bottlenose whales

Sam F. Walmsley[1]*, Laura J. Feyrer[1,2], Claire Girard[1], Elizabeth Zwamborn[1], Hal Whitehead[1]

Summary

How social behaviour changes as individuals age has important consequences for the health and function of both human and non-human societies. However, the extent of inter-individual variation in social ageing has been underappreciated, especially in natural populations of animals. Here, we leverage a photo-identification dataset spanning 35 years to examine social ageing in an Endangered population of northern bottlenose whales (*Hyperoodon ampullatus*), an oceanic beaked whale that exhibits fission-fusion social dynamics. Patterns of social ageing were sex-specific: males experienced a decline in social behaviour with age, shedding direct social connections and holding less central social roles. Conversely, female social traits were generally stable throughout adulthood, while the average strength of their relationships increased with age. Beyond sex, additional inter-individual variation played a large role in how animals responded socially to age. This study shows that inter-individual variation can play a key role in how animals experience behavioural senescence.

*Lead contact: sam.walmsley@dal.ca

---

[1] Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada.

[2] Bedford Institute of Oceanography, Fisheries and Oceans Canada, Dartmouth, Nova Scotia B2Y 4A2, Canada.

Introduction

For humans and other social species, ageing can involve changes in how individuals interact with and relate to others. Reciprocally, these changes in late-life social behaviour can influence health and ageing itself. The causes of "social ageing" are multifaceted and are increasingly recognized as operating in a range of species[1]. Social ageing can result from senescence in physiology, cognition, or other capacities. For example, declines in physical mobility are linked to reduced social interaction in ageing American humans[2]. Social ageing can also result from compensation for senescence in other traits, e.g., decreasing one's social interactions as a means to reduce risk of transmissible disease. More generally, changes in social behaviour through adulthood often stem from changing social or reproductive roles. This might involve declining social interactions as reproductive effort wanes, for example, but may also be associated with increases in other aspects of social behaviour. A reliance on experienced individuals for group leadership may result in the centering of older individuals within their social network. Beyond these mechanisms, age-related changes in an individual's social environment will also be important, for example, if long-term associates die and are not readily replaced. One difficulty in developing clear theoretical predictions for how social ageing should vary across taxa is that these mechanisms may act simultaneously.

One pattern of social ageing that has garnered interest, in part due to its prevalence in human populations, is increasing social selectivity with age[3]. Here, ageing individuals increasingly prioritize preferred relationships, detectable as a reduction in the number of associates despite maintaining a consistent amount of overall social engagement. This "proactive" social ageing has been detected in several primates such as chimpanzees (*Pan troglodytes*;[4]), rhesus macaques (*Macaca mulatta*;[5]), and tufted capuchins (*Sapajus* species;[6]), suggesting that it may be more prevalent than expected in non-humans. However, to date, the majority of social ageing research has focused on primates[7], with fewer studies devoted to other groups (but see exceptions: forked fungus beetles[8], red deer[9]). Thus a comparative understanding of social ageing is in its infancy, with few broad hypotheses for how social ageing should vary across and within populations.

Sex is one dimension which may influence social ageing within populations. Sex-specific differences in senescence and longevity are found in many species, though differences in mammals tend to be less pronounced than in some other groups[10]. Of mammals that do exhibit differences in longevity, females typically live longer (as in many human populations, for example). And while sex differences in social ageing are expected[1], most studies in non-humans have focused on a single sex (e.g., male chimpanzees,[4]; female red deer,[9]; female rhesus macaques[5]; female Assamese macaques[11]). This may be for logistical reasons (e.g., targeting the sex that does not disperse), so that most studies of primate social ageing have focused on philopatric females[7]. However, few studies have compared trajectories of social ageing in male and female individuals of the same population (but see[10]). This is mirrored by a lack of general theory that can provide testable predictions for how sexes should differ in their social ageing. One suggestion is that the "socially dominant" sex in primate species may be more likely to maintain stable social traits or even become more socially active with age[7]. On close examination, however, of the various mechanisms thought to contribute to social ageing (reviewed in[1]), nearly all could vary with sex. Even simple mechanisms like reductions in mobility can be sex-specific: for example, wild male moose (*Alces alces*) are more likely to experience chronic bone diseases than females[12].

Beyond sex, additional sources of individual-specific variation may play an important role in social ageing. This seems obvious when considering behavioural ageing humans, where despite a high prevalence of social isolation in the elderly[13], some individuals exhibit increases in social connection, e.g., living in communal residences or taking on influential political roles. While we naturally expect *some* inter-individual variation in how animals experience social ageing, the extent of this variation remains unclear. One of the few studies of non-humans that examines variation in within-individual social ageing found that rhesus macaques responded similarly to age, with population-level patterns dwarfing individual-specific effects[5]. Characterizing the variability in social ageing within populations has implications both for how social ageing is studied, as well as its ecological and evolutionary consequences.

Toothed whales have proven to be a valuable group for developing a comparative understanding of both social behaviour and life history. However, surprisingly little is known about social ageing in this group. Several observational studies have suggested that lone male sperm whales (*Physeter macrocephalus*) tend to be larger, and likely older, than males found in pairs or groups[14] [15], indicating a possible reduction in social associations with age. Evidence of post-reproductive lifespans in several odontocetes suggests that older females can play important social roles in some species (killer whales, *Orca orcinus*; false killer whales, *Pseudorca crassidens*; short-finned pilot whale, *Globicephala macrorhynchus*; narwhal, *Monodon monoceros*; beluga; *Delphinapterus leucas*), though it is unclear how this translates to measures of individual social behaviour, as measured by number of associates, strength of relationships, etc. A recent study of southern resident killer whales found that both males and females became less central with age[16]. Similarly, a study of repeatability in social activities of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) found that older adults were alone more often than other adult age classes and that individuals were more likely to be in large groups during middle age[17]. Systematic studies of social behaviour in older whales are lacking, and necessary to distinguish whether apparent declines in social behaviour are driven by within-individual changes (social ageing) or other processes such as selective disappearance of certain phenotypes from the population.

Here we leverage a 35-year study to test for evidence of social ageing in an Endangered population of northern bottlenose whales (*Hyperoodon ampullatus*). Unlike other cetaceans that rely on stable kin-based units, male and female northern bottlenose whales live together, forming many weak (i.e., less frequent) social associations. While social bonds tend to be strongest within the sexes, male-female associations are also common[18]. Northern bottlenose whales are known to live for up to 37 years[19], and males may live longer than females[20]. As one of very few long-term studies of beaked whales that has spanned an approximate lifespan[21], this population offers a rare opportunity to understand interactions between age and social behaviour. Our analysis aims to address three main questions. First, do northern bottlenose whales exhibit age-related declines in social behaviour? Second, if declines are present, are bottlenose whales becoming more selective in their social connections with age, as found in humans and some other mammals? Third, how do sex and individual variation shape social ageing? Understanding patterns of ageing across sexes and individuals could also provide clues as to the function(s) of social behaviour in northern bottlenose whales, which appear to diverge in social structure from what is known of other deep-diving toothed whales.

Results

In total, our social ageing models included 107 individuals (49 males, 58 females) in 10 annual social networks spanning 2000-2023 (See STAR Methods). For models based on social network traits, we were able to include an average of 3 separate years of observation per individual as an adult (range 2 - 8). Additional animals were included for the group size models, from years with too few data to fit a social network, resulting in a total of 61 males and 68 females. Dyadic estimates of the proportion of time animals were detected together (i.e., edge weights) generally corresponded with previous findings. Mean edge weights were low (often < 5%). The Bayesian approach assumes that individuals never observed together still have some probability of associating, adjusted appropriately given sample sizes and the distribution of relationships in the wider social network. However, when excluding edge weights for individuals that were never observed together, the resulting mean "non-zero" edge weights suggested that social partners spent approximately 20% of their time together on average, similar to previous studies[18];[22].

Group size and number of social partners stable for ageing whales

Mean typical group sizes were similar for males (4.11, 1-27) and females (3.79, range 1-27). Effects of minimum age on group size were small, with males showing a slight decrease in group size with age (both between- and within-individual effects) and females showing a slight increase in group size with age. Credible intervals for both effects overlapped with zero, suggesting weak evidence that age affected group size. Similar effects were detected in our robustness checks based on individuals with genetically confirmed sex only, though the negative between-individual trend for males was more certain (β = -0.02, CI -0.04 – -3.10 x 10^-3). Notably, sex appeared to play a role in inter-individual variability in social ageing, with females showing a wider range of positive and negative responses when compared to males (Figure S1).

The number of social partners that individuals associated with during a given field season was similar for males (mean 6.80, range 0-34) and females (mean 6.35, range 0-37), though we expected these values to be heavily influenced by sampling intensity. Indeed, the number of days during which each individual was observed had a strong positive effect on the number of social partners for male (β = 0.29, CI 0.25 – 0.34) and female (β = 0.28, CI 0.23 – 0.32) specific models . Minimum age did not appear to have much influence on the number of social partners in either sex (Figure 1).

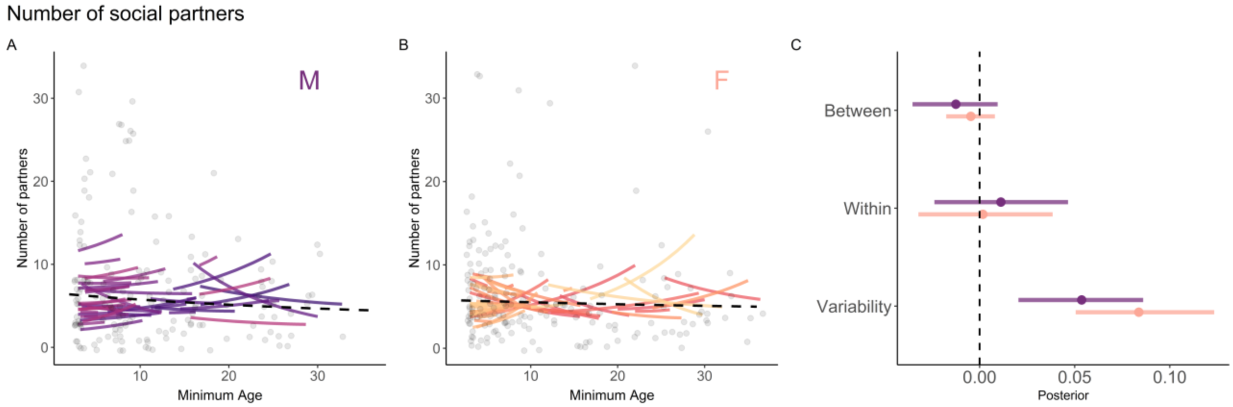

Figure 1 – Effects of minimum age on number of social partners in male (A) and female (B) northern bottlenose whales. Coloured lines represent within-individual effects fit with a random slopes model while the black dashed line represents between-individual effects. Panel C shows the 90% CI of the posteriors of both between and within-individual effects by sex. Grey points represent raw data so may not reflect fitted lines.

Declining social connections for ageing males

Next, we considered ageing in social network strength and eigenvector centrality. Measures of social network strength, representing direct social connections, were very similar across males (mean = 2.64, range 0.63 - 9.04) and females (mean = 2.54, range 0.68 - 8.52), and were also strongly influenced by sampling intensity (males: β = 0.16, CI 0.13 – 0.19; females: β = 0.19, CI 0.16 – 0.23). While estimates of within-individual effects and inter-individual variability were similar for both sexes and quite uncertain, older males had fewer direct social connections (β = -0.01, CI -0.02 – -2.50 x 10^-3; Figure S2). As the within- and between-individual effects for males overlapped, there is no evidence for selective disappearance (i.e., that some phenotypes are being disproportionately lost from the population) and the decline in social network strength among older males is expected to be driven by within-individual processes. Similarly, a negative relationship between minimum age and male network strength was detected in the model based on biopsied individuals only, thought the effect was less certain (β = -0.03, CI -0.08 – 0.01).

Sampling intensity had a positive effect on eigenvector centrality for both males (β = 0.37, CI 0.3 – 0.45) and females (β = 0.44, CI 0.36 – 0.52). Male northern bottlenose whales became less central in their social networks as they aged, as evidenced by negative between- and within-individual effects of minimum age (Figure 2). These effects were moderate in size: for example, a typical male is expected to fall from a centrality of 0.43 (~ 74th percentile of all males) to 0.13 (~ 18th percentile of all males) throughout their adult lifetime. For females, centrality appeared to be very stable through adulthood, with both within- and between-individual effects of age tightly centered on zero (Figure 2c).

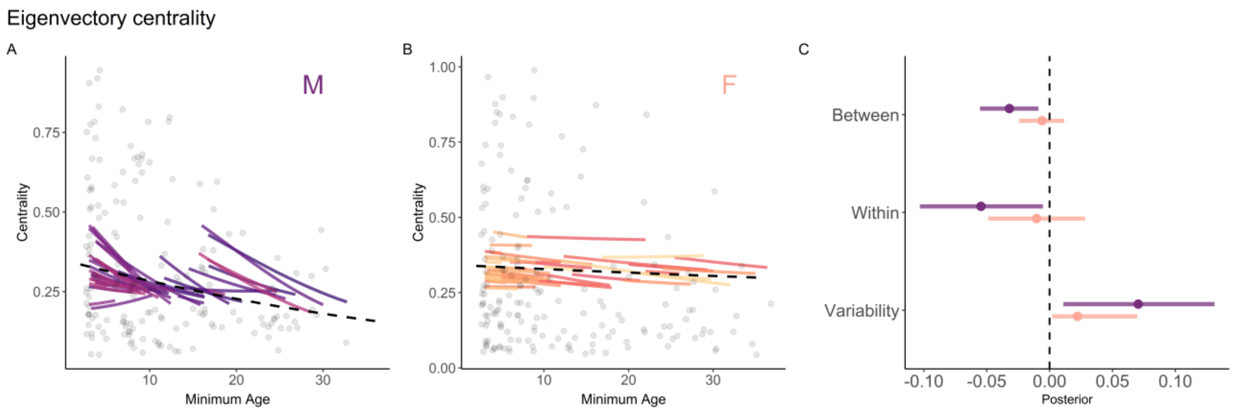

Figure 2 – Effects of minimum age on social centrality in male (A) and female (B) northern bottlenose whales. Coloured lines represent within-individual effects fit with a random slopes model while the black dashed line represents between-individual effects. Panel C shows the 90% CI of the posteriors of both between and within-individual effects by sex. Grey points represent raw data so may not reflect fitted lines.

Strengthening social relationships for ageing females

We then considered social ageing in the mean strength of relationships for each individual, excluding dyads that were never detected together in the given year. Mean bond strengths were similar for males (mean 0.24, range 0.07 - 0.60) and females (mean 0.25, range 0.1 - 0.63). For males, mean bond strength was relatively stable across adulthood, with a slightly negative between-individual effect and a slightly positive within-individual effect, each associated with high uncertainty (Figure 3). In contrast, female bottlenose whales formed stronger social bonds as they aged (β = 0.03, CI 3.30 x 10^-3 – 0.05). This corresponded to a relatively large effect: our model predicted that a typical female would spend 19% of their time with an average social partner on average in early adulthood, and 33% of their time with an average social partner in late adulthood.

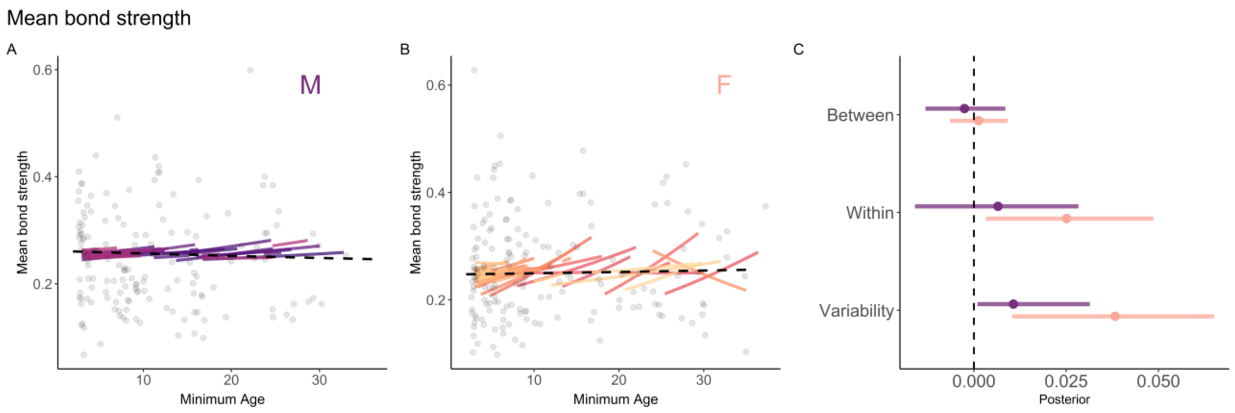

Figure 3 – Effects of minimum age on mean bond strength in male (A) and female (B) northern bottlenose whales. Coloured lines represent within-individual effects fit with a random slopes model while the black dashed line represents between-individual effects. Panel C shows the 90% CI of the posteriors of both between and within-individual effects by sex. Grey points represent raw data so may not reflect fitted lines.

Sex-specific and inter-individual variation in social ageing

Patterns of social ageing varied by sex (MANOVA: all individuals, $p < 0.001$; only individuals with genetic sex information, $p < 0.001$). This was evident in the principal components analysis based on within-individual effects from all models, in which males and females tended to be clustered together (Figure 4). Individuals with genetically confirmed sex were distributed evenly among visually-sexed animals, suggesting that issues in sex classification did not underlie observed variation. Here, the first principal component (PC1) had positive loadings for within-individual slopes of all traits, with especially high values for network strength and centrality, meaning that PC1 corresponds to age-related changes in general social connectedness (See Table S1 for all loadings). The second dimension, PC2, had positive loadings for mean relationship strength and centrality, but negative loadings for number of social partners and group size. Thus, more positive values of PC2 would result from a focus on fewer, stronger relationships with age, similar to social selectivity (Figure 4). Accordingly, the PCA suggests that some females may be exhibiting social selectivity, while others are not, dynamics that were masked when considering the population as a whole. Consistent with this, we detected a substantial amount of inter-individual variation in the multilevel models. For example, while the *average* female formed stronger social bonds with age, at least one female showed the opposite trend, forming weaker bonds with age (Figure 3). In some instances, directional individual-specific effects were masked by the lack of a population trend (e.g., female group size; Figure S1)

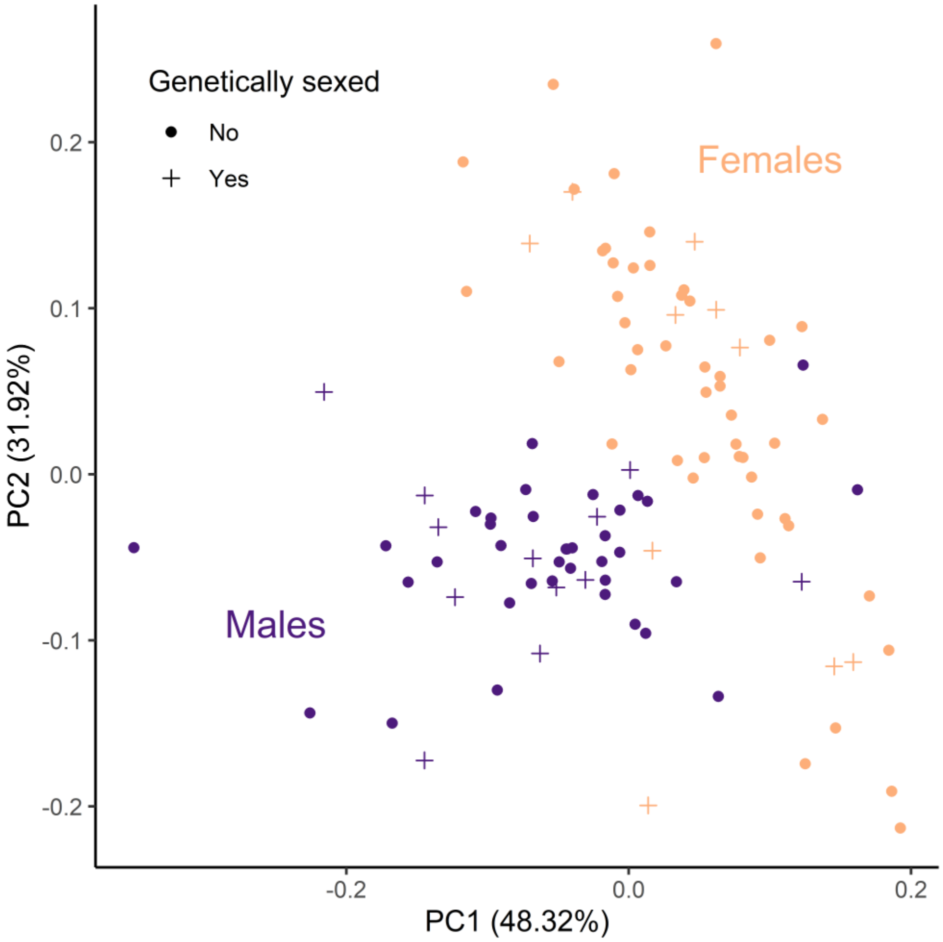

Figure 4 – Patterns of social ageing vary by sex and individual. Results of Principal Components Analysis applied to mean estimated effects of social ageing for each individual. PC1 captures change in general social connectedness with age while PC2 captures a change in the quality vs. quantity of social relationships with age. Individuals for which we lacked genetic sex information were sexed visually based on dimorphic characteristics of melon (forehead) shape and size (See STAR Methods).

Robustness checks for female models focusing on individuals detected over a span of at least 10 years revealed very similar results (i.e., stability). The within-individual effect of minimum age on mean bond strength was weaker than in the original model, but still mostly positive (β = 0.03, CI -5.30 x 10^-3 – 0.07). Similarly, models based on females with genetically confirmed sex alone did not show directional changes in any traits, though these models were limited in sample size (N = 10 biopsied females).

Discussion

Here we leverage a long-term study to investigate how ageing influences social behaviour in northern bottlenose whales. Patterns of social ageing varied by trait and were strongly shaped by within-population effects. While female social traits were generally stable throughout adulthood, males shed social connections and held less central roles in their society as they aged. Neither of these sex-specific patterns was consistent with increasing social selectivity, however. For each, the lack of a decline in the number of social partners suggests that northern bottlenose whales were not focusing their social effort on a narrowing set of preferred individuals, as is found in humans and some other species. Consideration of ageing across all social traits revealed both sex differences as well as unexpected individual variation in the trajectories of social ageing for females. More specifically, females varied in whether they prioritized quality vs. quantity of social bonds as they got older (Figure 4). This multivariate perspective raises the possibility of behavioural syndromes in social ageing, i.e., correlations in individual-specific traits[23];[24]. Together, these findings show that population and individual-level effects should be considered in tandem when trying to infer patterns of social ageing.

Male northern bottlenose whales experienced declines in social connectedness as they aged. This was evident in both direct connections (i.e., social network strength), as well as in their centrality within their social networks. Stability in the number of associates that males had suggests that this decline did not result from social selectivity, i.e., an increasing focus on key social relationships. This also makes social withdrawal for purposes like disease avoidance or reduced mobility seemingly less likely. One possibility is that the decline in social centrality is linked to changing reproductive roles, i.e., reproductive senescence. Male northern bottlenose whales have been observed performing a “headbutting” ritual whereby they align underwater and smash their melons together, which often occurs several times in sequence[25]. The headbutting behaviour of northern bottlenose whales is reminiscent of male contests in terrestrial ungulates and may be indicative of competition for mating opportunities. This, paired with evidence of long-term bonds between males[18], points to competitive behaviour centered on reproduction. If reproductive value declines with age it may be that the associated social behaviour (e.g., possible male-male coalitions) are lost as well. Alternatively, it may be that ageing males reduce their social connectedness in an effort to avoid potentially aggressive interactions. Currently, the processe(s) underlying this decline in male social behaviour are unclear.

In contrast, social ageing in females was characterized by relative stability at the population level as well as a high degree of variation across individuals. In fact, female northern bottlenose whales appeared to develop stronger social bonds as they aged. Perhaps relating to the same underlying social process, there was also some evidence that older females may be found in larger groups. These results run counter to an emerging trend from mammalian species where females shed social connections with age[9];[5], and suggests that physical declines are not driving social ageing for these animals. Generally, female bottlenose whales are thought to have weaker and more homogenous relationships when compared to males[18]. One explanation for the relative stability of female social traits is that a reliance on relatively interchangeable bonds may buffer females from the loss of preferred social partners. Extending this idea, one might generally expect that species, populations, and sexes with less differentiated social relationships should experience reduced social ageing stemming from the mortality of conspecifics.

A reliance on “replaceable” relationships would not explain the apparent strengthening of social relationships for ageing females, however. Increases in female social behaviour might be expected for menopausal species, which can indicate a role for older females in offspring care, as repositories of knowledge, or as leaders in collective movements. A recent study of Baird’s beaked whales (*Berardius* *bairdii*) suggests that cultural knowledge may play a role in fine-scale space-use of deep waters, for example[26]. However, older female killer whales exhibit menopause and were found to have reduced social centrality[16], and there is currently no evidence that northern bottlenose whales are among the toothed whales that exhibit menopause[20]. In fact, there is some indication that male northern bottlenose whales may live longer than females, contrary to the general mammalian pattern[27]. Evidence for this difference in longevity comes from analysis of dentine growth layers in a single study however[19], and may not generalize across populations. Kinship dynamics, defined as predictable changes in the local relatedness[28], are another process which likely influences patterns of social ageing. For example, ageing female bottlenose whales likely vary in the number of offspring and grand-offspring that persist in the population. If these ageing females interact differently with kin (e.g., perhaps being more likely to provide care) compared to non-kin, we would predict some increases in social behaviour with age as well as substantial variability, as is observed in this population.

Amid these population-level and sex-specific effects, individual bottlenose whales showed substantial variation in how they responded socially to old age. Beyond the structural factors discussed above (e.g., kinship dynamics), this variation may also simply result from differences in personality[29]. We detected individual-level social ageing in traits where no overall trend was found, such as in female group size. Here, there was strong evidence that both positive and negative within-individual effects of minimum age were simultaneously present in the population. The implications of this are two-fold: first, it suggests that individuals can experience substantial social ageing in the absence of a population-level effect. This reifies the benefit of exploring social ageing using a random slopes approach that can partition variation at multiple scales. Second, the extent of within-individual variation may provide some insights into the type(s) of underlying mechanisms at hand. We propose that processes like leadership or changing social roles are most likely to explain large inter-individual differences, including opposite effects among individuals, e.g., if a subset of individuals become leaders while others do not. Similarly, individual differences in the outcomes of kinship dynamics, i.e., how related older individuals are to their potential associates[28], could plausibly result in substantial differences in social ageing. In comparison, the scope of inter-individual variation seems somewhat narrower for other mechanisms of social ageing. For example, reductions in energy budgets will vary across individuals, but it would be more surprising to see individuals exhibit large increases in energy with age.

In conclusion, these findings show that social ageing can vary substantially within populations and that sex and individual variation play a role in how individuals respond behaviourally to age. Of particular interest is the lack of evidence for increasing social selectivity with age in this population, which has been detected in several species. This raises the intriguing possibility that social selectivity is driven by ecological and/or phylogenetic patterns that are more specific to primates or terrestrial mammals, though evidence from a wider set of species will be necessary to confirm this. Our results also challenge the most common finding that social bonds decline for ageing females, indicating that studies from diverse animal societies will be necessary to fully understand these patterns and build a more general theory on why social ageing should vary by sex.

Limitations of the study

Our reliance on minimum age rather than true age is a weakness of our study and is expected to result in slight underestimates of the effects of social ageing generally. We aimed to minimize this issue by focusing our analysis on the later years of the long-term research project when minimum age should more closely approximate true age. The use of minimum age was also mitigated by the within-individual centering approach, which allowed us to isolate patterns occurring within individual lifetimes. Hypothetically, a reliance on minimum age may also contribute to estimates of individual-specific variation, if there are strong non-linearities in how traits change during a lifetime. However, we do not expect this to play a major role in our results, as individuals observed for long periods in the dataset (e.g., 20+ years) still appeared to have varied within-individual slopes (Figure 7b). Despite these challenges, studying social ageing in wild populations like these is necessary if the goal is to generalize across species and avoid misinterpretation based on captive or otherwise accessible populations (see[30]). We expect that the development of quantitative approaches for managing the uncertainties implied by minimum ages will be valuable for the field.

It is also important to note that our analysis relies on associations between whales, rather than direct interactions. Thus the relationships we observe are not necessarily affiliative and may sometimes involve agonistic behaviour or be influenced by processes that are not initially social (e.g., shared attraction to a specific area)[31]. Whales in this population typically swim in close formations with conspecifics, and appear to breathe synchonously with one another[22]. Furthermore, focusing our analysis on relatively close spatial-temporal associations (i.e., 2 minutes) should help to exclude instances when animals were in the vicinity of one another for non-social reasons without interacting directly. Regardless, future work may benefit from the use of aerial video from drones, which can help to identify direct interactions between cetaceans (e.g.,[16]).

STAR Methods

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data necessary to complete analyses of social ageing in *Hyeroodon ampullatus*.	Github	https://github.com/swalmsley/Bottlenose-Social-Ageing
Software and algorithms		
Analysis pipeline for modelling social ageing in *Hyperoodon ampullatus*	Github	https://github.com/swalmsley/Bottlenose-Social-Ageing

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Sam Walmsley (sam.walmsley@dal.ca).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Data are publicly available at https://github.com/swalmsley/Bottlenose-Social-Ageing, alongside all original code used in this analysis. DOIs for both are listed in the above Key Resources Table. Please contact Sam Walmsley (sam.walmsley@dal.ca) for additional information.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

This study did not rely on experimental model animals, experimental *in vivo* animals, human participants, plants, microbe strains, cell lines, or primary cell cultures.

METHOD DETAILS

Study System and Data collection

Photographs of northern bottlenose whales were collected during 26 summers spanning 1988-2023. While northern bottlenose whales can travel large distances, this study focuses on a population of approximately 170 animals that is localized to the Scotian Shelf, centered on a large submarine canyon known as “The Gully”. Though individuals move between this and other nearby areas such as the Shortland and Haldimand canyons, acoustic data show that bottlenose whales are present in the Gully year-round[32]. Ocean-going sailing vessels were used for fieldwork, a 10-m boat for 1988-1990, and a 13-m boat for all subsequent years. These vessels allowed us to spend approximately two weeks in the Gully at a time, with one to three of these trips occurring during each summer fieldwork season. During these trips, we surveyed the canyon and searched for bottlenose whales visually (e.g., fins, blows) and using acoustic indicators (i.e., clicks in the appropriate frequency range). Bottlenose whales were then photographed *ad libitum* during encounters, during which we generally spent no more than one hour with the same group of whales. When possible, we aimed to photograph both sides of the dorsal fin of each animal. Traditional 35-mm film cameras were replaced by digital cameras in 2007. Though lens dimensions varied, typically a 300mm fixed lens was used.

Photo-identification

Photographic identifications of northern bottlenose whales based on side-specific (left/right) appearance of the dorsal fin and other markings were extracted from a long-term catalogue spanning 1988-2023[33]. Only high-quality photographs where the dorsal fin and surrounding area were clearly visible were used for identification. For this analysis, we focus on left-sided IDs only, as only a portion of heavily marked animals in the population can be reliably identified from each side. We also restricted our analysis to sightings within the Gully, excluding occasional sightings along the continental shelf or in other canyons, where group size and other aspects of social behaviour may vary.

Calves and juveniles were distinguished from adults visually by size comparison with adult whales when possible, and otherwise by several visible features. Calves are typically very dark in colouration, with a particularly dark band running along the dorsal plane of the body, and have few other markings. Additional distinguishing features include visible fetal folds and non-rigid dorsal fins which can appear folded and bend downwards. Newborn calves were likely born in the late spring or early summer, so would likely be just several months old when photographed in the summer during fieldwork. Next, we considered juveniles to be older than calves and up to 2/3 the size of adults (following[18]), and otherwise used the following features to distinguish them visually: a darker band of colouration at the dorsal plane, and often having relatively few scars or other markings. Fin shape and approximate size relative to the body were also characteristic of age class, with calves and juveniles relatively smaller dorsal fins with a much rounder trailing edge such that the tip of the fin points slightly downwards, whereas adults often have taller fin shapes, though there is substantial variation.

While calves can be identified unambiguously, the classification of juveniles is likely to be imperfect given that their traits will blend continuously into adult traits. To assess the accuracy of these classifications, we calculated Fleiss' kappa statistic for annually-indexed age classifications from two independent raters[34]. Visual classifications of young animals showed substantial inter-rater agreement for all classes (Fleiss' kappa for calves: 0.80, juveniles: 0.61, adults: 0.67; $p < 0.001$).

Sex classification was based on the appearance of melons (foreheads) in photographs, and confirmed with genetic analysis for a subset of individuals that have been biopsied (see[35] for additional details). Males, and particularly older males, have large flat melons that are often scarred or whitened, and may contain a "target"-like circle, presumably playing a function in headbutting behaviour[25]. However, these traits can be subtler for younger males, and individuals without these traits are classified as female/immature, which may include young males. In-depth description of the photo-identification and sex classification protocols can be found at[33].

Individuals with no high-quality melon photographs or where melons were not clearly distinguishable as male or female/immature were classified as "unknown". To mitigate possible misclassifications, we focused on adult individuals only (excluding younger animals), and conducted sensitivity analyses to determine whether our key findings changed when focusing on females that had been observed as adults for at least 10 years, or when using genetically-sexed animals only (see "Robustness Checks").

We assigned "minimum ages" for each ID for each year based on the age class at first identification. We assumed that calves had a minimum age of zero and that juveniles had a minimum age of one when first observed. Based on this assumption, individuals classified visually as juveniles rarely had a minimum age greater than two, and never greater than three. Accordingly, we assumed that adults had a minimum age of 3 when first observed. Note that these were intended as absolute minimums, and will not all capture biological or behavioural transitions to adulthood (e.g., sexual maturity occurs between 7-11 years old;[36]). Instead, our classifications for initial minimum ages align with the conclusion of weaning in northern bottlenose whales, which occurs between 3-4 years old[37]. We calculated these minimum age values based on left-sided identifications only. While this meant ignoring some information about minimum age if an ID had right-sided photographs from an earlier year where no left-sided photographs were available, it avoided the potential bias of individuals identifiable from both sides (and thus more heavily marked and potentially older) being assigned higher minimum ages than individuals with side-specific IDs only.

QUANTIFICATION AND STATISTICAL ANALYSIS

Bayesian inference of social relationships

We defined associations as the co-occurrence of two animals within 2 minutes of one another, based on the timing of photographs. This definition was intended to emphasize instances when whales were swimming in close proximity to one another. In between their dives of 6-70 minutes the bottlenose whales form tight, coordinated groups of about 1-7 individuals for roughly 5-120 min at the surface[18];[38], so our measure of association corresponds closely to membership in the same group. We used days as sampling periods, recording the presence or absence of an association for each possible dyad on each day when at least one animal in the dyad was observed. Accordingly, we considered instances when 1) hypothetical individual ‘A’ was seen on a given day but ‘B’ was not seen and 2) when ‘A’ and ‘B’ were both seen on a given day but never within 2 minutes of each other as equally implying no association on that day.

We then implemented a Bayesian approach to estimating dyad-specific estimates of the proportion of time that each pair of animals was detected together. Models were run separately for each year, resulting in annual social networks, and were estimated according to the following equation:

$$\begin{aligned} Together &\sim Bernoulli(1,p) \\ logit(p) &= \alpha_{overall} + \alpha_{[Dyad]} \\ \alpha_{overall} &\sim Normal(-1.5,1.5) \\ \alpha_{[Dyad]} &\sim Normal(\overline{\alpha},\sigma) \\ \overline{\alpha} &\sim Normal(0,1) \\ \sigma &\sim Exponential(1) \end{aligned}$$

Here, $\alpha_{overall}$ represents an overall intercept for the amount of time pairs of individuals were detected together while $\alpha_{[Dyad]}$ represents a varying effect for each dyad. The resulting dyad-specific deviations, when combined with the overall intercept, represent dyadic relationships or “edge weights” in social network parlance.

Fitting dyad ID as a varying effect allowed us to benefit from partial pooling, which induces “shrinkage’ towards a mean dyadic effect (see[39]), which will be strongest for dyads that have few observations and/or those that would otherwise have extreme edge weight values. This is valuable for our study system, where we have relatively few observations in each year to infer social relationships, but a relatively large number of individuals from which we can pool information to generate more accurate dyad-specific estimates.

Social networks were fit using a non-centered parameterization in the brms package in R[40]. For these network models and all other models in this study, the posterior was estimated using the Hamiltonian Monte Carlo algorithm with 2,000 iterations (1,000 warmup) and 4 chains. Models were then assessed using standard diagnostics such as trace plots, R-hat values, and effective sample sizes before interpreting results.

Calculating individual social traits

Group size

We extracted group sizes from photo-identifications by binning identifications into consecutive temporal groups using a window of 10 minutes (similar to[18]). We then combined any groups that included identifications less than 5 minutes apart from one another. From these groups, we calculated group sizes for each individual in each group that it was observed in. This offered a broader measure of social activity compared to the finer temporal scale of associations used for social network analysis.

Number of social partners

The number of social partners (i.e., social network degree) was calculated directly from annual association data as the number of unique animals that each individual had an association with. We expected this and other social traits to be strongly influenced by asymmetries in sampling intensity across individuals, so we also tracked the number of sampling periods during which each individual was observed in each year to serve as a control in subsequent models.

Social network traits

We used the annual social networks to extract three social traits for each individual in each year it was observed. *Strength* is the summed weight of all edge weights, capturing a general level of social effort and direct connections with others. *Eigenvector centrality* (hereafter centrality) is similar to strength but incorporates "connections of connections" to measure both direct and indirect relationships, with higher centrality values for individuals who are well-connected and whose connections are also well-connected. See[41] for further discussion of social network measures. *Mean bond strength* is the average of edge weights for each individual, excluding any zero-edges, defined as dyads that were never observed associating in the given year. In the Bayesian framework, these zero-edges will often be assigned a very small edge weight value, based on the assumption that they may interact occasionally. The average of all non-zero bonds is a measure of the intensity of social relationships, with lower values indicating that individuals spend less time with specific partners.

To propagate uncertainty from edge weights into individual social traits, we iteratively sampled from the posterior of each network model to create 100 "draws" of each annual network. We then calculated the social network traits for each draw, using the igraph package for strength and centrality[42]. From these values, we calculated the mean and standard deviation of each trait for each individual in each year in which it was observed.

Modelling social traits as a function of minimum age

Next, we used multilevel models to explore within-individual variation in social traits, using the inferred minimum age of each animal. Importantly, northern bottlenose whales were observed for different parts of their lives (i.e., some individuals were only seen from minimum ages 2-10 while others were seen from 2-30). Even when using a varying effects approach, failing to account for variation in a *predictor* variable across clusters (here, minimum age across individuals) can result in the conflation of between- and within-individual effects (see[43] as well as[44] for discussion of the causal implications). Accordingly, we used a within-individual centering approach, equivalent to a group-mean centering approach, which decomposes the effect of a predictor into between- and within-individual components. While these effects may often be aligned, when they differ the overall effect of the variable (here, minimum age) may mask the true underlying relationships[45]. See[46] which applies a very similar approach to jackdaws (*Corvus monedula*) of unknown age. Here, evidence of demographic processes like selective disappearance would be demonstrated by a difference between the coefficients of the within- and between-individual effects, not simply the presence of a between-individual effect. Whether within-individual effects are statistically identifiable in a given dataset will depend on various aspects of the data, particularly the number of repeat observations for each individual. When between- and within-individual effects are not statistically distinct, within-individual effects can be assumed to dominate observed patterns[5].

All models included the mean minimum age for each individual across the years where observations were included (i.e., the between-individual effect of age), the change from this mean (i.e., the within-individual effect of age). We incorporated a varying effects approach for the within-individual age term (i.e., random slopes) which allows us to consider how individuals differ in their social responses to ageing (see[43]). This also allowed for the possibility that a few individuals become more social with age (e.g., matriarchs or other types of leaders), while others might show stable or declining social traits. We also included a varying effect on the intercept for each year, which accounts for variation across years and variation in edge weights for each annual social network. Lastly, we expected that the number of social partners, network strength, and network centrality would scale positively with sampling intensity, and so for these models we adjusted for the number of sampling periods (days) that each individual was observed in during a given year.

For these models, we focused on adults only, excluding any individuals in years that they were classified as calves or juveniles. We also excluded individuals seen in just one year: first, these may be “transient” individuals visiting the population temporarily and thus might exhibit different social behaviour compared to individuals with longer-term residency and social familiarity. Secondly, as our social network traits were indexed annually, these individuals would not be usable for within-individual comparisons, which was necessary for our analysis. We focused our analysis on years after 2000, as we expected the bias between minimum age and true age to be greatest in the first years of the project (e.g., all adults observed in 1988 would be assigned a minimum age of 2 that year). For models based on network traits, we excluded small amounts of data from years with very few photo-identifications (< 100 photographs) or just a single sampling period (1 day of effort).

These models were fit using the brms package in R[40]. Group sizes and number of social partners were modelled as counts in Poisson models with log link functions. Eigenvector centrality and mean bond strength were modelled using a Beta family (which ranges from 0 to 1) with a logit link function, while network strength was modelled using a Gamma family with a log link function. Prior to fitting, we subtracted 0.001 from all values of eigenvector centrality as there were 2 measures of 1.0 that were incompatible with the Beta distribution (N = 2 of 635 measures). Standard deviations of strength, centrality, and mean relationship strength were included as measurement error around the response in order to propagate uncertainty from social network models through the analysis. Weakly informative priors were selected based on prior predictive simulation and varied across models. All priors for age effects were symmetric around 0, i.e., we did not encode any expectation of negative or positive changes in social behaviour with age. Unless stated otherwise, summaries of effects are reported as 90% credible intervals[39]. If the 90% CI does not include 0, the posterior probability of a directional effect is greater than 95%.

Models with female centrality and mean edge weight (both sexes) as response variables showed convergence issues and divergent transitions when uncertainty in network traits was incorporated as an error term around the response variable. Though these models produced similar results, we proceed to present and interpret versions of these models without a measurement error term. Otherwise, all models ran successfully with no evidence of non-convergence or other pathologies based on standard diagnostics. Numerical summaries of all social ageing models are found in the supplementary material (Tables S2-S26).

Multivariate analyses

Given that social network traits are often interrelated, we used a simple multivariate analysis to visualize patterns of social ageing across traits. First, we fit a principal components analysis (PCA) to the within-individual effects extracted from each model. The PCA was fit using the *stats* package in R, all effects were scaled, and only individuals for which we had effects for all five social traits were included. We also ran a MANOVA to assess whether male and female bottlenose whales varied in multivariate patterns of social ageing. All analyses were organized and stored using the targets package[47], and are available at https://github.com/swalmsley/Bottlenose-Social-Ageing.

Robustness checks

We carried out several checks to assess the robustness of our findings across several key analytic decisions. First, we re-ran all analyses using a 10-minute threshold for demarcating associations in the social network. Results were nearly identical, so we proceeded to present the results from the 2-minute association models only. We also assessed whether our sex classification procedure may have influenced our results. First, we re-fit each of the “Female” models while excluding individuals seen over a span of less than 10 years, as younger males can be difficult to distinguish from females and can be visually misclassified as females on occasion. We also fit versions of all social ageing models and the MANOVA using only individuals for whom we had confirmed genetic sex information from biopsies. While models based on genetic sex had smaller sample sizes and presumably less power to detect age-related effects, we aimed to check if the sign and magnitude of the effects were similar. Though results from these sex-related robustness checks were generally similar to the main models, we highlight any differences in the Results.

Acknowledgements

We thank all members of the Whitehead Lab for helpful comments on an earlier version of these ideas. We also thank the organizers of a Royal Society Meeting, “Understanding Age and Society Using Natural Populations” for inspiring parts of this work. SFW is supported by the Izaak Walton Killam Memorial Scholarship and the NSERC Alexander Graham Bell Canada Graduate Scholarship. HW is supported by an NSERC Discovery Grant. Fieldwork, data processing, and data management were supported through funding provided by Fisheries and Oceans Canada.

Author contributions

Conceptualization: SFW, HW. Methodology: SFW, HW. Validation: SFW. Formal analysis: SFW. Data curation: SFW, LJF, EZ, CG. Writing - original draft: SFW. Writing - review and editing: SFW, HW, LFJ, EZ, CG.

Declarations of interest

The authors declare no competing interests.

Supplemental information titles and legends

Document S1. Figures S1-S2, Tables S1-S26.

References

1. Siracusa, E.R., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Social ageing: exploring the drivers of late-life changes in social behaviour in mammals. Biology Letters *18*, 20210643. https://doi.org/10.1098/rsbl.2021.0643.

2. Rosso, A.L., Taylor, J.A., Tabb, L.P., and Michael, Y.L. (2013). Mobility, disability, and social engagement in older adults. J Aging Health *25*, 617–637. https://doi.org/10.1177/0898264313482489.

3. Lang, F.R., and Carstensen, L.L. (1994). Close emotional relationships in late life: Further support for proactive aging in the social domain. Psychology and Aging *9*, 315–324. https://doi.org/10.1037/0882-7974.9.2.315.

4. Rosati, A.G., Hagberg, L., Enigk, D.K., Otali, E., Emery Thompson, M., Muller, M.N., Wrangham, R.W., and Machanda, Z.P. (2020). Social selectivity in aging wild chimpanzees. Science *370*, 473–476. https://doi.org/10.1126/science.aaz9129.

5. Siracusa, E.R., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Within-individual changes reveal increasing social selectivity with age in rhesus macaques. Proceedings of the National Academy of Sciences *119*, e2209180119. https://doi.org/10.1073/pnas.2209180119.

6. Schino, G., and Pinzaglia, M. (2018). Age-related changes in the social behavior of tufted capuchin monkeys. American J Primatol *80*, e22746. https://doi.org/10.1002/ajp.22746.

7. Machanda, Z.P., and Rosati, A.G. (2020). Shifting sociality during primate ageing. Phil. Trans. R. Soc. B *375*, 20190620. https://doi.org/10.1098/rstb.2019.0620.

8. Cook, P.A., Costello, R.A., Formica, V.A., and Brodie, E.D. (2023). Individual and population age impact social behavior and network structure in a long-lived insect. The American Naturalist *202*, 667–680. https://doi.org/10.1086/726063.

9. Albery, G.F., Clutton-Brock, T.H., Morris, A., Morris, S., Pemberton, J.M., Nussey, D.H., and Firth, J.A. (2022). Ageing red deer alter their spatial behaviour and become less social. Preprint at bioRxiv, https://doi.org/10.1101/2021.06.11.448092 https://doi.org/10.1101/2021.06.11.448092.

10. Rudd, L., Packer, C., Biro, D., Firth, J.A., and Albery, G.F. (2024). Sex-specific social ageing in wild African lions. Preprint, https://doi.org/10.2139/ssrn.4761072 https://doi.org/10.2139/ssrn.4761072.

11. Sadoughi, B., Mundry, R., Schülke, O., and Ostner, J. (2024). Social network shrinking is explained by active and passive effects but not increasing selectivity with age in wild macaques. Proc. R. Soc. B. *291*, 20232736. https://doi.org/10.1098/rspb.2023.2736.

12. Hoy, S.R., Vucetich, J.A., Vucetich, L.M., Hindelang, M., Huebner, J.L., Kraus, V.B., and Peterson, R.O. (2024). Links between three chronic and age-related diseases, osteoarthritis, periodontitis, and osteoporosis, in a wild mammal (moose) population. Osteoarthritis and Cartilage *32*, 281–286. https://doi.org/10.1016/j.joca.2023.11.016.

13. Bull, A., Iciaszczyk, N., and Sinha, S.K. (2023). Understanding the factors driving the epidemic of social isolation and loneliness among older Canadians (National Institute on Ageing).

14. Ohsumi, S. (1971). Some investigations on the school structure of sperm whale. Sci. Rep. Whales Res. Inst., 1–25.

15. Gaskin, D.E. (1970). Composition of schools of sperm whales *Physeter catodon* Linn. east of New Zealand. New Zealand Journal of Marine and Freshwater Research *4*, 456–471. https://doi.org/10.1080/00288330.1970.9515359.

16. 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. R. Soc. B. *288*, 20210617. https://doi.org/10.1098/rspb.2021.0617.

17. Evans, T., Krzyszczyk, E., Frère, C., and Mann, J. (2021). Lifetime stability of social traits in bottlenose dolphins. Commun Biol *4*, 1–8. https://doi.org/10.1038/s42003-021-02292-x.

18. Gowans, S., Whitehead, H., and Hooker, S.K. (2001). Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: Not driven by deep-water foraging? Animal Behaviour *62*, 369–377. https://doi.org/10.1006/anbe.2001.1756.

19. Christensen, I. (1973). Age determination, age distribution and growth of bottlenose whales, *Hyperoodon ampullatus*, in the Labrador Sea. Norwegian Journal of Zoology *21*, 331–340.

20. Ellis, S., Croft, D.P., Nielsen, M.L.K., Franks, D.W., and Weiss, M.N. (2023). Bayesian inference of toothed whale lifespans. Preprint, https://doi.org/10.1101/2023.02.22.529527 https://doi.org/10.1101/2023.02.22.529527.

21. Hooker, S.K., Soto, N.A.D., Baird, R.W., Carroll, E.L., Claridge, D., Feyrer, L., Miller, P.J.O., Onoufriou, A., and Schorr, G. (2019). Future directions in research on beaked whales. Frontiers in Marine Science *5*. https://doi.org/10.3389/fmars.2018.00514.

22. O'Brien, K. (2013). MSc Thesis: Population status and social structure of northern bottlenose whales (*Hyperoodon ampullatus*) on the Scotian Shelf.

23. Martin, J.S., Massen, J.J.M., Šlipogor, V., Bugnyar, T., Jaeggi, A.V., and Koski, S.E. (2019). The EGA+GNM framework: An integrative approach to modelling behavioural syndromes. Methods in Ecology and Evolution *10*, 245–257. https://doi.org/10.1111/2041-210X.13100.

24. Sih, A., Bell, A., Johnson, J., and Ziemba, R. (2004). Behavioral syndromes: An integrative overview. The Quarterly Review of Biology *79*, 241–277. https://doi.org/10.1086/422893.

25. Gowans, S., and Rendell, L. (2006). Head-butting in northern bottlenose whales (*Hyperoodon ampullatus*): A possible function for big heads? Marine Mammal Science *15*, 1342–1350. https://doi.org/10.1111/j.1748-7692.1999.tb00896.x.

26. Filatova, O.A., Fedutin, I.D., Meschersky, I.G., Mamaev, E.G., and Hoyt, E. (2024). Unusual use of shallow habitats may be evidence of a cultural tradition in Baird's beaked whales. Animal Behaviour *209*, 121–128. https://doi.org/10.1016/j.anbehav.2023.12.021.

27. Lemaître, J.-F., Ronget, V., Tidière, M., Allainé, D., Berger, V., Cohas, A., Colchero, F., Conde, D.A., Garratt, M., Liker, A., et al. (2020). Sex differences in adult lifespan and aging rates of mortality across wild mammals. Proc. Natl. Acad. Sci. U.S.A. *117*, 8546–8553. https://doi.org/10.1073/pnas.1911999117.

28. Croft, D.P., Weiss, M.N., Nielsen, M.L.K., Grimes, C., Cant, M.A., Ellis, S., Franks, D.W., and Johnstone, R.A. (2021). Kinship dynamics: Patterns and consequences of changes in local relatedness. Proceedings of the Royal Society B: Biological Sciences *288*. https://doi.org/10.1098/rspb.2021.1129.

29. Laskowski, K.L., Chang, C.-C., Sheehy, K., and Aguiñaga, J. (2022). Consistent individual behavioral variation: What do we know and where are we going? Annu. Rev. Ecol. Evol. Syst. *53*, 161–182. https://doi.org/10.1146/annurev-ecolsys-102220-011451.

30. Webster, M.M., and Rutz, C. (2020). How STRANGE are your study animals? Nature *582*, 337–340. https://doi.org/10.1038/d41586-020-01751-5.

31. Whitehead, H., and James, R. (2015). Generalized affiliation indices extract affiliations from social network data. Methods in Ecology and Evolution *6*, 836–844. https://doi.org/10.1111/2041-210X.12383.

32. Feyrer, L.J., Stanistreet, J.E., Gomez, C., Adams, M., Lawson, J.W., Ferguson, S.H., Heaslip, S.G., Lefort, K.J., Davidson, E., Hussey, N.E., et al. (2024). Identifying important habitat for northern

bottlenose and Sowerby's beaked whales in the western North Atlantic. Aquatic Conservation *34*, e4064. https://doi.org/10.1002/aqc.4064.

33. Feyrer, L., and Walmsley, S. (2024). A guide to northern bottlenose whale photo ID: Version 4.0. https://doi.org/10.17605/OSF.IO/XD7EK.

34. Landis, J.R., and Koch, G.G. (2016). The measurement of observer agreement for categorical data. International Biometric Society *33*, 159–174.

35. Feyrer, L.J., Einfeldt, A., Bentzen, P., Whitehead, H., and Paterson, I.G. (2019). Evolutionary impacts differ between two exploited populations of northern bottlenose whale (*Hyperoodon ampullatus*). Ecology and Evolution, 13567–13584. https://doi.org/10.1002/ece3.5813.

36. Benjaminsen, T., and Christensen, I. (1979). The natural history of the bottlenose whale, Hyperoodon ampullatus. In Behavior of Marine Animals, pp. 143–164.

37. Feyrer, L.J., Zhao, S.T., Whitehead, H., and Matthews, C.J.D. (2020). Prolonged maternal investment in northern bottlenose whales alters our understanding of beaked whale reproductive life history. PLoS ONE *15*, 1–19. https://doi.org/10.1371/journal.pone.0235114.

38. Hooker, S.K., and Baird, R.W. (1999). Deep–diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). Proc. R. Soc. Lond. B *266*, 671–676. https://doi.org/10.1098/rspb.1999.0688.

39. McElreath, R. (2020). Statistical Rethinking2: A Bayesian Course with Examples in R and Stan (CRC Press).

40. Bürkner, P.-C. (2021). Bayesian item response modeling in *R* with **brms** and *Stan*. J. Stat. Soft. *100*. https://doi.org/10.18637/jss.v100.i05.

41. Whitehead, H. (2008). Analyzing animal societies: Quantitative methods for vertebrate social analysis (University of Chicago Press).

42. Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. InterJournal.

43. Van De Pol, M., and Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. Animal Behaviour *77*, 753–758. https://doi.org/10.1016/j.anbehav.2008.11.006.

44. Byrnes, J.E.K., and Dee, L.E. (2024). Causal inference with observational data and unobserved confounding variables (Ecology) https://doi.org/10.1101/2024.02.26.582072.

45. Hamaker, E.L., and Muthén, B. (2020). The fixed versus random effects debate and how it relates to centering in multilevel modeling. Psychological Methods *25*, 365–379. https://doi.org/10.1037/met0000239.

46. Verhulst, S., Geerdink, M., Salomons, H.M., and Boonekamp, J.J. (2014). Social life histories: jackdaw dominance increases with age, terminally declines and shortens lifespan. Proc Biol Sci *281*, 20141045. https://doi.org/10.1098/rspb.2014.1045.

47. Landau, W.M. (2021). The targets R package: a dynamic Make-like function-oriented pipeline toolkit for reproducibility and high-performance computing. Journal of Open Source Software *6*, 2959.