Social aging in dolphins

Authors: Kelley Meehan[1*], Barbara Class[2], Shinichi Nakagawa[3], Meredith MacQueeney[4], Vivienne Foroughirad[4,5], Janet Mann[5], Celine Frere[1]

[1]School of the Environment, The University of Queensland, St. Lucia, Queensland 4072, Australia

[2]Department of Biology, Ludwig-Maximilians-Universität München, 82152 Planegg-Martinsried, Germany

[3]Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2R3, Canada

[4]Department of Biology, Georgetown University, Washington DC 20057, USA

[5]Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77554, USA

*Corresponding author: k.meehan@uq.edu.au

Classification: Biological Sciences – Ecology; Biological Sciences – Evolution

Keywords: Social behaviour, Predictability, Malleability, Plasticity, Social aging, Cetaceans, Group size, Sociability, Social evolution, Within-individual variation

Authorship and Conflicting Interests Statement:

KM and CF conceived the study, KM devised and carried out the analysis with support from SN and BC. KM wrote the manuscript. JM, VF, MM and KM collected behavioural data. JM, CF, SN, VF, MM, and BC commented on the manuscript. JM, CF, and VF oversaw wider running of the project. The authors declare no competing interests.

Abstract

Recent work has unearthed strong relationships between aging and average sociability. Clear patterns of decreases in average sociability are observed across taxa; many of these are sex-specific. Individuals, however, generally deviate from population averages, and discounting individual variance in behaviour could disguise mechanisms of adaptation, selection, and developmental stability. Using forty years of behavioural data from Indo-Pacific bottlenose dolphins, we provide new insights into social aging. We achieve this by simultaneously measuring both mean (repeatability) and variance (predictability) in group size—a trait reflecting social interaction preference—across the population and throughout individual lifespans. Double hierarchical location-scale modelling reveals a multidimensional response; at both the population and individual level, the mean trait response (plasticity) and variance (malleability) of group size changes with age. At a population level and for most individuals, average group size increases then declines in later life. This decline is more pronounced in males, though males are consistently in larger and more predictable groups than females at all life stages. Population predictability of group size increases throughout life, consistent with our prediction that social preferences strengthen with age. Individuals which are highly sociable are also highly predictable, and increased sociability and predictability both appear correlated with longevity. The positive correlation between increasing predictability and longevity leads us to hypothesise that individuals develop social competence by refining their social experiences. This process likely involves increasing social selectivity and optimizing social choices to achieve a net fitness benefit. These findings provide novel insights into social aging and illustrate how studying variance in social traits can capture processes of social competence, selectivity, and adaptation of social phenotypes occurring within an individuals' social environment.

Introduction

Throughout ontogeny, animals are subject not only to the bounds of their physical world, but to a world defined by the other individuals around them: their social environment. Interaction with conspecifics is unavoidable, particularly for group living species, but patterns of engagement can be flexible and shaped by the individual. These choices, in turn, are highly consequential, as ultimate fitness outcomes are often influenced by social integration[55,101,107,109,125]. Recent literature has focused on the relationship between social behaviour and age[72,103]. Aging is known to drive shifts in sociability in many taxa, such as decreased network size and increased social selectivity reported in humans[16,19,135], non-human primates[72,93,104], and birds[2,98], reduced affiliative interactions and social influence in rodents[63,130], and lessened social connectedness in deer[3]. These age-related patterns, however, are not one-size-fits-all even within species, as sex-specific variation has been documented in lions[94], giraffes[17,18,67], whales[124,126], and macaques[25].

Though the metrics, species, and methods of analysis have been different across these studies, all have focused on trait changes at the average level. Individuals, however, are more than their averages, and as such, the relationship between aging and individual variance in social behaviour remains poorly understood. Individual behaviour can be measured through both trait averages (i.e., behavioural syndromes[33,100], 'personality', repeatability[8]), and trait variance. This variation, the differences that exist within repeated measures of an individual, has been described with multiple terms: (1) within-individual or intraindividual variation (IIV)[108], or, (2) predictability, which measures the same variation but scales in reverse (increased variance in repeated measures means decreased predictability)[21]. Individual average behaviour may change over time or across environments (i.e., behavioural reaction norms, plasticity[128]). Variance in individual behaviour, too, is hypothesised to change, a phenomenon called 'malleability'[87]. At this time, malleability has not been empirically demonstrated in wild animals,

81 though varied predictability of movement in two age classes of owls suggests its presence[13].

82 These four components of behaviour (personality, plasticity, predictability, malleability) are

83 described in Table 1 alongside a conceptual graphic (Figure 1).

84

85 **Table 1:** The four components used to measure behaviour, including definitions and literature where each
86 term is explicitly used to describe a trait in the context of aging. Each term is categorised into the
87 dimension measured (average or variance) as well as the state of the variable: static (e.g. intercepts) or
88 dynamic (e.g. slopes). Broadly, studies of aging in the behavioural ecology literature focus on plasticity of
89 traits, though the use of the term varies from study to study.

Term	Trait dimension	Variable state	Definition	Empirical example studies with age components
Repeatability; Personality	Average	Static	The portion of behavioural variation that stems from differences among individuals [8]	Dolphins: [38] Birds: [117] Insects: [48] Rodents: [99] Meta-analysis: [6]
Plasticity	Average	Dynamic	The way behaviour changes situationally; a within-individual change in trait average [34,100,128]	Birds: [2,9,27,98,117] Insects: [1] Ungulates: [84] Non-human primates: [104]
Intraindividual variation; Predictability	Variance	Static	Within-individual trait variation in a given environment [21]	Owls: [13]
Malleability	Variance	Dynamic	Plastic changes in within-individual variation[87]	This study

90

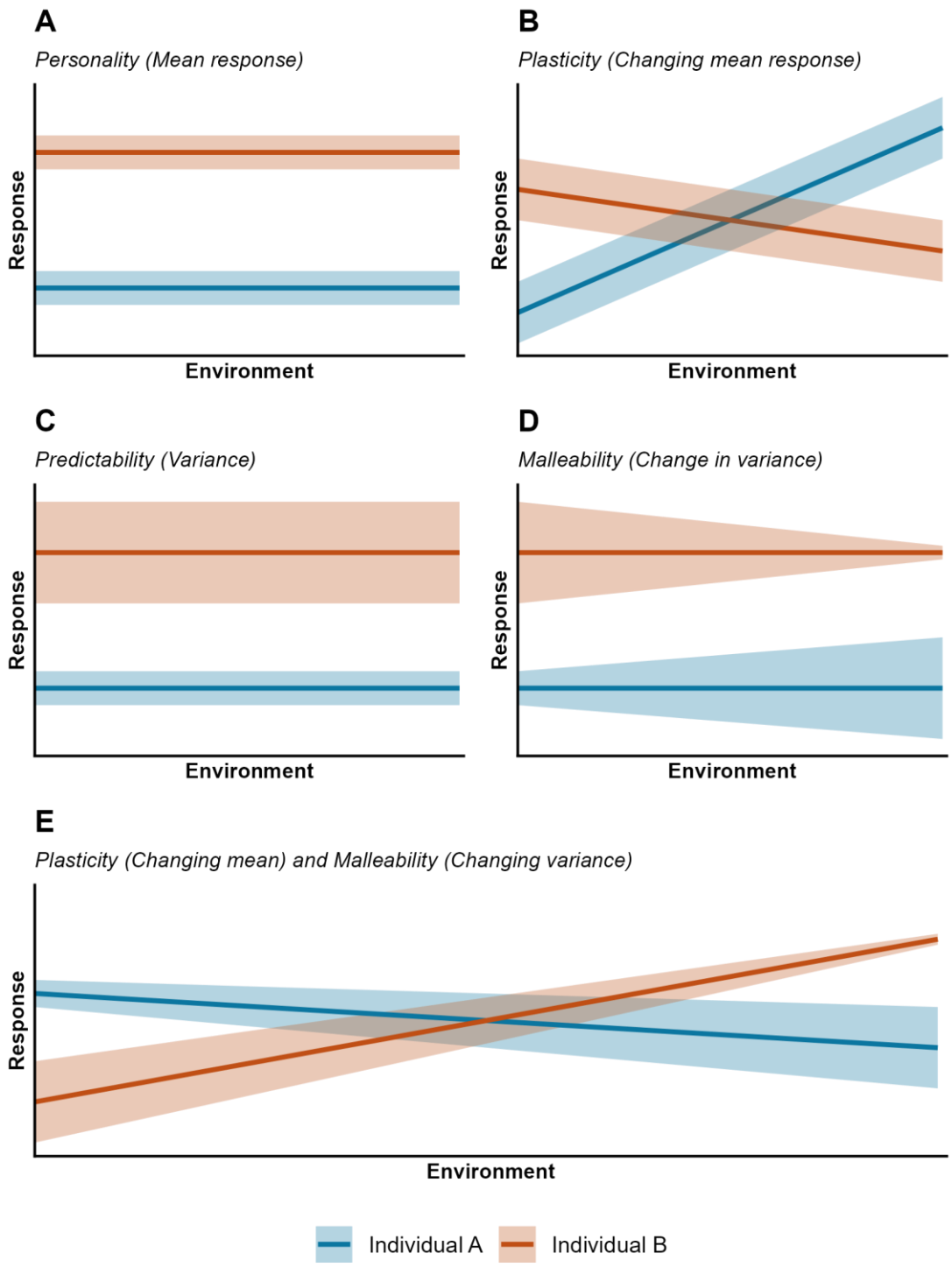


Figure 1: A series of conceptual plots illustrating the four components of behaviour in individuals A (blue) and B (orange). Lines represent average responses, and shading represents the spread of points around the average. In plot A, personality/repeatability, individuals have different average responses but the same variance. Plot B, plasticity, shows individual A increasing their average response across an environmental gradient and B decreasing, but in both cases variance is unchanged. Plot C, predictability, shows B has a higher variance than A. Plot D, malleability, shows A and B have unchanging average responses, but A becomes less predictable over an environmental gradient, and B becomes more predictable. Plot E describes how average response (plasticity) and variance-level change (malleability) can covary simultaneously, though this covariance need not occur in a consistent direction.

Within-individual variance has long been considered random noise in ecological data, but recent studies indicate that predictability can describe a host of hidden biological processes[129], such as adaptation or learning. Day to day, individuals generate a broad range of phenotypic responses to various external stimuli, but upon receiving feedback, are able to modify their behaviour[40,57], thereby reducing the variation they display in favour of stabilising their behaviour around a preferred phenotype[110,129]. When applied to a social phenotype associated with positive fitness, this ability is defined as "social competence"[88,115] and is hypothesised to be a trait upon which selection may act depending on social and environmental pressures[111]. Because social competence is developed through experience and feedback[95,114,115], in dynamic social environments, early development is likely to correspond to a period of low predictability. As individuals age and develop social competence, predictability should be malleable, reducing the degree of variation around an optimal reaction norm.

Taborsky (2021) further proposed a positive feedback loop between sociability and social competence, where environments favouring group formation would in turn select for individuals who are more socially competent in their groups, leading to increasing sociability and increasing favour for highly gregarious, highly competent animals[114]. If predictability can reflect social competence, in such a loop, a positive correlation would emerge between an individual's average sociability and their predictability, a pattern recently described and linked to fitness benefits in a social reptile[20]. However, optimum sociability can change depending on age and sex. For example, male and female life history strategies can differentially favour social interaction[43], leading to sex-specific patterns of social aging in many species.

Here, we use a 40-year study of wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) to investigate predictability and malleability in group size, a measurable social trait and critical component of social structure. Indo-Pacific bottlenose dolphins are long-lived marine mammals with a fission-fusion social structure characterised by high relational complexity[71].

126 Interactions among conspecifics in this population are dynamic and unbounded[41,42,44], and
127 individuals can independently change their group compositions 5-6 times per hour[44].
128 Delphinids, like primates, are posited to have evolved large brains to navigate cognitively
129 demanding social environments[12,36,121,131], which has enabled intricate, long-term social
130 strategies to develop in this population[23,24,42,46,80]. *T. aduncus* are demonstrably segregated
131 socially by sex[106]; female relationships are influenced by biparental kinship, shared habitat
132 preferences, and foraging behaviours[42,80], whereas males of this population engage in highly
133 structured, multi-tier alliance systems with unrelated individuals of similar age to compete for
134 access to cycling females[23,24,46]. Long lifespans (>52 years[81]), bisexual natal philopatry[118], and an
135 extended developmental period[60] have allowed us to collect many repeated measures for
136 hundreds of individuals, providing rare insights into the fine-scale behavioural changes that are
137 often difficult to detect in a wild population.

138 We hypothesise that patterns of average group size will correspond to changing socio-
139 ecological strategies throughout life, while predictability will reflect the development of social
140 competence. We expect average group sizes, especially for males, to increase from birth
141 through the juvenile period as individuals explore their social environment for appropriate social
142 partners[43,47,65], stabilise in adulthood as they codify social relationships and foraging
143 strategies[46,90], then decline with age as close conspecifics are lost to age-related mortality[39,92].
144 We also expect to see variation in predictability among individuals if some animals are more
145 socially competent than others, but because social competence develops through prior
146 experiences and feedback[95,114,115], early development is likely to correspond to a period of lower
147 predictability. As individuals learn to balance the benefits and costs of grouping as they age,
148 predictability of group size should canalise[129], as individuals selectively stabilise their
149 behavioural choices[93]. We predict a correlation between group size and its predictability, such
150 that individuals who are more gregarious are also more predictable. We also hypothesise that
151 the presence of sex-specific reproductive strategies present in this population will drive

differences in predictability and malleability, as the purpose and value of sociability differs between the sexes[39].

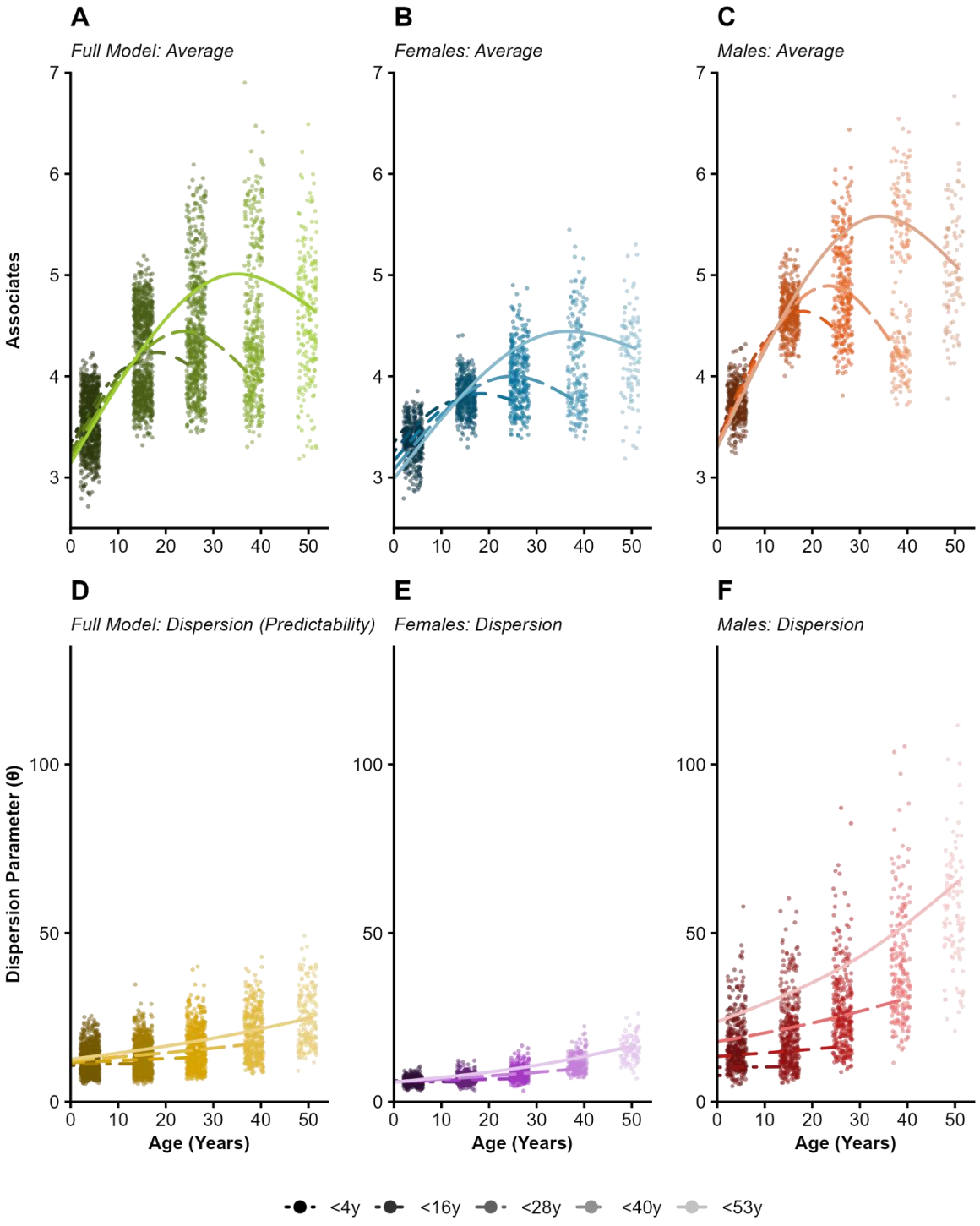
Results

Summary statistics

This dataset included 64,914 individual observations (mean per individual = 142, min 40, max 942) collected between 1988 and 2025. The number of observations, number of individuals, and average observations per individual for each sex is described in Table S2. Age at time of observation ranged from 0 days to an estimated 19,253 days (0 years to 52.7 years) old. Males were slightly more gregarious than females, with a mean of 6.05 (sd 5.37) associates per male observation and 5.14 (sd 5.00) associates per female observation (whole population average = 5.58, sd 5.20).

Fixed and random effects at the mean level (personality, plasticity)

Sex, age, and age at last sighting all had a quadratic effect on mean level sociability (Figure 2, Table 2, Table 3). Males had higher average gregariousness than females (Figure 2, Table 2, Table 3, Table S3). Mean group size increased throughout the juvenile and early adult years, peaked, and then declined with continuing age; this quadratic pattern was more pronounced in males (Figure 2, Table 2). Earlier declines in average group size appeared to precede earlier disappearance of individuals in the population, while longer lived individuals continued to increase in average group size (Figure 2, Table 2). Groups with newborns present were largest, followed by those with calves with groups made by juveniles and adults the smallest on average (Table 2, Table 3). Though most individual followed population level trends in group size, Individual varied substantially among one another in their group size intercept and age slopes across repeated measures (Figure 3, Table 2). Date of observation had a larger effect on mean sociability than year **(**Table 2).



176

177 **Figure 2:** Model predictions of group size at the mean and dispersion (predictability) scales, for the full
178 model (A, green, and D, yellow) and for female-only (B, blue, and E, purple) and male-only (C, orange, and
179 F, red) models. For visual simplicity, lifespan projections are binned into 5 ages of disappearance from
180 darkest to lightest shades of colour, 4 (approximating weaning age), 16, 28, 40, and 53 years. Increasingly
181 lighter shades represent prediction patterns associated with longer lifespan.

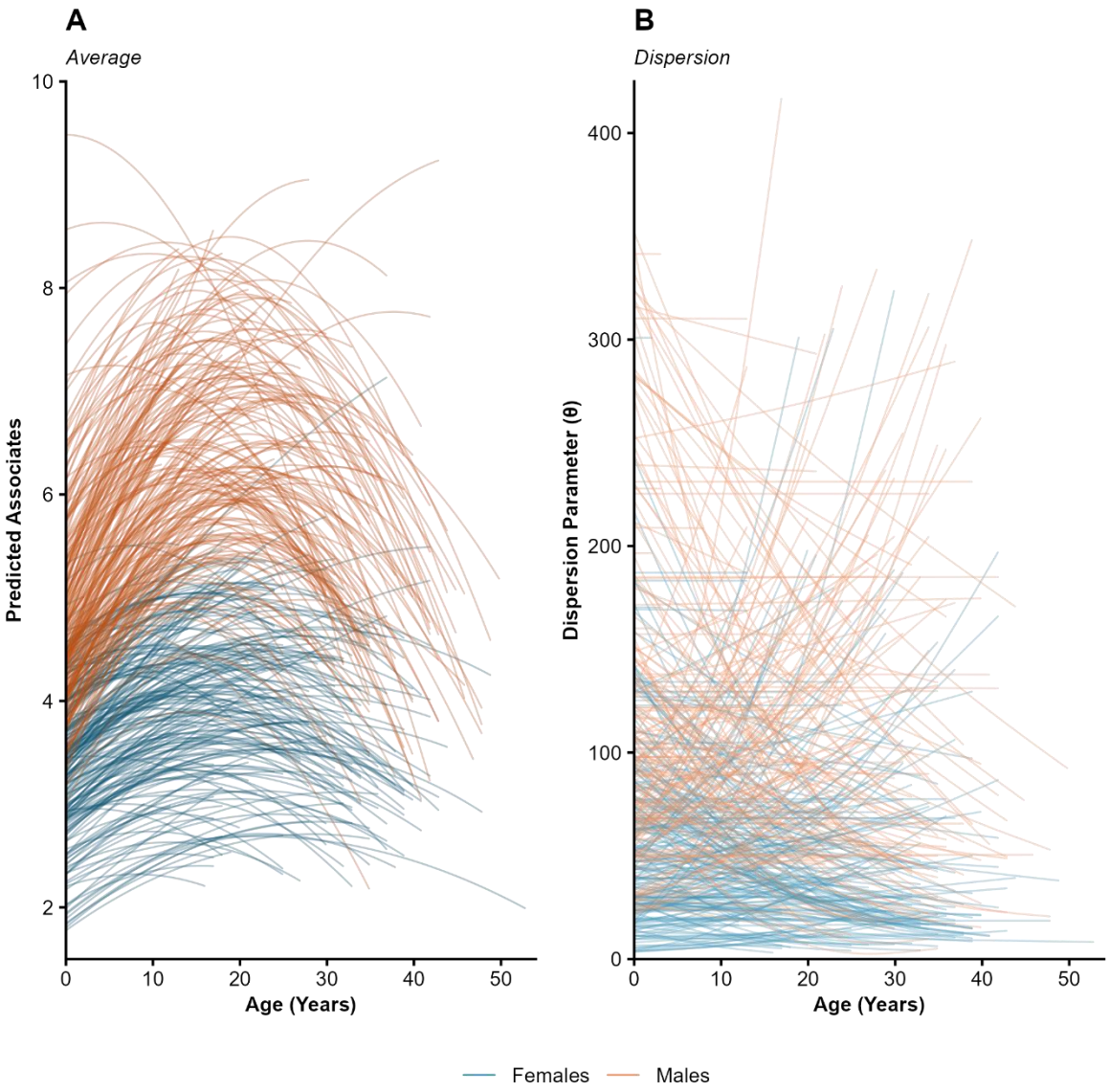


Figure 3: Random slopes for individual group size (A) and predictability (B). Each random slope is trimmed to within one year of the individual's age at last sighting. Males are represented in orange, females in blue. Because θ is directly reported, increasing values correspond to increasing predictability of individuals over their lifespan.

Table 2: Summary estimates (median, 95% credible interval) obtained from a double hierarchal generalised linear model estimating mean (sociability) and dispersion (predictability of sociability) parameters. Italicised terms are slopes; other terms are intercepts. Mean model effects are given on the log scale, while dispersion parameters are reported in standard deviations on the log scale.

		Estimate
Mean	**Fixed effects (coefficients):**	
	Intercept	1.28 (1.31,1.36)
	Sex (male)	0.14 (0.10, 0.19)
	Age	2.98 (-3.71, 9.59)
	Age²	-16.20 (-21.53, -10.99)
	Age at Last Sighting	0.03 (0.00, 0.06)
	*Age*Age at Last Sighting*	12.85 (6.29, 19.58)
	*Age²*Age at Last Sighting*	3.53 (-0.26, 7.41)
	Sex (male)**Age*	-1.14 (-9.30, 7.36)
	Sex (male)**Age²*	-13.24 (-19.47, -7.06)
	Sex (male)**Age at Last Sighting*	0.02 (-0.01, 0.06)
	Sex (male)**Age*Age at Last Sighting*	4.95 (-3.33, 13.32)
	Sex (male)**Age²*Age at Last Sighting*	4.23 (-0.34, 8.89)
	Reproductive State (Newborn)	0.12 (0.05, 0.19)
	Reproductive State (Not Calf)	-0.06 (-0.09, -0.04)
	Random effects (SD):	
	Individual	0.20 (0.18, 0.22)
	Age of Individual	28.00 (23.78, 32.75)
	Age² of Individual	4.06 (0.23, 9.16)
	Date	0.62 (0.60, 0.64)
	Year	0.18 (0.13, 0.24)
Dispersion	**Fixed effects (coefficients):**	
	Intercept	2.38 (2.08, 2.69)
	Sex (male)	0.55 (0.38, 0.72)
	Age	0.05 (0.03, 0.08)
	Age at Last Sighting	0.07 (0.04, 0.12)
	*Age*Age at Last Sighting*	0.05 (0.03, 0.08)
	Sex (male)**Age*	0.05 (0.03, 0.09)
	Sex (male)**Age at Last Sighting*	0.15 (0.07, 0.25)
	Sex (male)**Age*Age at Last Sighting*	0.05 (0.03, 0.08)
	Reproductive State (Newborn; <2 months age)	0.48 (0.12, 1.07)
	Reproductive State (Not Calf; post-weaning)	0.07 (0.03, 0.11)
	Random effects (SD):	
	Individual	0.80 (0.73, 0.87)
	Age of Individual	0.60 (0.53, 0.67)
	Date	1.56 (1.47, 1.66)
	Year	0.76 (0.57, 1.02)
Mean – Dispersion	**Correlations:**	
	Mean Individual – Dispersion Individual	0.93 (0.89, 0.96)
	Mean Date – Dispersion Date	-0.38 (-0.43, -0.32)
	Mean Year – Dispersion Year	0.16 (-0.24, 0.52)

Table 3: Computed Average Marginal Effects (AMEs) for each population parameter in the model. AMEs are calculated by marginalising out the reference condition applied by the model to reveal the true effect of a given parameter separate from other conditions specified in the model. Credible intervals are 95%. All estimates are given on the log scale.

	Fixed effects (coefficients):	Estimate
Mean	Sex (Female)	3.55 (3.29, 3.80)
	Sex (Male)	4.16 (3.86, 4.46)
	Age (scaled, centred)	3.85 (3.57, 4.10)
	Age at Last Sighting (scaled, centred)	3.85 (3.57, 4.10)
	Reproductive State (Newborn; < 2 months age)	4.59 (4.13, 5.03)
	Reproductive State (Calf; > 2 months, pre-weaning)	4.07 (3.77, 4.36)
	Reproductive State (Not Calf; post-weaning)	3.82 (3.54, 4.07)
Dispersion	Sex (Female)	2.47 (2.17, 2.77)
	Sex (Male)	3.06 (2.75, 3.36)
	Age (scaled, centred)	2.71 (2.44, 3.01)
	Age at Last Sighting (scaled, centred)	2.76 (2.47, 3.05)
	Reproductive State (Newborn; < 2 months age)	3.18 (2.65, 3.76)
	Reproductive State (Calf; > 2 months, pre-weaning)	2.71 (2.41, 3.00)
	Reproductive State (Not Calf; post-weaning)	2.77 (2.50, 3.08)

Fixed and random effects at the dispersion level (predictability, malleability)

Similar to mean level gregariousness, group size predictability was affected by sex and age. At the dispersion level, every level of every effect tested differed from other levels (Table 3, Table S3). Males were, on average, more predictable than females (Table 2, Table 3, Table S3). Group size predictability increased with age (Table 3), though the rate of increase in predictability was highest in the longest-lived individuals (Figure 2, Table 2), and this relationship was more pronounced in males than females (Figure 2, Table 2). Groups containing newborns were more predictable in size than calf or non-calf groups, and calf groups were slightly less predictable than non-calf groups (Table 2, Table 3, Table S3). Individual ID and year of observation had small effects on predictability and, while the date of observation had a much larger effect (Table 2). Consistent with the population trend, predictability within individuals generally increased with age (malleability: Figure 3, Table 2), though more individual differences in this pattern appeared in males, with some independently appearing to contradict this trend (Figure 3).

Correlations between mean and dispersion components

Within individuals, there was a positive relationship between mean group size and predictability, where individuals with a higher mean group size also exhibited higher group size predictability (Table 2, Figure 4). We analysed two temporal correlations, effects of the day of observation and effects caused by the year of observation. At the per-day level, average sociability and social predictability were negatively correlated; days with larger mean group sizes were also less predictable (Table 2). Between years, mean group size and social predictability did not have a relationship (Table 2.)

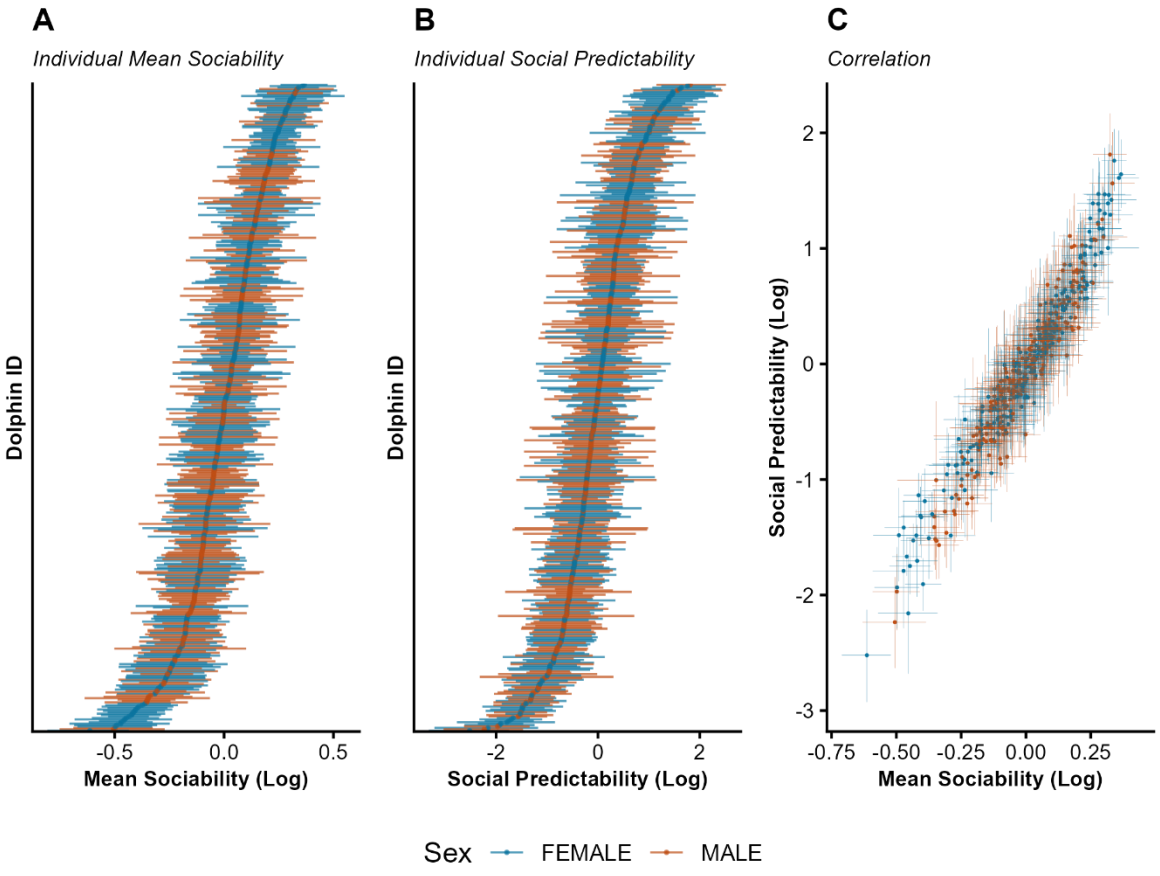


Figure 4: Individual posterior distributions for mean sociability (A), social predictability (B) and the correlation between sociability and social predictability (C) for each of the 457 individuals used in this study. Females are given in blue; males are given in orange. All values are reported on the log scale.

Discussion

This study provides unique insights into the sex-specific effects of aging on sociability in a long-lived mammal population. Specifically, we found strong patterns regarding sociability, its plasticity, social predictability, and its malleability. Throughout the population, group size increases and subsequently decreases in averages with age, though this later life decline is more pronounced in males. However, at the dispersion level, group size predictability increases with age, with this increase stronger in males. Males are more sociable and predictable in their grouping patterns than females, however, at the individual level, some males become less predictable with age, and some do not appear to be malleable. However, both increased group size and increased group size predictability appear correlated within individuals, and higher trait values in both group size and its predictability show links to longevity. We discuss these results in the context of social aging and life history.

Average sociability in the Shark Bay dolphins follows a quadratic curve: group sizes rise steadily for several decades, then subsequently fall in later life, with this decline's intensity depending on sex. Literature generally relates group formation to predation or conspecific harassment. Adult females and young calves are particularly vulnerable to tiger shark predation[81], but increased group sizes around newborns and calves suggest that mothers may mitigate this risk through increased group vigilance[70], a pattern found in other populations[127]. Risk of conspecific aggression is highest among juvenile males[43,50,51,68,81] and cycling females, but grouping patterns do not appear to change during this higher-risk juvenile period, a pattern also seen in previous study of this population[65]. We suggest that additional drivers serve to moderate grouping patterns, one of these being the changing value of social information. Conspecifics are a critically important source of knowledge as the use of socially transmitted information provides a suite of evolutionary advantages[28,29,66], and the size of conspecific groups may be defined by each individual's need for, and ability to process, social information[35]. As individuals mature,

253 their socio-cognitive competence increases, enabling the formation of preferential bonds and
254 ever-larger groups, which would maximise the social information gained from these
255 interactions. Age and accrued knowledge may also improve social position[7,32,96] which may be
256 attractive to other individuals, leading to the maintenance of larger group sizes into later years
257 for long-lived individuals.

258 Average group sizes decreased at various times throughout adulthood, with the timing of this
259 decline appearing proportional to total lifespan: individuals whose group sizes began to decline
260 earlier in life also disappeared earlier. We suggest this stems from several factors co-occurring,
261 namely: social selectivity, social and physical senescence, and loss of preferred conspecifics.
262 Forming conspecific groups comes with individual cost, such as increased disease risk[5],
263 visibility to predators, and intragroup competition (for a comparison table, see Makuya and
264 Schradin[74]). In early life, when individuals have limited knowledge of the world, seeking social
265 interaction can provide fitness benefits which may outweigh the costs of grouping[119]. Aging
266 individuals might place less value on social information since they have well-established home
267 ranges and foraging tactics[10]. Such experience-modulated social selectivity has been
268 documented in aging macaques[4,10], and similarly increasing preference for individual decision-
269 making with age is frequently reported in humans[31,105] particularly when dealing with everyday
270 problem solving[30,113].

271 Aging also comes with physical costs. Poor health and old age negatively affects physiological
272 condition in numerous ways that may influence sociability[103]. Declining body condition impacts
273 movement capacity[3,56] and foraging efficiency[73], reducing individual ability to engage socially. To
274 that end, individuals which disappear earlier than expected may be experiencing health
275 conditions which preclude social engagement, leading to visible declines in average group size
276 in the years preceding disappearance. Furthermore, aging also comes with a loss of
277 conspecifics. Animals may die from old age, sickness, starvation, predation, or any number of

causes. Those which live to advanced age may often be one of the few remaining from their cohort, particularly for males since their long-term alliance members are often close in age[23]. As the Shark Bay dolphins are known to form long-term, stable bonds, declining group sizes may stem from a loss of closely bonded, socially irreplaceable conspecifics[92]. These outcomes correspond to similar changes in social phenotypes seen in primates, deer, rodents, and other species with age[103]. These losses may then further exacerbate mortality risk for remaining individuals (e.g. widowhood effect)[92], a pattern also seen in humans[83].

Though average group size rises and falls throughout life, the trait variance underpinning these averages follows a different pattern: individuals generally become more predictable with age, with predictability positively correlated with longevity. Although not explicitly tested in this study, this patterns appears consistent with the development of social competence in individuals because social competence is characterised by the use of available social information to optimise behaviour based on context[115]. Young individuals form groups of varying sizes through social and individual learning, then upon accruing experience, reduce the variance in their behaviour in favour of what may be more optimal group sizes for the given individual. This suggests canalisation-like processes[62,110,129] are occurring within individuals throughout their lifetime similar to processes in developmental studies, for example, where achieving a specific outcome leads to more consistent behaviour producing that outcome (winner-loser effect[69]), e.g. less variation in behaviour (and outcome) over time. Malleability, which is the measure of changes in variation as they occur, may then be indicative of behavioural adaptation happening within an individual.

Social selectivity found in similar systems (humans and non-human primates[4,10,116]) may also contribute to increasing predictability with age, as these individuals form strong, irreplaceable bonds with certain conspecifics while young, then invest in those bonds throughout life[23,78]. This would lead to older dolphins becoming more selective and joining groups of consistent sizes

303 that meet specific criteria (e.g., close allies, kin, foraging on large fish shoals). However,
304 becoming too socially isolated (e.g. smaller groups) and too unpredictable in later years may
305 foretell disappearance. While context-dependent, social connectedness has frequently been
306 linked to increased survival[109] and longevity[37,101,107,119], and consistency of behaviour is also
307 thought to improve outcomes in social scenarios (social niche hypothesis,[58,134]). This is
308 supported by the correlations found in this study; sociability and predictability are strongly
309 correlated within individuals and increases in both appear to merit a fitness benefit; individuals
310 who continue to become more gregarious and predictable with age also live the longest, while
311 declining group sizes and failure to increase in predictability correspond to early disappearance
312 from the population. Taken together, maintaining more predictably larger group sizes may be a
313 sign of stronger or more stable social position leading to improved longevity[92].

314 Although lifelong patterns in average group size and its predictability are similar in both sexes,
315 variation between males and females is tightly linked to reproductive strategies. Females are
316 typically in smaller, less predictable groups, as females have a broader range of viable social
317 strategies, including predominantly solitary ones[78], they can select from based on kinship and
318 individual foraging profiles. Starting at age 13 (on average), females in this population produce
319 one calf at a time and nurse that calf for 2.5 to 8 years (average 4 years)[60]. Extensive lone
320 foraging to maintain energetic demand[76,79] reduces average group size[47] and leaves calves at
321 greater risk[81]. To compensate, mothers increase their sociability with other females[75] during
322 critical periods, a pattern also seen in primates[26]. Decreasing calving frequency due to
323 reproductive senescence[60], however, may lead to smaller groups in old age.

324 For male dolphins in Shark Bay, however, sociability forms the backbone of their reproductive
325 strategy. Extended maternal investment and large interbirth intervals (primates, hyenas,
326 elephants, cetaceans, humans[137]) make oestrus females a rare and valuable resource, requiring
327 males to form varied-term coalitions to guard these females and ultimately pass on

genes[22,120,122]. Male Shark Bay dolphins have evolved a complex multi-tier alliance system[23] comprised of long-term, stable social bonds allowing teams of male dolphins to mate-guard and consort with a reproductive female[23,24,89]. Increased sociability necessarily enhances alliance formation, the strength of these bonds which then improves reproductive success[45]. Because males spend the vast majority of their time with their alliance partners[106] in persistent, structured groups where numbers can influence acquisition, guarding, and mating access to females, they are ultimately in larger and more predictably sized groups. Some males, however, became less predictable with age. This might be related to changes in alliance partners due to social or demographic shifts (e.g., death of an alliance partner).

The strong positive correlation between increasing group size and increasing predictability of group size we observe provides support for the theory of sociality and social competence existing in a positive feedback loop[114]. Variation among individuals forms the basis for evolution such that directional selection may act; and correlations with increased sociability and predictability appear linked to increased longevity, a common measure of fitness. Previous work has also identified correlations between average and variance responses in behavioural traits[52,59,82,87] and extended such associations to improved fitness outcomes; increased gregariousness, and in females, more social predictability, was positively associated with survival[20]. As social integration can influence longevity and reproductive success[14,101], and predictability of social traits can influence mate choice for reproduction[97], the relationship becomes clear: variation itself can underpin ultimate fitness consequences in social systems. Future work should endeavour to identify explicit causal links between personality, predictability, and fitness outcomes to better understand the role of predictability in social evolution.

This study unifies personality, plasticity, predictability, and malleability to broaden our understanding of the relationship between aging and sociability in a long-lived mammal. We

353 support the growing body of work exploring sex-specific differences in personality and
354 predictability, provide empirical evidence that predictability is malleable due to aging, and
355 describe how mean and variance responses in a trait correlate to form personality-predictability
356 associations. We posit that variation is not solely random noise within a dataset, but a
357 biologically meaningful component of animal behaviour, and its malleability may have the
358 potential to provide information about behavioural adaptation. While we cannot explicitly state
359 a causal link between social competence and fitness outcomes, our findings suggest that
360 understanding group formation, particularly in the context of social aging, requires us to
361 incorporate both life history and social considerations, like the theory of social competence,
362 into our framework, and informs future research directions. This study highlights the importance
363 of within-individual variation and how it relates to our understanding of social aging.

364 **Methods**

365 *Data collection*

366 Data used in this study were collected as part of an extensive long-term wild population study
367 by the Shark Bay Dolphin Research Project (SBDRP) offshore of Monkey Mia in the eastern gulf
368 of Shark Bay, Australia (25˚ 47`S, 113˚ 43`E). Since 1984, >2000 resident animals have been
369 observed primarily between May and November each year, with detailed behaviour and location
370 data available from 1988. Behavioural data were collected via five-minute scan sampling during
371 boat-based surveys, with each sighting capturing group size and composition along with
372 location and environmental data[61]. Inclusion in a group was determined via a 10m chain rule
373 where membership required individuals to be within 10m of at least one group member[106]. To
374 mitigate spatial and temporal autocorrelation, we retained only a single sighting per individual
375 per day[118]. Sex determination was conducted via visual inspection of the ventrum, association
376 with a calf, or genetic analysis[64,106]. Birthdates were estimated based on sighting of the mother
377 before and after calf birth and physical characteristics (body size, speckling, foetal lines)[77].

Ethics statement

All research utilised in this study was conducted under Georgetown University Animal Care and Use Permits: IACUC-13-069, 07-041, 10-023, and 2016-1235; The University of Queensland Animal Ethics Approval: 2022/AE000612, and Department of Parks and Wildlife (Western Australia) Permits: SF-009876, SF-010347, SF-008076, SF009311, and SF007457.

Response variable

This study used number of associates as a proxy for sociability. This population exhibits a unique characteristic in that grouping decisions are made by identifiable individuals who are known to have distinct social preferences and avoidances which moderate social interactions[112]. Further, associate count is a metric common to all observations made in the population, providing us the extensive volumes of repeated measures essential for accurately estimating predictability and malleability[21]. Prior study of this population used 15 or more measures per individual to robustly measure mean social traits[38]; this threshold was more than doubled to a minimum of 40 repeat measurements per individual based on minimum variance requirements suggested by Hill and Mulder[54]. Individuals sighted less than 40 times were removed from analysis, leaving 457 individuals, 228 male and 229 female, that met our requirements (Table S1). All individuals in the dataset were sighted in at least two years, with an average of 17.3 years of sightings per individual (min 2, max 35) spanning ages between 0 years and 52 years old. To calculate the number of associates, the focal animal of a given observation was subtracted from recorded group size. If a precise group size was not collected, range estimates were used (n = 2,320 of 64,914 observations, <4% of the total dataset.)

Analysis

To best model the variance in residuals of the mean using the same fixed and random effects, we fit a location-scale double-hierarchical generalised linear model (DHGLM[21]) to decompose

behavioural variance[15,20,52,133] , using the brms package[11] in R (version 4.2.3)[91]. The mean (location) model directly estimates mean trait responses (repeatability and plasticity), while the dispersion (scale) model estimates the variation present around the mean effect (predictability and malleability).

Data best fit a negative binomial distribution with no prior transformation for normality. All parameters in the dispersion portion of the models were assigned inv_gamma (0.4,0.3) priors to approximate penalised complexity priors, which are the current best practice for modelling negative binomial distributions[102]. Default uninformative priors were assigned to the mean model. Convergence and fit were determined based on trace plots, posterior predictive checks, R-hat values < 1.01, and leave-one-out (LOO) cross-validation to estimate out-of-sample prediction accuracy of a given model fit using the loo package[123].

In the mean model we fit fixed effects for: i) sex, as dolphins have sex-specific social strategies[106], ii) a scaled (mean-centred and z-scored) quadratic effect of age to measure plasticity as animals age and accrue experience, iii) a scaled value representing the age of each individual at their last or oldest sighting, and iv) a three-level factor to account for reproductive state of the focal individual, newborn (0-2 months), calf (2 months to weaning) and not calf (post-weaning), to account for group sizes when affected by the presence of a newborn or calf. Random effects on mean trait response included: i) linear and quadratic age slopes by individual ID to calculate age slopes for each individual, ii) the year of observation to account for short-term, external environmental effects, and iii) the date of observation, to mitigate non-independence of social interaction data and to account for unique occurrences on a given day (such as large once-off foraging events). All fixed and random effects in the dispersion model were identical apart from replacing quadratic age terms with linear-scaled age terms, as this fit the data better during model construction. Description of all model terms is provided in Table S1.

Average Marginal Effects (AMEs)

A technical limitation of generalised linear mixed modelling types is the conditional interpretation of regression parameters[86], wherein the model must select a reference category to compare different levels of a discrete parameter. This can make population-level inferences challenging, as estimates are subject-specific[136]. To counteract this limitation, Hedeker et al. developed a numerical approach to obtain population-level estimates, known as Average Marginal Effects (AMEs), from mixed models[49]. We utilised the brmsmargins package[132] to calculate these AMEs and their credible intervals for each population-level parameter. In both mean and dispersion models, when credible intervals of different levels of a fixed effect AME did not cross each other, effects of the level were considered statistically different from one another.

Understanding variance components and effect direction

Interpreting the directional effects on predictability from a model is contingent on the model's distributional family. These models are negative binomial models, which have mean and variance parameters calculated by the following equations:

a)
$$y_{ij} \sim \mathrm{NB}(\lambda_{ij}, \theta),$$

b)
$$E[y] = \lambda$$

c)
$$\mathrm{var}[y] = \lambda + \frac{\lambda^2}{\theta}$$

In this equation, λ is the mean and θ is a shape parameter (also known as the dispersion parameter, and, in some cases, size parameter)[85] measuring overdispersion. The brms modelling package reports the shape parameter θ directly, so larger dispersion values (decreased variation[53]) correspond to higher predictability in this model.

Acknowledgments

We acknowledge the Malgana peoples, the traditional custodians of the lands and waters of Guthaaguda, of Elders past and present, on which this work was conducted. We thank all members of the Shark Bay Dolphin Research Project (SBDRP) for their efforts in data collection used for this project. This research is supported by an Australian Government Research Training Program (RTP) Scholarship and the Holsworth Wildlife Research Endowment, as well as grants to JM [NSF-REU: 0847922, 1755229, 0941487, 0918308, 2106909, 2139712, 0316800, 2146995,1559380, 2128134, 1515197, 0521763, 0820722, 1927619, 9753044; ONR 10230702] and MM [NSF-GRFP], Georgetown University, and special thanks to Monkey Mia Resort, the Royal Automobile Club of Australia, and the local community of Shark Bay.

References

1. Abe, T., Fujiyama, N., Tomimatsu, H., & Nagayama, T. (2018). Age-dependent and social status-dependent behavioural plasticity of the cricket Gryllus bimaculatus. *Animal Behaviour*, *141*, 1-7. https://doi.org/https://doi.org/10.1016/j.anbehav.2018.05.003
2. Acácio, M., Gahm, K., Anglister, N., Vaadia, G., Hatzofe, O., Harel, R., Efrat, R., Nathan, R., Pinter-Wollman, N., & Spiegel, O. (2024). Behavioral plasticity shapes population aging patterns in a long-lived avian scavenger. *Proceedings of the National Academy of Sciences*, *121*(35), e2407298121. https://doi.org/doi:10.1073/pnas.2407298121
3. Albery, G. F., Clutton-Brock, T. H., Morris, A., Morris, S., Pemberton, J. M., Nussey, D. H., & Firth, J. A. (2022). Ageing red deer alter their spatial behaviour and become less social. *Nat Ecol Evol*, *6*(8), 1231-1238. https://doi.org/10.1038/s41559-022-01817-9
4. Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, Alexandra M., & Fischer, J. (2016). Motivational Shifts in Aging Monkeys and the Origins of Social Selectivity. *Current Biology*, *26*(13), 1744-1749. https://doi.org/10.1016/j.cub.2016.04.066
5. Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M., & Pulliam, J. R. C. (2003). Social Organization and Parasite Risk in Mammals: Integrating Theory and Empirical Studies. *Annual Review of Ecology, Evolution, and Systematics*, *34*(Volume 34, 2003), 517-547. https://doi.org/https://doi.org/10.1146/annurev.ecolsys.34.030102.151725
6. Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim Behav*, *77*(4), 771-783. https://doi.org/10.1016/j.anbehav.2008.12.022
7. Berdoy, M., Smith, P., & Macdonald, D. W. (1995). Stability of Social Status in Wild Rats: Age and the Role of Settled Dominance. *Behaviour*, *132*(3-4), 193-212. https://doi.org/https://doi.org/10.1163/156853995X00694
8. Boake, C. R. B. (1989). Repeatability: Its role in evolutionary studies of mating behavior. *Evolutionary Ecology*, *3*(2), 173-182. https://doi.org/10.1007/BF02270919
9. Bonamour, S., Chevin, L.-M., Réale, D., Teplitsky, C., & Charmantier, A. (2020). Age-dependent phenological plasticity in a wild bird. *Journal of Animal Ecology*, *89*(11), 2733-2741. https://doi.org/https://doi.org/10.1111/1365-2656.13337

10. Brent, L. J. N., Ruiz-Lambides, A., & Platt, M. L. (2017). Family network size and survival across the lifespan of female macaques. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1854), 20170515. https://doi.org/doi:10.1098/rspb.2017.0515
11. Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*(1), 1 - 28. https://doi.org/10.18637/jss.v080.i01
12. Byrne, R. W. (1996). Machiavellian intelligence. *Evolutionary Anthropology: Issues, News, and Reviews*, *5*(5), 172-180. https://doi.org/https://doi.org/10.1002/(SICI)1520-6505(1996)5:5<172::AID-EVAN6>3.0.CO;2-H
13. Cain, S., Solomon, T., Leshem, Y., Toledo, S., Arnon, E., Roulin, A., & Spiegel, O. (2023). Movement predictability of individual barn owls facilitates estimation of home range size and survival. *Movement Ecology*, *11*(1), 10. https://doi.org/10.1186/s40462-022-00366-x
14. Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, *106*(33), 13850-13853. https://doi.org/doi:10.1073/pnas.0900639106
15. Carslake, C., Occhiuto, F., Vázquez-Diosdado, J. A., & Kaler, J. (2022). Repeatability and Predictability of Calf Feeding Behaviors—Quantifying Between- and Within-Individual Variation for Precision Livestock Farming [Original Research]. *Frontiers in Veterinary Science*, *9*. https://doi.org/10.3389/fvets.2022.827124
16. Carstensen, L. L. (1992). Social and emotional patterns in adulthood: Support for socioemotional selectivity theory. *Psychology and Aging*, *7*(3), 331-338. https://doi.org/10.1037/0882-7974.7.3.331
17. Carter, K. D., Brand, R., Carter, J. K., Shorrocks, B., & Goldizen, A. W. (2013). Social networks, long-term associations and age-related sociability of wild giraffes. *Animal Behaviour*, *86*(5), 901-910. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.08.002
18. Castles, M. P., Brand, R., Carter, A. J., Maron, M., Carter, K. D., & Goldizen, A. W. (2019). Relationships between male giraffes' colour, age and sociability. *Animal Behaviour*, *157*, 13-25. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.08.003
19. Charles, S. T., & Carstensen, L. L. (2010). Social and Emotional Aging. *Annual Review of Psychology*, *61*(Volume 61, 2010), 383-409. https://doi.org/https://doi.org/10.1146/annurev.psych.093008.100448
20. Class, B., Strickland, K., Potvin, D., Jackson, N., Nakagawa, S., & Frère, C. (2024). Sex-Specific Associations between Social Behavior, Its Predictability, and Fitness in a Wild Lizard. *The American Naturalist*, *204*(5), 501-516. https://doi.org/10.1086/732178
21. Cleasby, I. R., Nakagawa, S., & Schielzeth, H. (2015). Quantifying the predictability of behaviour: statistical approaches for the study of between-individual variation in the within-individual variance. *Methods in Ecology and Evolution*, *6*(1), 27-37. https://doi.org/https://doi.org/10.1111/2041-210X.12281
22. Connor, R., & Whitehead, H. (2005). Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fusion societies. *Animal Behaviour*, *69*(1), 127-132. https://doi.org/https://doi.org/10.1016/j.anbehav.2004.02.022
23. Connor, R. C., & Krützen, M. (2015). Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Animal Behaviour*, *103*, 223-235. https://doi.org/https://doi.org/10.1016/j.anbehav.2015.02.019
24. Connor, R. C., Krützen, M., Allen, S. J., Sherwin, W. B., & King, S. L. (2022). Strategic intergroup alliances increase access to a contested resource in male bottlenose dolphins. *Proceedings of the National Academy of Sciences*, *119*(36), e2121723119. https://doi.org/doi:10.1073/pnas.2121723119
25. Corr, J. (2003). Social behavior in aged rhesus macaques. *Collegium antropologicum*, *27*(1), 87-94.

26. Creighton, M. J. A., Lerch, B. A., Lange, E. C., Silk, J. B., Tung, J., Archie, E. A., & Alberts, S. C. (2024). Re-evaluating the relationship between female social bonds and infant survival in wild baboons. *bioRxiv*, 2024.2008.2020.608854. https://doi.org/10.1101/2024.08.20.608854
27. Crouchet, T., Cauchoix, M., Heeb, P., & Chaine, A. S. (2026). Plasticity in social foraging is a matter of age in great tits. *Animal Behaviour*, *236*, 123565. https://doi.org/https://doi.org/10.1016/j.anbehav.2026.123565
28. Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*(4), 187-193. https://doi.org/10.1016/j.tree.2005.01.010
29. Danchin, É., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public Information: From Nosy Neighbors to Cultural Evolution. *Science*, *305*(5683), 487-491. https://doi.org/doi:10.1126/science.1098254
30. Delaney, R., Strough, J., Parker, A. M., & Bruine de Bruin, W. (2015). Variations in decision-making profiles by age and gender: A cluster-analytic approach. *Personality and Individual Differences*, *85*, 19-24. https://doi.org/https://doi.org/10.1016/j.paid.2015.04.034
31. Delaney, R. K., Turiano, N. A., & Strough, J. (2018). Living longer with help from others: Seeking advice lowers mortality risk. *Journal of Health Psychology*, *23*(12), 1590-1597. https://doi.org/10.1177/1359105316664133
32. Deniz, M., de Sousa, K. T., do Vale, M. M., & Dittrich, J. R. (2021). Age and body mass are more important than horns to determine the social position of dairy cows. *Journal of Ethology*, *39*(1), 19-27. https://doi.org/10.1007/s10164-020-00667-x
33. Dingemanse, N. J., Dochtermann, N. A., & Nakagawa, S. (2012). Defining behavioural syndromes and the role of 'syndrome deviation' in understanding their evolution. *Behavioral Ecology and Sociobiology*, *66*(11), 1543-1548. https://doi.org/10.1007/s00265-012-1416-2
34. Dingemanse, N. J., Kazem, A. J., Reale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol Evol*, *25*(2), 81-89. https://doi.org/10.1016/j.tree.2009.07.013
35. Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, *22*(6), 469-493. https://doi.org/https://doi.org/10.1016/0047-2484(92)90081-J
36. Dunbar, R. I. M. (2009). The social brain hypothesis and its implications for social evolution. *Annals of Human Biology*, *36*(5), 562-572. https://doi.org/10.1080/03014460902960289
37. Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M. L., & Brent, L. J. N. (2019). Deconstructing sociality: the types of social connections that predict longevity in a group-living primate. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1917). https://doi.org/10.1098/rspb.2019.1991
38. Evans, T., Krzyszczyk, E., Frère, C., & Mann, J. (2021). Lifetime stability of social traits in bottlenose dolphins. *Communications Biology*, *4*(1), 759. https://doi.org/10.1038/s42003-021-02292-x
39. Foroughirad, V., Frère, C. H., Levengood, A. L., Kopps, A. M., Krzyszczyk, E., & Mann, J. (2023). Small effects of family size on sociality despite strong kin preferences in female bottlenose dolphins. *Animal Behaviour*, *195*, 53-66. https://doi.org/10.1016/j.anbehav.2022.10.011
40. Frank, S. A. (1997). The design of adaptive systems: optimal parameters for variation and selection in learning and development. *Journal of Theoretical Biology*, *184*(1), 31-39.
41. Frere, C. H., Krutzen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc Natl Acad Sci U S A*, *107*(46), 19949-19954. https://doi.org/10.1073/pnas.1007997107

42. Frère, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., Connor, R., Bejder, L., & Sherwin, W. B. (2010). Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Animal Behaviour*, *80*(3), 481-486. https://doi.org/10.1016/j.anbehav.2010.06.007
43. Galezo, A. A., Foroughirad, V., Krzyszczyk, E., Frère, C. H., & Mann, J. (2020). Juvenile social dynamics reflect adult reproductive strategies in bottlenose dolphins. *Behavioral Ecology*, *31*(5), 1159-1171. https://doi.org/10.1093/beheco/araa068
44. Galezo, A. A., Krzyszczyk, E., & Mann, J. (2017). Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behavioral Ecology*, *29*(2), 377-386. https://doi.org/10.1093/beheco/arx177
45. Gerber, L., Connor, R. C., Allen, S. J., Horlacher, K., King, S. L., Sherwin, W. B., Willems, E. P., Wittwer, S., & Krützen, M. (2022). Social integration influences fitness in allied male dolphins. *Current Biology*, *32*(7), 1664-1669.e1663. https://doi.org/https://doi.org/10.1016/j.cub.2022.03.027
46. Gerber, L., Connor, R. C., King, S. L., Allen, S. J., Wittwer, S., Bizzozzero, M. R., Friedman, W. R., Kalberer, S., Sherwin, W. B., Wild, S., Willems, E. P., & Krützen, M. (2019). Affiliation history and age similarity predict alliance formation in adult male bottlenose dolphins. *Behavioral Ecology*, *31*(2), 361-370. https://doi.org/10.1093/beheco/arz195
47. Gibson, Q. A., & Mann, J. (2008). The size, composition and function of wild bottlenose dolphin (Tursiops sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour*, *76*(2), 389-405. https://doi.org/https://doi.org/10.1016/j.anbehav.2008.01.022
48. Han, C. S., & Dingemanse, N. J. (2023). Age-related reductions in within-individual variation increase the repeatability of mating behaviour. *Behavioral Ecology and Sociobiology*, *77*(8), 94. https://doi.org/10.1007/s00265-023-03368-w
49. Hedeker, D., du Toit, S. H. C., Demirtas, H., & Gibbons, R. D. (2017). A Note on Marginalization of Regression Parameters from Mixed Models of Binary Outcomes. *Biometrics*, *74*(1), 354-361. https://doi.org/10.1111/biom.12707
50. Heithaus, M. R. (2001). SHARK ATTACKS ON BOTTLENOSE DOLPHINS (TURSIOPS ADUNCUS) IN SHARK BAY, WESTERN AUSTRALIA: ATTACK RATE, BITE SCAR FREQUENCIES, AND ATTACK SEASONALITY. *Marine Mammal Science*, *17*(3), 526-539. https://doi.org/https://doi.org/10.1111/j.1748-7692.2001.tb01002.x
51. Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, *83*(2), 480-491. https://doi.org/10.1890/0012-9658(2002)083[0480:Faatsp]2.0.Co;2
52. Hertel, A. G., Royauté, R., Zedrosser, A., & Mueller, T. (2021). Biologging reveals individual variation in behavioural predictability in the wild. *Journal of Animal Ecology*, *90*(3), 723-737. https://doi.org/10.1111/1365-2656.13406
53. Hilbe, J. M. (2011). *Negative Binomial Regression*. Cambridge University Press. https://books.google.com.au/books?id=0Q_ijxOEBjMC
54. Hill, W. G., & Mulder, H. A. (2010). Genetic analysis of environmental variation. *Genetics Research*, *92*(5-6), 381-395. https://doi.org/10.1017/S0016672310000546
55. House, J. S., Landis, K. R., & Umberson, D. (1988). Social Relationships and Health. *Science*, *241*(4865), 540-545. https://doi.org/doi:10.1126/science.3399889
56. INGRAM, D. K. (2000). Age-related decline in physical activity: generalization to nonhumans. *Medicine & Science in Sports & Exercise*, *32*(9), 1623-1629. https://journals.lww.com/acsm-msse/fulltext/2000/09000/age_related_decline_in_physical_activity_.16.aspx
57. Jackson, R. R., & Wilcox, R. S. (1993). Spider flexibly chooses aggressive mimicry signals for different prey by trial and error. *Behaviour*, 21-36.
58. Johnstone, R. A. (2001). Eavesdropping and animal conflict. *Proc Natl Acad Sci U S A*, *98*(16), 9177-9180. https://doi.org/10.1073/pnas.161058798

59. Jolles, J. W., Briggs, H. D., Araya-Ajoy, Y. G., & Boogert, N. J. (2019). Personality, plasticity and predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish. *Animal Behaviour*, *154*, 193-202. https://doi.org/10.1016/j.anbehav.2019.06.022
60. Karniski, C., Krzyszczyk, E., & Mann, J. (2018). Senescence impacts reproduction and maternal investment in bottlenose dolphins. *Proc Biol Sci*, *285*(1883), 20181123. https://doi.org/10.1098/rspb.2018.1123
61. Karniski, C., Patterson, E. M., Krzyszczyk, E., Foroughirad, V., Stanton, M. A., & Mann, J. (2015). A comparison of survey and focal follow methods for estimating individual activity budgets of cetaceans. *Marine Mammal Science*, *31*(3), 839-852. https://doi.org/10.1111/mms.12198
62. Kok, E. M. A., Burant, J. B., Dekinga, A., Manche, P., Saintonge, D., Piersma, T., & Mathot, K. J. (2019). Within-Individual Canalization Contributes to Age-Related Increases in Trait Repeatability: A Longitudinal Experiment in Red Knots. *The American Naturalist*, *194*(4), 455-469. https://doi.org/10.1086/704593
63. Kroeger, S. B., Blumstein, D. T., & Martin, J. G. A. (2021). How social behaviour and life-history traits change with age and in the year prior to death in female yellow-bellied marmots. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1823), 20190745. https://doi.org/doi:10.1098/rstb.2019.0745
64. Krützen, M., Barré, L. M., Möller, L. M., Heithaus, M. R., Simms, C., & Sherwin, W. B. (2006). A Biopsy System for Small Cetaceans: Darting Success and Wound Healing in Tursiops Spp. *Marine Mammal Science*, *18*(4), 863-878. https://doi.org/10.1111/j.1748-7692.2002.tb01078.x
65. Krzyszczyk, E., Patterson, E. M., Stanton, M. A., & Mann, J. (2017). The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins. *Animal Behaviour*, *129*, 43-59. https://doi.org/https://doi.org/10.1016/j.anbehav.2017.04.011
66. Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, *32*(1), 4-14. https://doi.org/10.3758/BF03196002
67. Lavista Ferres, J. M., Lee, D. E., Nasir, M., Chen, Y.-C., Bijral, A. S., Bercovitch, F. B., & Bond, M. L. (2021). Social connectedness and movements among communities of giraffes vary by sex and age class. *Animal Behaviour*, *180*, 315-328. https://doi.org/https://doi.org/10.1016/j.anbehav.2021.08.008
68. Lee, H. H., Wallen, M. M., Krzyszczyk, E., & Mann, J. (2019). Every scar has a story: age and sex-specific conflict rates in wild bottlenose dolphins. *Behavioral Ecology and Sociobiology*, *73*(5), 63. https://doi.org/10.1007/s00265-019-2674-z
69. Lehner, S. R., Rutte, C., & Taborsky, M. (2011). Rats Benefit from Winner and Loser Effects. *Ethology*, *117*(11), 949-960. https://doi.org/10.1111/j.1439-0310.2011.01962.x
70. Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*(1), 11-20. https://doi.org/https://doi.org/10.1016/0003-3472(95)80149-9
71. Lukas, D., & Clutton-Brock, T. (2018). Social complexity and kinship in animal societies. *Ecology Letters*, *21*(8), 1129-1134. https://doi.org/https://doi.org/10.1111/ele.13079
72. Machanda, Z. P., & Rosati, A. G. (2020). Shifting sociality during primate ageing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1811), 20190620. https://doi.org/doi:10.1098/rstb.2019.0620
73. MacNulty, D. R., Smith, D. W., Vucetich, J. A., Mech, L. D., Stahler, D. R., & Packer, C. (2009). Predatory senescence in ageing wolves. *Ecology Letters*, *12*(12), 1347-1356. https://doi.org/https://doi.org/10.1111/j.1461-0248.2009.01385.x
74. Makuya, L., & Schradin, C. (2024). Costs and benefits of solitary living in mammals. *Journal of Zoology*, *323*(1), 9-18. https://doi.org/https://doi.org/10.1111/jzo.13145

75. Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (Tursiops sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, *11*(2), 210-219. https://doi.org/10.1093/beheco/11.2.210
76. Mann, J., & Sargeant, B. L. (2003). Like mother, like calf: the ontogeny of foraging traditions in wild Indian ocean bottlenose dolphins (*Tursiops* sp.). In D. Fragaszy & S. Perry (Eds.), *The Biology of Traditions: Models and Evidence* (pp. 236-266). Cambridge Univeristy Press. http://www.monkeymiadolphins.org/wp-content/uploads/2019/10/Mann-2003-Like-mother-like-calf-the.pdf
77. Mann, J., & Smuts, B. (1999). Behavioral Development in Wild Bottlenose Dolphin Newborns (Tursiops sp.). *Behaviour*, *136*(5), 529-566. http://www.jstor.org/stable/4535627
78. Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & Singh, L. O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nature Communications*, *3*(1), 980. https://doi.org/10.1038/ncomms1983
79. Mann, J., & Watson-Capps, J. J. (2005). Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Tursiops* sp. *Animal Behaviour*, *69*(4), 899-909. https://doi.org/10.1016/j.anbehav.2004.04.024
80. Marfurt, S. M., Allen, S. J., Bizzozzero, M. R., Willems, E. P., King, S. L., Connor, R. C., Kopps, A. M., Wild, S., Gerber, L., Wittwer, S., & Krützen, M. (2022). Association patterns and community structure among female bottlenose dolphins: environmental, genetic and cultural factors. *Mammalian Biology*, *102*(4), 1373-1387. https://doi.org/10.1007/s42991-022-00259-x
81. McEntee, M. H. F., Foroughirad, V., Krzyszczyk, E., & Mann, J. (2023). Sex bias in mortality risk changes over the lifespan of bottlenose dolphins. *Proc Biol Sci*, *290*(2003), 20230675. https://doi.org/10.1098/rspb.2023.0675
82. Mitchell, D. J., Fanson, B. G., Beckmann, C., & Biro, P. A. (2016). Towards powerful experimental and statistical approaches to study intraindividual variability in labile traits. *Royal Society Open Science*, *3*(10), 160352. https://doi.org/10.1098/rsos.160352
83. Moon, J. R., Kondo, N., Glymour, M. M., & Subramanian, S. V. (2011). Widowhood and Mortality: A Meta-Analysis. *PLoS One*, *6*(8), e23465. https://doi.org/10.1371/journal.pone.0023465
84. Moquin, P., Curry, B., Pelletier, F., & Ruckstuhl, K. E. (2010). Plasticity in the rumination behaviour of bighorn sheep: contrasting strategies between the sexes? *Animal Behaviour*, *79*(5), 1047-1053. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.01.020
85. Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface*, *14*(134), 20170213. https://doi.org/doi:10.1098/rsif.2017.0213
86. Neuhaus, J. M., Kalbfleisch, J. D., & Hauck, W. W. (1991). A Comparison of Cluster-Specific and Population-Averaged Approaches for Analyzing Correlated Binary Data. *International Statistical Review / Revue Internationale de Statistique*, *59*(1), 25-35. https://doi.org/10.2307/1403572
87. O'Dea, R. E., Noble, D. W. A., & Nakagawa, S. (2022). Unifying individual differences in personality, predictability and plasticity: A practical guide. *Methods in Ecology and Evolution*, *13*(2), 278-293. https://doi.org/10.1111/2041-210x.13755
88. Oliveira, R. F. (2009). Social behavior in context: Hormonal modulation of behavioral plasticity and social competence. *Integrative and Comparative Biology*, *49*(4), 423-440. https://doi.org/10.1093/icb/icp055
89. Orbach, D. N. (2019). Sexual Strategies: Male and Female Mating Tactics. In B. Würsig (Ed.), *Ethology and Behavioral Ecology of Odontocetes* (pp. 75-93). Springer International Publishing. https://doi.org/10.1007/978-3-030-16663-2_4

90. Patterson, E. M., Krzyszczyk, E., & Mann, J. (2016). Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins. *Behavioral Ecology*, *27*(2), 401-410. https://doi.org/10.1093/beheco/arv164
91. R Core Team. (2023). *R: A Language and Environment for Statistical Computing*. In https://www.R-project.org/
92. Rankin, R. W., Foroughirad, V. J., Krzyszczyk, E. B., Frère, C. H., & Mann, J. (2022). Changes in social position predict survival in bottlenose dolphins. *bioRxiv*, 2022.2008.2025.505273. https://doi.org/10.1101/2022.08.25.505273
93. Rosati, A. G., Hagberg, L., Enigk, D. K., Otali, E., Emery Thompson, M., Muller, M. N., Wrangham, R. W., & Machanda, Z. P. (2020). Social selectivity in aging wild chimpanzees. *Science*, *370*(6515), 473-476. https://doi.org/doi:10.1126/science.aaz9129
94. Rudd, L. F., Packer, C., Biro, D., Firth, J. A., & Albery, G. F. (2024). Sex-specific social aging in wild African lions. *Current Biology*, *34*(17), 4039-4046.e4032. https://doi.org/10.1016/j.cub.2024.07.040
95. Rutte, C., Taborsky, M., & Brinkhof, M. W. (2006). What sets the odds of winning and losing? *Trends Ecol Evol*, *21*(1), 16-21. https://doi.org/10.1016/j.tree.2005.10.014
96. Šárová, R., Špinka, M., Stěhulová, I., Ceacero, F., Šimečková, M., & Kotrba, R. (2013). Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle. *Animal Behaviour*, *86*(6), 1315-1323. https://doi.org/https://doi.org/10.1016/j.anbehav.2013.10.002
97. Scherer, U., Kuhnhardt, M., & Schuett, W. (2018). Predictability is attractive: Female preference for behaviourally consistent males but no preference for the level of male aggression in a bi-parental cichlid. *PLoS One*, *13*(4), e0195766. https://doi.org/10.1371/journal.pone.0195766
98. Schroeder, J., Dunning, J., Chan, A. H. H., Chik, H. Y. J., & Burke, T. (2024). Not so social in old age: demography as one driver of decreasing sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*(1916), 20220458. https://doi.org/doi:10.1098/rstb.2022.0458
99. Schuster, A. C., Carl, T., & Foerster, K. (2017). Repeatability and consistency of individual behaviour in juvenile and adult Eurasian harvest mice. *The Science of Nature*, *104*(3), 10. https://doi.org/10.1007/s00114-017-1430-3
100. Sih, A., Bell, Alison M., Johnson, J C., & Ziemba, Robert E. (2004). Behavioral Syndromes: An Integrative Overview. *The Quarterly Review of Biology*, *79*(3), 241-277. https://doi.org/10.1086/422893
101. Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Current Biology*, *20*(15), 1359-1361. https://doi.org/10.1016/j.cub.2010.05.067
102. Simpson, D., Rue, H., Riebler, A., Martins, T. G., & Sørbye, S. H. (2017). Penalising Model Component Complexity: A Principled, Practical Approach to Constructing Priors. *Statistical Science*, *32*(1), 1-28, 28. https://doi.org/10.1214/16-STS576
103. Siracusa, E. R., Higham, J. P., Snyder-Mackler, N., & Brent, L. J. N. (2022). Social ageing: exploring the drivers of late-life changes in social behaviour in mammals. *Biology Letters*, *18*(3), 20210643. https://doi.org/doi:10.1098/rsbl.2021.0643
104. Siracusa, E. R., Negron-Del Valle, J. E., Phillips, D., Platt, M. L., Higham, J. P., Snyder-Mackler, N., & 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*(49), e2209180119. https://doi.org/doi:10.1073/pnas.2209180119

105. Smith, K., Strough, J., Parker, A. M., & Bruine de Bruin, W. (2023). Age differences in social decision-making preferences and perceived ability. *Psychol Aging*, *38*(3), 167-173. https://doi.org/10.1037/pag0000736
106. Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex Differences in Patterns of Association Among Indian Ocean Bottlenose Dolphins. *Behaviour*, *123*(1-2), 38-69. https://doi.org/10.1163/156853992x00101
107. Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., Harris, K. M., Shively, C. A., Alberts, S. C., & Tung, J. (2020). Social determinants of health and survival in humans and other animals. *Science*, *368*(6493), eaax9553. https://doi.org/doi:10.1126/science.aax9553
108. Stamps, J. A., Briffa, M., & Biro, P. A. (2012). Unpredictable animals: individual differences in intraindividual variability (IIV). *Animal Behaviour*, *83*(6), 1325-1334. https://doi.org/10.1016/j.anbehav.2012.02.017
109. Stanton, M. A., & Mann, J. (2012). Early Social Networks Predict Survival in Wild Bottlenose Dolphins. *PLoS One*, *7*(10), e47508. https://doi.org/10.1371/journal.pone.0047508
110. Stearns, S. C., & Kawecki, T. J. (1994). Fitness Sensitivity and the Canalization of Life-History Traits. *Evolution*, *48*(5), 1438-1450. https://doi.org/10.1111/j.1558-5646.1994.tb02186.x
111. Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291-309. https://doi.org/10.1007/s002650050390
112. Strickland, K., Levengood, A., Foroughirad, V., Mann, J., Krzyszczyk, E., & Frere, C. H. (2017). A framework for the identification of long-term social avoidance in longitudinal datasets. *R Soc Open Sci*, *4*(8), 170641. https://doi.org/10.1098/rsos.170641
113. Strough, J., Cheng, S., & Swenson, L. M. (2002). Preferences for collaborative and individual everyday problem solving in later adulthood. *International Journal of Behavioral Development*, *26*(1), 26-35. https://doi.org/10.1080/01650250143000337
114. Taborsky, B. (2021). A positive feedback loop between sociality and social competence [Review]. *Ethology*, *127*(10), 774-789. https://doi.org/10.1111/eth.13201
115. Taborsky, B., & Oliveira, R. F. (2012). Social competence: an evolutionary approach. *Trends Ecol Evol*, *27*(12), 679-688. https://doi.org/10.1016/j.tree.2012.09.003
116. Thompson González, N., Machanda, Z., & Emery Thompson, M. (2023). Age-related social selectivity: An adaptive lens on a later life social phenotype. *Neuroscience & Biobehavioral Reviews*, *152*, 105294. https://doi.org/https://doi.org/10.1016/j.neubiorev.2023.105294
117. Thys, B., Pinxten, R., & Eens, M. (2021). Long-term repeatability and age-related plasticity of female behaviour in a free-living passerine. *Animal Behaviour*, *172*, 45-54. https://doi.org/https://doi.org/10.1016/j.anbehav.2020.11.021
118. Tsai, Y. J. J., & Mann, J. (2013). Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science*, *29*(2), 261-279. https://doi.org/10.1111/j.1748-7692.2011.00559.x
119. Turner, J. W., Robitaille, A. L., Bills, P. S., & Holekamp, K. E. (2021). Early-life relationships matter: Social position during early life predicts fitness among female spotted hyenas. *Journal of Animal Ecology*, *90*(1), 183-196. https://doi.org/https://doi.org/10.1111/1365-2656.13282
120. Van Schaik, C. P. (1996). Social evolution in primates: the role of ecological factors and male behaviour. Proceedings-British Academy,
121. van Schaik, C. P., & Burkart, J. M. (2011). Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1008-1016. https://doi.org/doi:10.1098/rstb.2010.0304

122. Van Schaik, C. P., & Hooff, J. A. R. A. M. V. (1983). On the Ultimate Causes of Primate Social Systems. *Behaviour*, *85*(1/2), 91-117. http://www.jstor.org/stable/4534256
123. Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, *27*(5), 1413-1432. https://doi.org/10.1007/s11222-016-9696-4
124. Walmsley, S. F., Feyrer, L. J., Girard, C., Zwamborn, E., & Whitehead, H. (2024). *Social ageing varies within a population of bottlenose whales PREPRINT*. https://doi.org/10.32942/X2MW52
125. Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: fitness consequences of social partner choice in female house mice. *Animal Behaviour*, *75*(3), 801-808. https://doi.org/https://doi.org/10.1016/j.anbehav.2007.06.017
126. 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., Nielsen, M. L. K., Grimes, C., & Croft, D. P. (2021). Age and sex influence social interactions, but not associations, within a killer whale pod. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1953), 20210617. https://doi.org/doi:10.1098/rspb.2021.0617
127. Wells, R. S. (2014). Social Structure and Life History of Bottlenose Dolphins Near Sarasota Bay, Florida: Insights from Four Decades and Five Generations. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies* (pp. 149-172). Springer Japan. https://doi.org/10.1007/978-4-431-54523-1_8
128. West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution*. Oxford University Press. https://books.google.com.au/books?id=7DQNTPYaHlYC
129. Westneat, D. F., Wright, J., & Dingemanse, N. J. (2015). The biology hidden inside residual within-individual phenotypic variation. *Biol Rev Camb Philos Soc*, *90*(3), 729-743. https://doi.org/10.1111/brv.12131
130. Wey, T. W., & Blumstein, D. T. (2010). Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, *79*(6), 1343-1352. https://doi.org/https://doi.org/10.1016/j.anbehav.2010.03.008
131. Whiten, A., & van Schaik, C. P. (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 603-620. https://doi.org/doi:10.1098/rstb.2006.1998
132. Wiley, J. F., & Hedeker, D. (2022). *brmsmargins: Bayesian Marginal Effects for 'brms' Models*. In https://joshuawiley.com/brmsmargins/
133. Winter, G., Wirsching, L., & Schielzeth, H. (2023). Condition dependence of (un)predictability in escape behavior of a grasshopper species. *Behavioral Ecology*, *34*(5), 741-750. https://doi.org/10.1093/beheco/arad047
134. Wolf, M., Van Doorn, G. S., & Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proc Biol Sci*, *278*(1704), 440-448. https://doi.org/10.1098/rspb.2010.1051
135. Wrzus, C., Hänel, M., Wagner, J., & Neyer, F. J. (2013). Social network changes and life events across the life span: a meta-analysis. *Psychol Bull*, *139*(1), 53-80. https://doi.org/10.1037/a0028601
136. Zeger, S. L., Liang, K.-Y., & Albert, P. S. (1988). Models for Longitudinal Data: A Generalized Estimating Equation Approach. *Biometrics*, *44*(4), 1049-1060. https://doi.org/10.2307/2531734
137. Zipple, M. N., Reeve, H. K., & Peniston, O. J. (2024). Maternal care leads to the evolution of long, slow lives. *Proc Natl Acad Sci U S A*, *121*(25), e2403491121. https://doi.org/10.1073/pnas.2403491121

Table S1: Description and language of all components of the model used in this analysis. Where multiple parts of a model are described in a single part of the model formula, the specific part of the model formula is bolded.

Model portion	Effect	Fixed or Random	Intercept or Slope	Model formula component	Levels
Response	Associates			Associates	Integer: 0 to 49
Mean (Location)	Sex	Fixed	Intercept	Sex	"MALE", "FEMALE"
	Age	Fixed	Slope	Poly(z.Age,2)	Scaled measure of age [-1.63 to 3.29] derived from age in days [0 to 19253]
	Age at last sighting (selective disappearance)	Fixed	Slope	z.ALS	Scaled measure of age at last sighting [-2.59 to 2.19] derived from last sighting age in days [715 to 19253]
	Reproductive state	Fixed	Intercept	Repro.Stat	"Newborn" – Under 2 months age "Calf" – 2 months to weaning "Not Calf" – All ages post-weaning
	Individual	Random	Intercept	(poly(z.Age,2)|a|**Individual**)	3-letter ID codes for each animal
	Age within individual	Random	Slope	**(poly(z.Age,2)**|a|Individual)	Scaled measure of age [-1.63 to 3.29] per individual
	Year	Random	Intercept	(1|b|Year)	1988 to 2025
	Observation Date	Random	Intercept	(1|c|Observation.Date)	Date in YYYYMMDD format
*Dispersion (scale)** ** all vars post "shape ~" in the model formula*	Sex	Fixed	Intercept	Sex	"MALE", "FEMALE"
	Age	Fixed	Slope	z.Age	Scaled measure of age [-1.63 to 3.29] derived from age in days [0 to 19253]
	Age at last sighting (selective disappearance)	Fixed	Slope	z.ALS	Scaled measure of age at last sighting [-2.59 to 2.19] derived from last sighting age in days [715 to 19253]
	Reproductive state	Fixed	Intercept	Repro.Stat	"Newborn" – Under 2 months age "Calf" – 2 months to weaning "Not Calf" – All ages post-weaning
	Individual	Random	Intercept	(z.Age|a|**Individual**)	Factor with 3-letter ID codes for each animal
	Age within individual	Random	Slope	**(z.Age**|a|Individual)	Scaled measure of age [-1.63 to 3.29] derived from age in days [0 to 19253]
	Year	Random	Intercept	(1|b|Year)	1988 to 2025
	Observation Date	Random	Intercept	(1|c|Observation.Date)	Date in YYYYMMDD format

Table S2: Number of observations, number of individuals, and average observations per individual, total and per sex. Averages are rounded to the nearest whole number.

	Individuals	Total Obs	Average obs/ind	Std err obs/ind
Total	457	64914	142	6.89
Male	*228*	*31287*	*137*	*8.58*
Female	*229*	*33627*	*147*	*10.8*

Table S3: Computed Average Marginal Effect (AME) contrasts for each population level parameter in the model. Negative estimates indicate the effect of the second compared level is higher, while a positive relationship indicates the first compared level is higher. Differences are significant (asterisk) if the AME contrast credible intervals do not cross zero. Confidence intervals represent 95% significance.

	Contrasting coefficients	Contrast Estimate
Mean	Sex (Female vs Male)	-0.61 (-0.78, -0.45)*
	Age (scaled, centred)	0.21 (0.13, 0.29)*
	Age at Last Sighting (scaled, centred)	0.17 (0.08, 0.27)*
	Reproductive State (Newborn vs Calf)	0.52 (0.20, 0.86)*
	Reproductive State (Newborn vs Not Calf)	0.77 (0.43, 1.13)*
	Reproductive State (Calf vs Not Calf)	0.25 (0.13, 0.37)*
Dispersion	Sex (Female vs. Male)	-0.59 (-0.75, -0.41)*
	Age (scaled, centred)	0.06 (0.03, 0.09)*
	Age at Last Sighting (scaled, centred)	0.14 (0.09, 0.20)*
	Reproductive State (Newborn vs Calf)	0.48 (0.08, 0.96)*
	Reproductive State (Newborn vs Not Calf)	0.41 (0.01, 0.86)*
	Reproductive State (Calf vs Not Calf)	-0.07 (-0.10,-0.03)*

Table S4: Additional summary estimates from correlations in the main model.

	Correlations:	Estimate
Mean – Mean	Mean Individual – Mean Age of Individual	0.23 (0.07, 0.38)
	Mean Individual – Mean Age^2 of Individual	0.24 (-0.44, 0.73)
	Mean Age of Individual – Mean Age^2 of Individual	0.33 (-0.34, 0.80)
Mean – Dispersion	Mean Age of Individual – Dispersion Individual	0.41 (0.26, 0.55)
	Mean Age^2 of Individual – Dispersion Individual	0.33 (-0.39, 0.79)
	Mean Individual – Dispersion Age of Individual	0.23 (0.09, 0.36)
	Mean Age of Individual – Dispersion Age of Individual	0.96 (0.91, 0.99)
	Mean Age^2 of Individual – Dispersion Age of Individual	0.39 (-0.31, 0.83)
Dispersion – Dispersion	Dispersion Individual – Dispersion Age of Individual	0.40 (0.27, 0.52)

Table S5: Variance components (sd_* variables) extracted from each portion of the model, including estimate, error, and lower and upper credible intervals. Decimals have been rounded to two places.

		Estimate	Error	Lower CI	Upper CI
Mean	*Individual*	0.20	0.01	0.18	0.22
	Age of Individual	28.00	2.31	23.78	32.75
	Age^2 of Individual	4.06	2.39	0.23	9.16
	Year	0.18	0.03	0.13	0.24
	Observation Date	0.62	0.01	0.60	0.64
Dispersion	*Individual*	0.80	0.04	0.73	0.87
	Age of Individual	0.60	0.04	0.53	0.67
	Year	0.76	0.12	0.57	1.02
	Observation Date	1.56	0.05	1.47	1.66