The age of change: social aging in dolphins

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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. Here, we leverage four decades of behavioural data on a population of Indo-Pacific bottlenose dolphins to bring new perspectives on social aging by exploring individual differences in sociability (repeatability, i.e. personality), its variance (predictability), and how sociability changes (plasticity) and its variance changes (malleability) with age. Novel analytical methods reveal a multidimensional response: individual sociability (group size) changes significantly throughout life, both in average response and underlying variance. Sociability increases for the first two decades of life, then declines with age, a trend more pronounced with males. Predictability of individual sociability, however, increases throughout life, indicating that individual social preferences strengthen (despite oscillations) with age. These patterns suggest that individuals develop social competence, defined as accruing social

information via experience, presumably optimising their social relationships for a net fitness benefit. These findings provide novel insights into sex-specific social aging and illustrate how studying variance can reveal processes of competence, selection, and adaptation.

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[48,90,95,97,111]. Recent literature has focused on the relationship between social behaviour and age[66,92]. Aging is known to drive shifts in sociability in many taxa, such as decreased network size and increased social selectivity reported in humans[13,16,119], non-human primates [66,84], and birds[88], reduced affiliative interactions and social influence in rodents[57,115], and lessened social connectedness in deer[1]. These age-related patterns, however, are not one-size-fits-all even within species, as sex-specific variation has been documented in lions[85], giraffes [14,15,61], whales [110,112], and macaques[22].

Though the metrics, species, and methods of analysis have been different across these studies, all have observed changes among individuals 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 wholly unstudied. Beyond average differences between individuals (i.e., behavioural syndromes[28,89], 'personality', repeatability[5]), differences exist within repeated measures of an individual. This variation has been described with multiple terms: (1) within-individual or intraindividual variation (IIV)[96], or, (2) predictability, which measures the same variation but scales in reverse (increased variance in repeated measures means decreased predictability)[18]. Just as averages may change over time or across environments (i.e., behavioural reaction norms, plasticity[113]), variance is theorised to be a plastic component of

behaviour, the change of which is known as 'malleability'[78]. At this time, no empirical evidence of malleability has been demonstrated in wild animals, though at least one study suggests its presence based on varied predictability of movement behaviour in two age classes of owls[10]. Predictability and malleability are also potentially valuable in studies of learning[78], as adaptive phenotypic plasticity is frequently observed in social learning and cognition studies[4,52,64]. A conceptual graphic describing these four components of behaviour (personality, plasticity, predictability, malleability) is presented in Figure 1.

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[114]. Of particular interest is the potential for describing adaptive processes, such as those of trial-and-error learning. In such processes, individuals generate a broad range of phenotypic responses, and upon receiving feedback, are able to modify their behaviour[35,51], reducing the variation they display in favour of stabilising their behaviour around a preferred phenotype[98,114]. When applied to social behaviour, this ability is defined as "social competence"[79,102] and is theorised to be a trait upon which selection may act depending on environmental needs[99]. Because social competence is developed through experience and feedback[86,101,102], in dynamic social environments, early development is likely to correspond to a period of low predictability. As individuals grow, age, and develop social competence, predictability should be malleable, reducing the degree of variation around an optimum reaction norm.

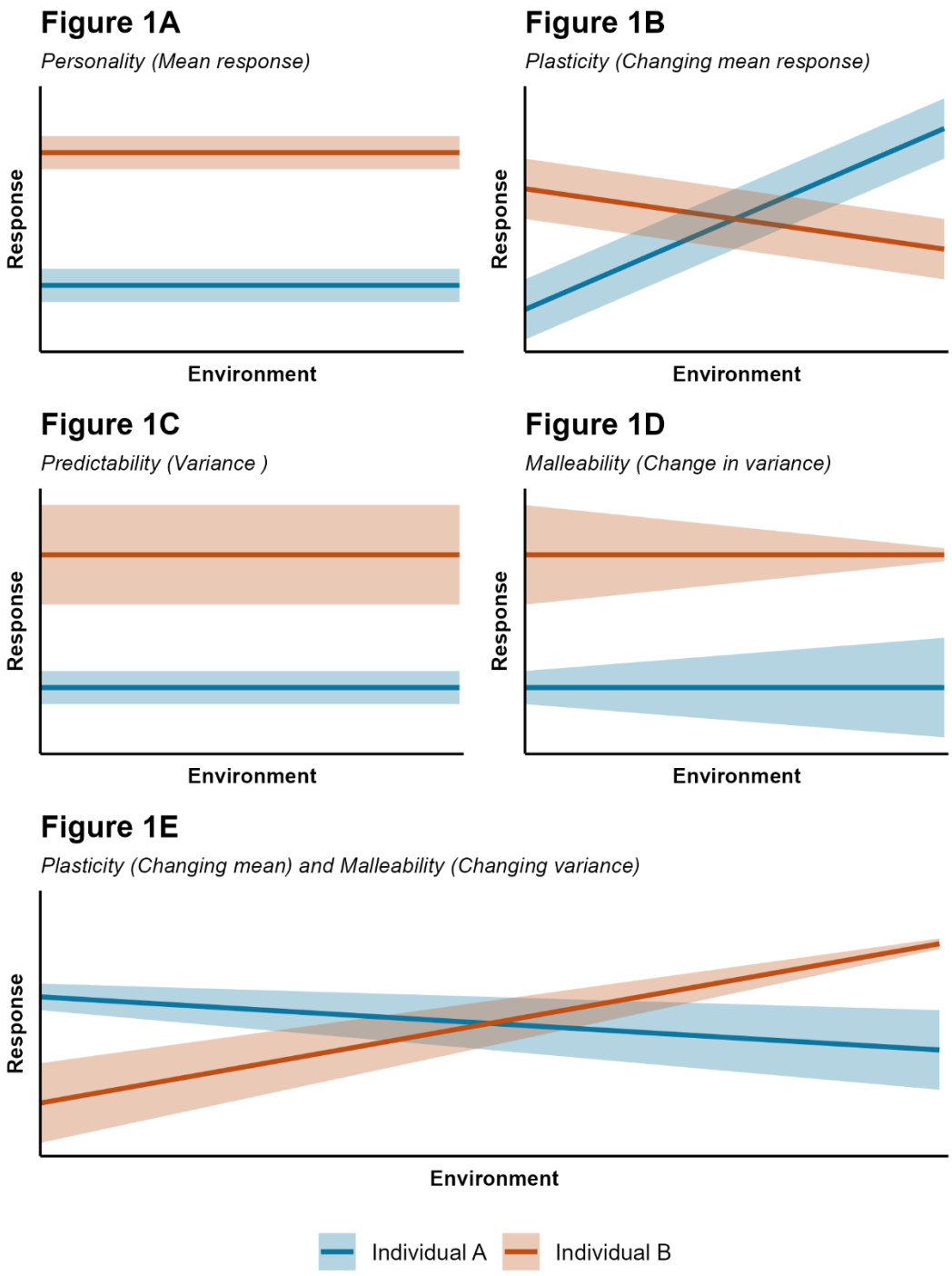


Figure 1: A series of conceptual plots illustrating the four components of behaviour in two individuals, A (blue) and B (orange). Lines represent average responses, and ribbons represent the spread of points around the average. In 1A, personality/repeatability, individuals have different average responses unaffected by the environment, but the same variance. 1B describes plasticity, where A increases their average response across an environmental gradient, while B decreases their response, but in both cases variance is unchanged. Figure 1C illustrates predictability, where B has a higher variance around their average response than A. Figure 1D describes malleability, where both A and B have unchanging average responses, but A becomes less predictable over an environmental gradient, and B becomes more predictable. Figure 1E describes how these components of behaviour can covary, where A decreases their average response (plasticity) while becoming less predictable (malleability), and B increases their average response while simultaneously becoming more predictable.

Taborsky (2021) further proposed a positive feedback loop between sociability and social competence. In such a case, environments favouring sociability would increasingly favour highly gregarious, highly competent animals[101], and correlations would emerge between average sociability and its predictability, such that individuals who are more sociable are also more predictable. This pattern has recently been described in a social reptile[17]. However, optimum sociability can change depending on age and sex. For example, life history strategies in each sex of a species can differentially favour social interaction[38], leading to sex-specific patterns of social aging are in many species. Similarly, in species where sociability is favoured in one sex, that sex is expected to be both more gregarious and more predictable.

Here, we use a decades-long study of wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) to investigate predictability and malleability in group size, a measurable social trait common to all observations of animals in a social system. Indo-Pacific bottlenose dolphins are long-lived marine mammals with a fission-fusion social structure characterised by high relational complexity[65]. Interactions among conspecifics in this population are dynamic and unbounded[36,37,39], and individuals can independently change their group compositions 5-6 times per hour[39]. Delphinids, like primates, are posited to have evolved large brains to navigate cognitively demanding social environments[9,30,107,116], which has enabled intricate, long-term social strategies to develop in this population[20,21,37,40,73]. *T. aduncus* are demonstrably segregated socially by sex[94]; female relationships are influenced by biparental kinship, shared habitat preferences, and foraging behaviours[37,73], whereas males of this population engage in highly structured, multi-tier alliance systems with unrelated individuals of similar age to compete for access to cycling females[20,21,40]. Long lifespans (>52 years[74]), bisexual natal philopatry[104], and an extended developmental period[54] have allowed us to collect hundreds of repeated measures for hundreds of individuals, providing rare insights into the fine-scale behavioural changes that are often difficult to detect in a wild population.

Here, we analyse sociability at both average and variance levels to understand how and why sex-specific sociability in dolphins changes with age. We hypothesise that patterns of average group size will correspond to changing socio-ecological strategies throughout life, while predictability will reflect the development of social competence. If some animals are more socially competent than others, we should see variation in predictability among individuals, but because social competence develops through prior experiences and feedback[86,101,102], early development is likely to correspond to a period of lower predictability. As individuals learn to balance the benefits and costs of grouping as they age, predictability of group size should canalise[114], as individuals selectively stabilise their behavioural choices[84]. We predict a correlation between group size and its predictability, such that individuals who are more gregarious are also more predictable. We also hypothesise that 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[33].

Methods

Data collection

Data used in this study were collected as a part of an extensive long-term wild population study by the Shark Bay Dolphin Research Project (SBDRP) offshore of Monkey Mia in the eastern gulf of Shark Bay, Australia (25˚ 47`S, 113˚ 43`E). Since 1984, >1900 resident animals have been observed repeatedly across decades primarily between May and November each year, with detailed behaviour and location data available from 1988. Sex determination was conducted via visual inspection of the ventrum, association with a calf, or genetic analysis[58,94]. Birthdates were estimated based on sighting of the mother before and after calf birth and physical characteristics (body size, speckling, foetal lines)[69].

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.

Survey and response variable

Behavioural data were collected via five-minute scan sampling during boat-based surveys, with each sighting capturing group size and composition along with location and environmental data[55]. Inclusion in a group was determined via a 10m chain rule where membership required individuals to be within 10m of at least one group member[94]. Spatial and temporal autocorrelation were mitigated by retaining only a single sighting of an individual per day[104]. 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 = 2,283 of 61,935 observations, <4% of the total dataset.)

Hill and Mulder suggest that a minimum of twice the repeated measures used to detect a mean behaviour effect will be required to detect a proportional effect on variance[47]. Prior study on mean social traits in this population used a minimum of 15 repeat measures to detect a mean response in the timeframe under observation[32] ; this threshold was more than doubled to a minimum of 40 repeat measurements per individual across the timeframe under observation (the full lifespan) for this analysis. Individuals which had been sighted less than 40 times were removed from analysis, leaving 431 individuals, 221 males and 210 females, that met our requirements (Table S1).

Analysis

To best model the variance in residuals of the mean using the same fixed and random effects, we fit a double-hierarchical generalised linear model (DHGLM[18]) to decompose behavioural

158 variance[12,17,45,118] , using the brms package[8] in R (version 4.2.3)[82]. A DHGLM is a mixed model
159 which contains both a mean and dispersion (residual) component. The mean model directly
160 estimates the mean effect of fixed and random effects on the response variable (number of
161 associates), while the dispersion model partitions the residual variance from the mean model
162 into separately specified fixed and random effects to estimate the variation present around the
163 mean effect. Larger variation is indicative of higher within-individual variation, or lower
164 predictability, and smaller variation is indicative of higher predictability.

165 To best understand the demographic drivers of within-individual variation at the population
166 level, we fit population-level parameters (fixed effects) in the mean model for: i) sex, as dolphins
167 have sex-specific social strategies[94], and ii) a mean-centred quadratic effect of age (z-score
168 scaling) to measure malleability as an organism ages and accrues experience. Random effects
169 unique to each individual, in the mean model included: i) quadratic effect of age (z-scaled)
170 within individual identity (ID), ii) the year of observation to account for short-term, external
171 environmental effects, and iii) the date of observation, to mitigate pseudoreplication caused by
172 multiple animals being treated as a focal individual within a given observation, and to account
173 for unique occurrences on a given day. All fixed and random effects in the dispersion model
174 were identical with the exception of replacing quadratic age terms with linear-scaled age terms,
175 as this fit the data better during model construction. Additionally, sex-specific models were run
176 on female and male data separately in case the combined model obscured sex-specific
177 patterns in behaviour.

178 Data best fit a negative binomial distribution with no prior transformation for normality. All
179 parameters in the dispersion portion of the models were assigned inv_gamma (0.4,0.3) priors to
180 approximate penalised complexity priors, which are the current best practice for modelling
181 negative binomial distributions[91]. Default uninformative priors were assigned to the mean
182 model. Models were run for 18000 iterations using 2 chains, no thinning intervals, and a burn-in

period of 12000 iterations. Fit was determined based on 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[109]. Convergence was determined by visual examination of trace plots and effective sample sizes above 1000.

Average Marginal Effects (AMEs)

A technical limitation of generalised linear mixed modelling types is the conditional interpretation of regression parameters[77], 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[120]. 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[42]. We utilised the brmsmargins package[117] 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 significantly 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)[76] measuring overdispersion. Decrease of θ

corresponds to increased variation, or less predictability, and an increase in θ results in decreased variation, or heightened predictability[46]. The brms modelling package reports the shape parameter θ directly, so larger dispersion values correspond to higher predictability in this model.

Results

Summary statistics

This dataset included 61,935 individual observations (mean per individual = 144, min 40, max 927) collected between 1988 and 2023. The number of observations, number of individuals, and average observations per individual for each sex is described in Table S1. All individuals were sighted across multiple years, with the average number of years of observation being 16.8 [min 2, max 33]. Age at time of observation ranged from 0 days to an estimated 18,631 days (0 years to 51.4 years) old. Males were slightly more gregarious than females, with a mean of 6.03 (sd 5.33) associates per male observation and 5.13 (sd 4.96) associates per female observation (whole population average = 5.56, sd 5.16).

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

Sex and age both had significant effects on mean level sociability (Table 1). Males had higher average gregariousness than females (-0.60 [95% CI: -0.78 to -0.45]; Figure 2, Table S2). Age followed a parabolic relationship throughout ontogeny, where mean group size increased throughout the juvenile and early adult years, peaked, and then declined with continuing age; this trend was more pronounced in males (Figure 3). Individual ID was responsible for a significant component of variation (0.19 [95% CI: 0.18 to 0.21]; Figure 2, Table 1), but a much larger effect was attributable to individual-specific aging patterns across repeated measures (3.78 [95% CI: 3.50 to 4.02]: Figure 2, Figure 4, Table 2). Date of observation had a larger effect

on individual variation in mean sociability (0.62 [95% CI: 0.61 to 0.64]) than year (0.18 [95% CI: 0.13 to 0.24]; Figure 2, Table 1).

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

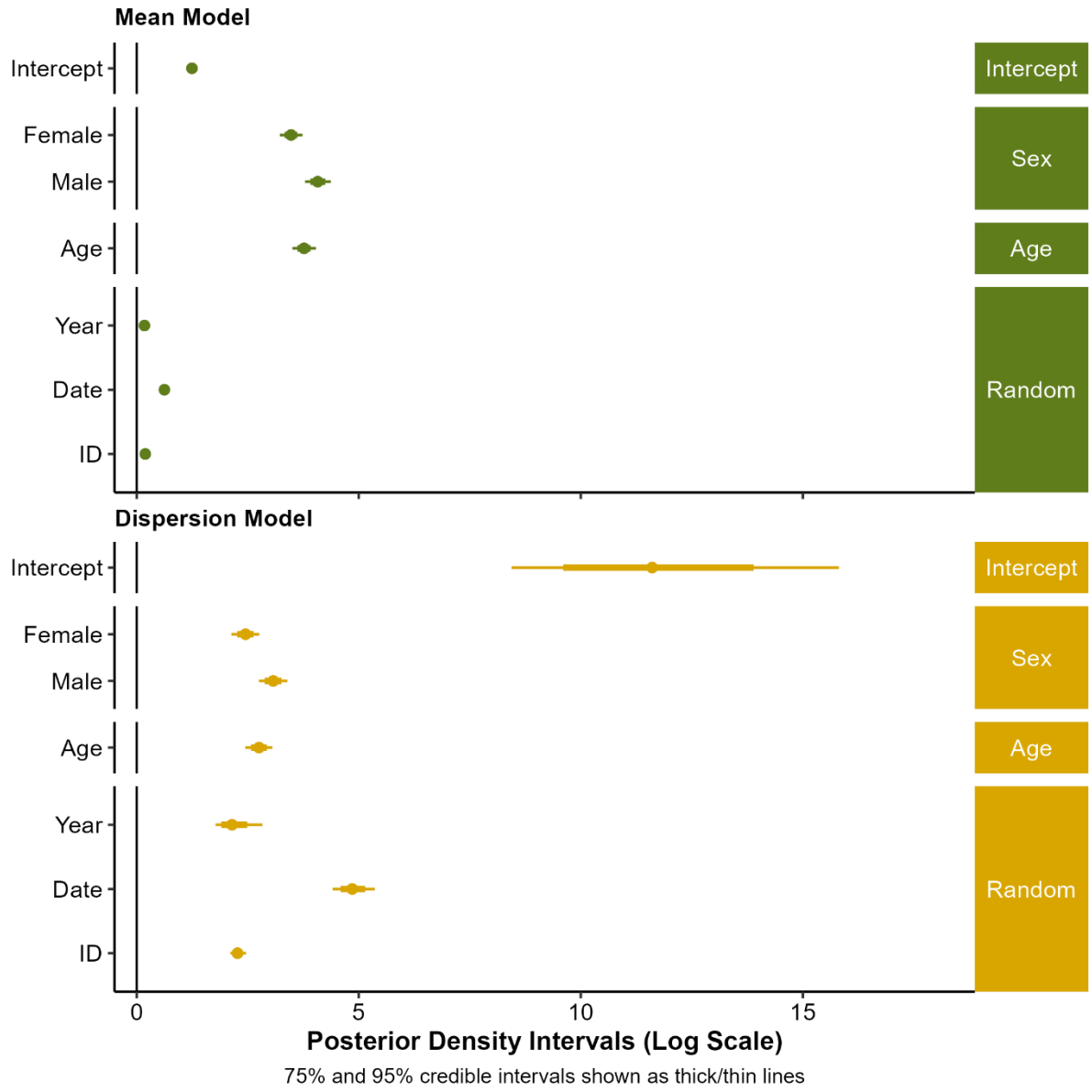
Similar to mean level gregariousness, group size predictability was affected by sex and age. At the dispersion level, every level of every effect tested differed from other levels (Figure 2, Table 1, Table S2). Males were, on average, more predictable than females (-0.62 [99% CI: -0.81 to -0.45]; Table S2). Group size predictability increased with age **(**2.75 [95% CI: 2.46 to 3.06], Table 2). Individual ID and year of observation had small effects on predictability (0.82 [95% CI: 0.75 to 0.90] and 0.78 [95% CI: 0.58 to 1.04]), while the date of observation had a much larger effect (1.58 [95% CI: 1.48 to 1.68], Figure 2, Table 1). Within individuals, predictability was malleable, increasing with age (0.59 [95% CI: 0.52 to 0.67], Table 1, Figure 4).

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 (0.94 [95% CI: 0.91 to 0.98], Table 1, Figure 5). Conversely, average sociability and social predictability between observation dates were negatively correlated, where increased mean group size resulted in decreased predictability on a given day (-0.36 [95% CI: -0.42 to -0.30], Table 1). The relationship between mean group size and social predictability specific to a given year was not significant (0.21 [95% CI: -0.19 to 0.57], Table 1).

Table 1: Summary estimates (median, 95% credible interval) obtained from a double hierarchal generalised linear model estimating mean (sociability) and dispersion (predictability of sociability) parameters in both sexes, with females only, and with males only. Mean model effects are given on the log scale, while dispersion parameters are reported in standard deviations on the log scale.

		Estimate (Empirical model)	Estimate (Female model)	Estimate (Male Model)
	Fixed effects (coefficients):			
Mean	Intercept	1.24 (1.17 to 1.32)	1.25 (1.17 to 1.32)	1.47 (1.41 to 1.53)
	Sex (male)	0.16 (0.12 to 0.20)		
	Individual:Age	3.21 (-0.56 to 7.14)	3.38 (-.90 to 7.53)	-3.24 (-7.98 to 1.55)
	Individual:Age^2	-11.89 (-14.84 to -9.21)	-7.57 (-10.59 to -4.71)	-13.20 (-16.31 to -10.17)
Dispersion	Intercept	2.45 (2.13 to 2.76)	2.18 (1.91 to 2.46)	3.15 (2.75 to 3.56)
	Sex (male)	0.62 (0.45 to 0.80)		
	z.Age	0.07 (0.03 to 0.11)	0.07 (0.04 to 0.12)	0.15 (0.06 to 0.29)
	Random effects (SD):			
Mean	Individual	0.19 (0.18 to 0.21)	0.23 (0.21 to 0.26)	0.15 (0.13 to 0.18)
	Individual:Age	27.42 (22.64 to 32.21)	9.79 (4.38 to 15.33)	19.48 (14.67 to 24.08)
	Individual:Age^2	5.67 (0.33 to 11.58)	6.62 (1.67 to 11.18)	3.74 (0.22 to 8.94)
	Date	0.62 (0.61 to 0.64)	0.61 (0.59 to 0.63)	0.58 (0.56 to 0.60)
	Year	0.18 (0.13 to 0.24)	0.16 (0.12 to 0.23)	0.15 (0.10 to 0.20)
Dispersion	Individual	0.82 (0.75 to 0.90)	0.99 (0.87 to 1.11)	1.00 (0.85 to 1.16)
	Individual:Age	0.59 (0.52 to 0.67)	0.47 (0.37 to 0.58)	0.99 (0.84 to 1.16)
	Date	1.58 (1.48 to 1.68)	1.37 (1.27 to 1.47)	1.71 (1.59 to 1.84)
	Year	0.78 (0.58 to 1.04)	0.56 (0.40 to 0.77)	0.97 (0.70 to 1.34)
	Correlations:			
Mean – Mean	Mean Individual – Mean Individual:Age	0.22 (0.04 to 0.39)	0.18 (-0.18 to 0.52)	0.15 (-0.08 to 0.38)
	Mean Individual – Mean Individual:Age^2	0.22 (-0.39 to 0.68)	0.05 (-0.38 to 0.44)	0.12 (-0.57 to 0.68)
	Mean Individual:Age – Mean Individual:Age^2	0.11 (-0.44 to 0.61)	-0.12 (-0.65 to 0.39)	-0.28 (-0.81 to 0.43)
Mean – Dispersion	Mean Individual – Dispersion Individual	0.94 (0.91 to 0.98)	0.83 (0.75 to 0.90)	0.82 (0.69 to 0.93)
	Mean Date – Dispersion Date	-0.36 (-0.42 to -0.30)	-0.21 (-0.28 to -0.14)	-0.12 (-0.20 to -0.05)
	Mean Year – Dispersion Year	0.21 (-0.19 to 0.57)	0.35 (-0.08 to 0.69)	0.31 (-0.10 to 0.65)
	Mean Individual:Age – Dispersion Individual	0.37 (0.20 to 0.53)	0.40 (0.05 to 0.70)	0.36 (0.13 to 0.56)
	Mean Individual:Age^2 – Dispersion Individual	0.28 (-0.35 to 0.73)	0.10 (-0.31 to 0.49)	0.02 (-0.62 to 0.63)
	Mean Individual – Dispersion Individual:Age	0.18 (0.03 to 0.33)	0.11 (-0.12 to 0.32)	0.02 (-0.20 to 0.24)
	Mean Individual:Age – Dispersion Individual:Age	0.91 (0.83 to 0.97)	0.78 (0.47 to 0.95)	0.64 (0.43 to 0.81)
	Mean Individual:Age^2 – Dispersion Individual	0.17 (-0.39 to 0.65)	-0.43 (-0.80 to 0.05)	0.03 (-0.59 to 0.64)
Dispersion – Dispersion	Dispersion Individual – Dispersion Individual:Age	0.35 (0.20 to 0.48)	0.31 (0.08 to 0.51)	0.34 (0.12 to 0.54)



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254 **Figure 2:** Posterior density intervals for the mean (green, top) and dispersion (yellow, bottom) portions of the DHGLM.
255 Each point corresponds to the posterior median, with 75% and 95% confidence intervals are represented by thick
256 and thin horizontal lines, respectively. Population level effects (sex, age) are marginalised to reflect the independent
257 effects of each level on the response.

Table 2: 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.

		Estimate (Empirical model)	Estimate (Female model)	Estimate (Male Model)
	Fixed effects (coefficients):			
Mean	Sex (Female)	3.48 (3.24 to 3.74)		
	Sex (Male)	4.08 (3.79 to 4.37)		
	Age (scaled, centred)	3.78 (3.50 to 4.02)	3.49 (3.24 to 3.73)	4.36 (3.98 to 4.71)
Dispersion	Sex (Female)	2.45 (2.14 to 2.77)		
	Sex (Male)	3.08 (2.74 to 3.38)		
	Age (scaled, centred)	2.75 (2.46 to 3.06)	2.17 (1.90 to 2.44)	3.16 (2.63 to 3.71)

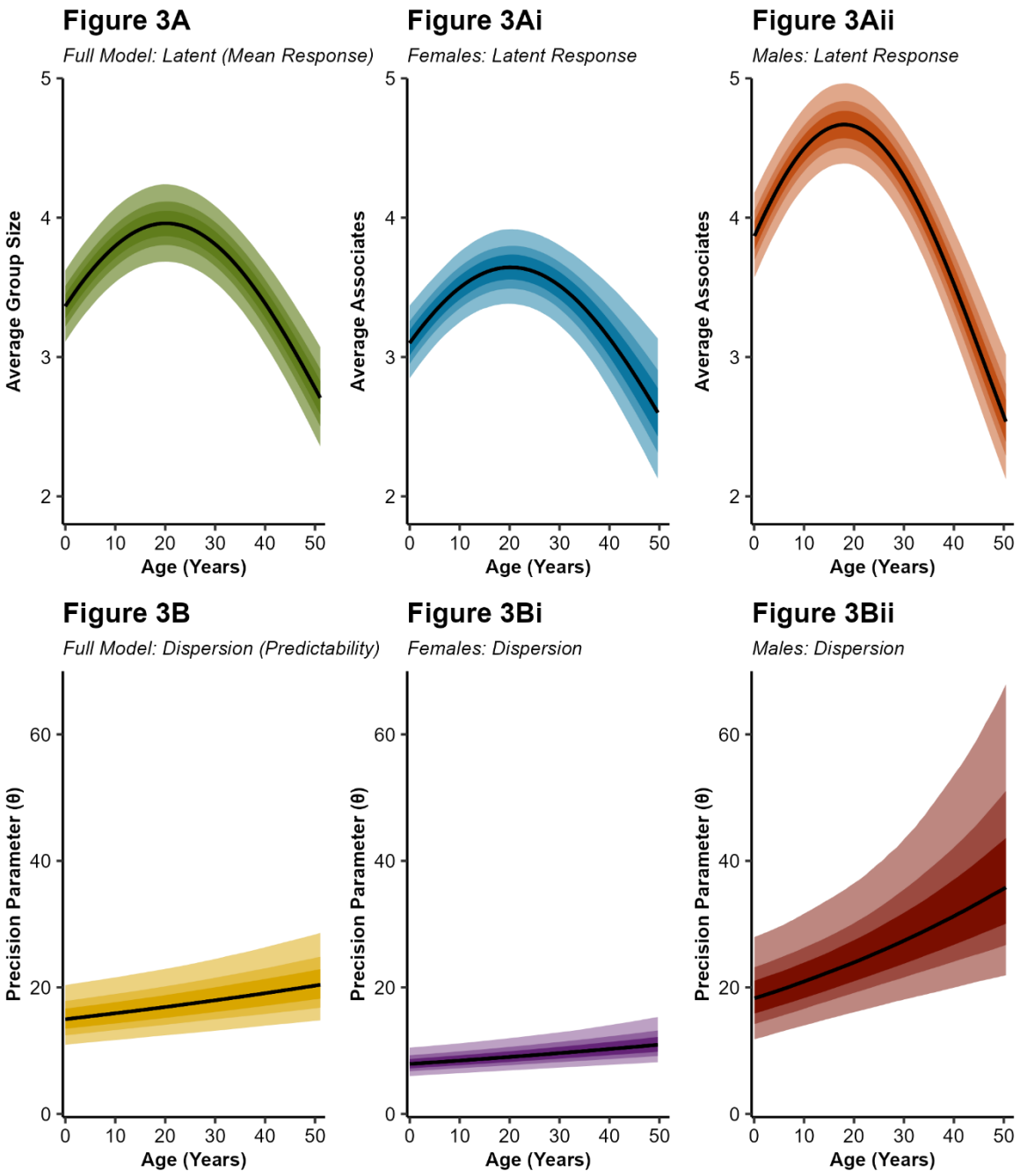
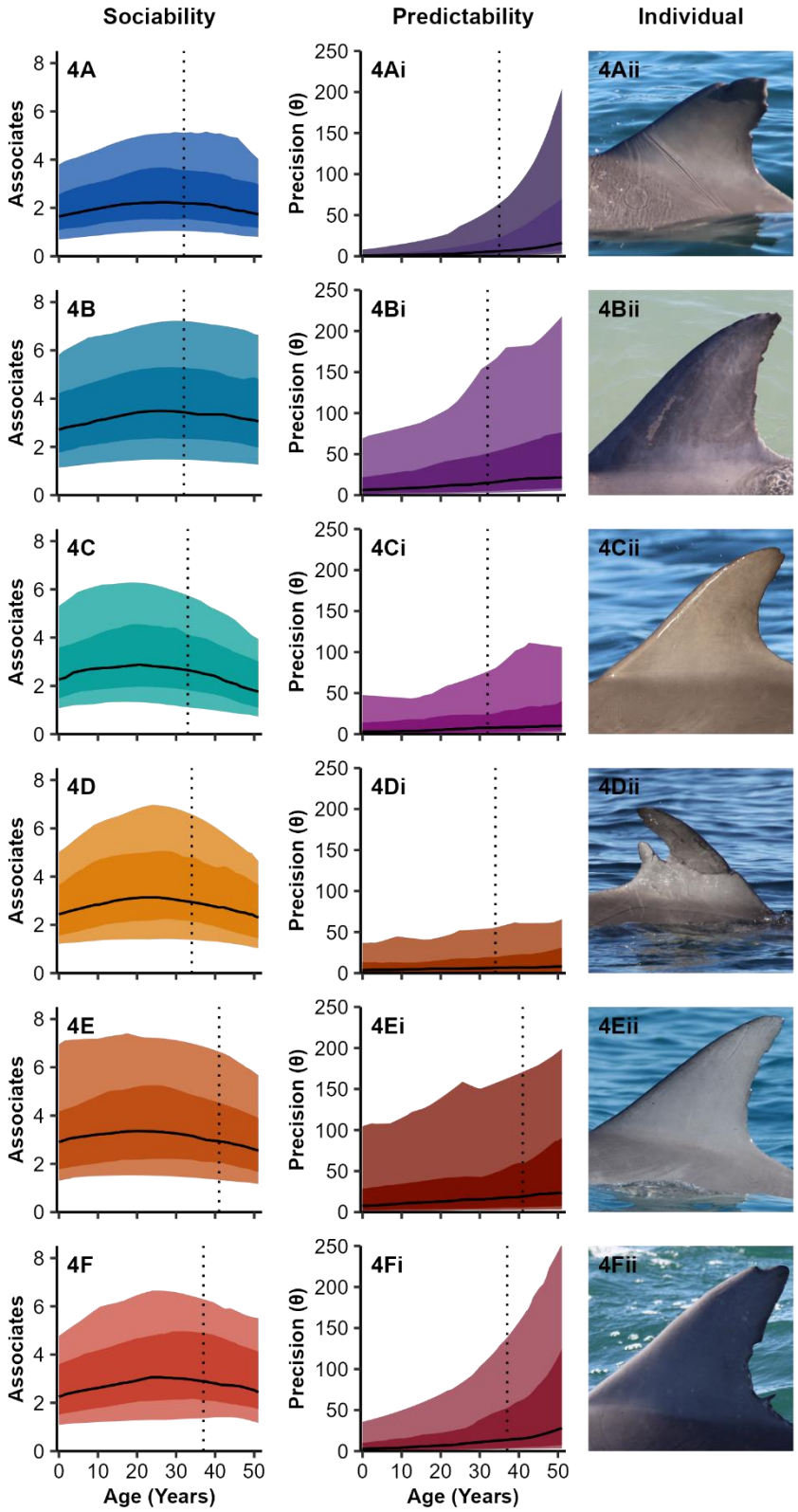


Figure 3: Posterior draws of group size at the latent (mean) response and dispersion (predictability) scale, for the full model (3A, green, and 3B, yellow) and for female-only (3Ai, blue, and 3Bi, purple) and male-only (3Aii, orange, and 3Bii, red) models. Colours represent confidence intervals of 50%, 75% and 95%, in darkest to lightest order. All variables have been back-transformed from z-score to the latent response scale.



269 **Figure 4:** Posterior draws of group size at the latent (Sociability, first column) and dispersion (Predictability, second
270 column) for six individuals (Female, A-C, blue and purple, and male, D-F, orange and red) in the population. Each row
271 is one individual, with the identifying dorsal fin for that individual on the right. Dashed lines indicate the age of the
272 individual at most recent sighting. Colours represent confidence intervals of 50% and 75%.

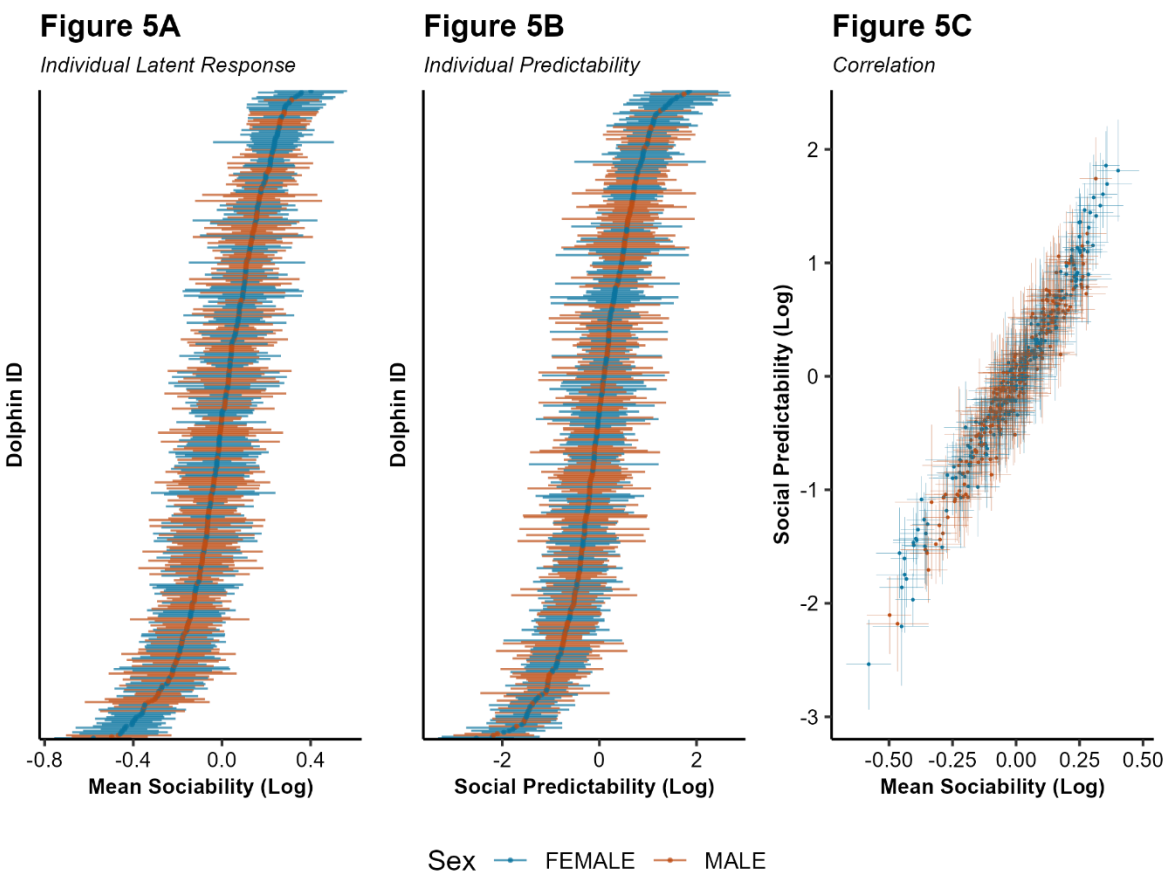


Figure 5: Individual posterior distributions for mean sociability (left), social predictability (centre) and the correlation between sociability and social predictability (right) for each of the 431 individuals used in this study. Females are given in blue; males are given in orange. All values are reported 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. Sociability follows a quadratic trend, but its underlying predictability is linear, decreasing with age as individuals become more predictable. While both sexes follow this pattern, males are more sociable and predictable in their grouping patterns than females. Further, we identify a significant individual component to group size and predictability, though age and sex have stronger effects than that of the individual's personality. Finally, we demonstrate a strong correlation between sociability and predictability, showing that more sociable individuals are also more consistent in their sociability. We discuss these results in the context of social aging and life history.

Sociability in the Shark Bay dolphins, on average, follows a quadratic curve: group sizes rise steadily into the early twenties, then subsequently fall in later life. Although literature generally relates group formation to predation or harassment, a threat highest in juvenile males[38,43,44,62,74] and adult females (while rearing calves, particularly those <1 year old[74]), these time periods are not where groups are largest, indicative of an unrelated force driving shifts in average group size. We suggest that this driver is 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[24,25,60], and the size of conspecific groups may be defined by each individual's need for, and ability to process, social information[29]. The juvenile and adolescent periods, for example, are periods where social information is highly valued for learning and development in many species[6,31,81]. Prior to weaning, calves are socially constrained by the mother, as separations are infrequent and of short duration[97]. It is only post-weaning that juveniles expand their social network[59]. As such, juvenile individuals prioritise quantity of social interactions. As individuals mature, their socio-cognitive competence

303 increases, enabling the formation of ever-larger groups, which would maximise the diversity of
304 these interactions. In long-lived species with similar life histories like humans, this process can
305 take nearly two decades[49], corresponding to the peak in dolphin group sizes around twenty
306 years old.

307 After this peak, average group sizes decline throughout adulthood. We suggest this decline
308 stems from the decreasing value of social information co-occurring with social senescence.
309 Forming a conspecific group comes with individual costs, such as increased disease risk[3],
310 increased visibility to predators, and intragroup social and feeding competition (for a
311 comparison table, see Makuya and Schradin[68]). In early life, when individuals have little
312 knowledge of the world around them, seeking social interaction can provide fitness benefits
313 which may outweigh the costs of grouping[105]. However, aging negatively affects body systems,
314 including motor function, immune strength, sensory capacity, and energetic function among
315 myriad other factors that may influence sociability[92]. Declining body condition impacts
316 movement capacity[1,50] and foraging efficiency[67], requiring individuals invest more in resource
317 acquisition, a largely solo activity in Shark Bay dolphins. Furthermore, aging individuals might
318 place less value on receiving information from conspecifics since they have well-established
319 home ranges and foraging tactics[7]. Such experience-modulated social selectivity has been
320 documented in aging macaques[2,7], and similarly increasing preference for individual decision-
321 making with age is frequently reported in humans[27,93] particularly when dealing with everyday
322 problem solving[26,100]. Thus, we expect that older dolphins would become more selective, joining
323 groups that meet specific criteria (e.g., close allies, kin, foraging on large fish shoals).

324 Aging also comes with a loss of conspecifics. Animals may die from old age, sickness,
325 starvation, predation, or any number of unseen causes. Individuals which live to advanced age
326 may often be one of the few remaining from their cohort, particularly for males since they form
327 long-term alliances with other males who are close in age[20]. As the Shark Bay dolphins are

known to form long-term, stable bonds, declining group sizes may be exacerbated by a loss of closely bonded, socially irreplaceable conspecifics[83]. These outcomes correspond to similar social declines seen in primates, deer, rodents, and other species with age[92], but of any species, the Shark Bay dolphins most closely mirror the patterns of social aging seen in humans, who parallel toothed whales in the evolution of long lifespans, large brains, and sophisticated social systems where social information modulates population dynamics[41].

Though average group size rises and falls throughout life, the variance that underpins these averages follows a different pattern: individuals become increasingly predictable with age. In the first two decades of life, despite a larger range of available group sizes, increasing predictability in this stage of life suggests that individuals of both sexes are actively selecting for optimally sized groups based on specific criteria. We suggest this is evidence of 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[102]. In earlier years, an individual forms groups of varying sizes through social and individual learning, then upon accruing experience, reduces the variance in their behaviour in favour of what may be more optimal group sizes for the given individual. This results in canalisation-like processes[56,98,114] within individuals throughout their lifetime. These processes are visible in developmental studies, for example, where achieving a specific outcome is known to lead to more consistent and efficient behaviour leading to that outcome (winner-loser effect[63]), i.e. less variation in behaviour (and outcome) over time. Malleability, which directly measures these changes in variation as they occur, may then be indicative of behavioural adaptation happening within an individual.

Predictability continues to increase even during the decline of average group sizes, though this increase is likely to stem from the same causes as declining group sizes. A declining value of social information and subsequent tendency towards smaller groups, coupled with shrinking

social networks as close associates die, could reduce the overall variance around average group size and explain increasing predictability with age. Social selectivity found in similar systems (humans, primates[2,7,103]) may also contribute, as these individuals form strong, irreplaceable bonds with certain conspecifics while young, then invest in and retain those bonds throughout life[20,71].

Although the lifelong patterns in average group size and its predictability are similar in both sexes, variation between males and females is tightly linked to reproductive strategies. Females are typically in smaller but less predictable groups, as females have a broader range of viable social strategies, including predominantly solitary ones[71], they can select from based on fluctuating reproductive states. Without a calf or pregnancy, predation risk and resource demands are lower, but starting at age 13 (on average), female Indo-Pacific bottlenose produce one calf at a time and nurse that calf for 2.5 to 8 years[69]. While nursing, predation risk and resource demands increase substantially. To maintain energetic demand, females forage extensively[72], a predominantly solo or calf-accompanied activity[70]. Calves <1 year old are especially vulnerable to predation[74], and mothers account for this risk by increasing their sociability with other females[69], a pattern also seen in primates[23]. Once calves surpass this age and predation risk decreases, females can prioritise smaller groups. Aging females also decrease in calving frequency due to reproductive senescence[54], leading to smaller, but less variable groups in old age.

In contrast with females, male dolphins in Shark Bay rely heavily on sociability as it forms the backbone of their reproductive strategy. In species with extended maternal investment and large interbirth intervals (primates, hyenas, elephants, cetaceans, humans[121]), fewer females are available to mate with annually relative to the total male population. With oestrus females a rare and valuable resource, the formation of short-term coalitions and longer-term alliances becomes necessary to effectively acquire and maintain access to these females and ultimately

reap the fitness consequence of passing on genes[19,106,108]. Male Shark Bay dolphins have evolved a multi-tier alliance system with a complexity second only to the systems developed by humans[20]. These alliances comprise long-term, stable social bonds allowing teams of male dolphins to mate-guard and cooperatively consort with a reproductive female for hours up to weeks[20,21,80]. Increased sociability necessarily enhances alliance formation, which occurs in the teens concurrent with peak average group sizes, and later reproductive success[34]. Because males spend the vast majority of their time with their alliance partners[94] in persistent, structured groups where numbers influence acquisition, guarding, and mating access to females, they are ultimately in larger, more predictably sized groups.

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[101]. Variation among individuals forms the basis for evolution such that directional selection may act; the direction in which this selection may act on fitness outcomes, though, is yet unclear. However, previous work has identified correlations between average and variance responses in behavioural traits[45,53,75,78] and extended such associations to improved fitness outcomes; increased gregariousness, and in females, more social predictability, was positively associated with survival[17]. As social integration can influence longevity and reproductive success[11,90], and predictability of social traits can influence mate choice for reproduction[87], the relationship becomes clear: variation itself can underpin ultimate fitness consequences in social systems. Future work should endeavour to identify 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 for the first time to broaden our understanding of the relationship between aging and sociability in a long-lived mammal. We provide evidence to support the growing body of work exploring sex-specific

differences in personality and predictability, demonstrate for the first time that predictability itself is malleable due to aging, and describe how mean and variance responses in a trait correlate to form personality-predictability associations. We posit that variation is not solely random noise within a dataset, but a biologically meaningful component of animal behaviour, and its malleability may have the potential to provide information about behavioural adaptation. The findings of this study suggest that understanding group formation, particularly in the context of social aging, requires us to incorporate both life history and social considerations, like the theory of social competence, into our framework. This study highlights the importance of within-individual variation and how it relates to our understanding of social aging in animal social systems.

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Table S1: 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	431	61935	144	7.10
Male	*221*	*30130*	*136*	*8.61*
Female	*210*	*31805*	*151*	*11.4*

Table S2: 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.

	AME Contrasts (Empirical model)	AME Contrasts (Female model)	AME Contrasts (Male model)
Mean model:			
Sex (Female vs. Male)	-0.60 (-0.78 to -0.45)*		
Age (scaled)	0.08 (0.03 to 0.14)*	0.10 (0.02 to 0.18)*	-0.01 (-0.11 to 0.08)
Dispersion model:			
Sex (Female vs. Male)	-0.62 (-0.81 to -0.45)*		
Age (scaled)	0.06 (0.02 to 0.10)*	0.07 (0.03 to 0.11)*	0.15 (0.05 to 0.27)*