Examining the fitness benefits of social plasticity to prey availability in bottlenose dolphins

Running title: Social buffering in bottlenose dolphins

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Abstract

A key explanation for phenotypic plasticity is that changing behaviour to match conditions increases fitness. Affiliative social associations with conspecifics can be important for coping with challenging conditions, and therefore plasticity in social behaviour in response to environment variation may bring fitness benefits. Here we test the adaptive benefit of social plasticity by quantifying female bottlenose dolphins' (*Tursiops truncatus*) plastic responses to salmon (*Salmo salar*) abundance and determine if either this plasticity or mean social behaviour is associated with calving success. We found that more gregarious females and those better connected to all parts of the entire social network had higher calving success, but plasticity in social behaviour in response to salmon abundance was not associated with this component

of fitness. This lack of relationship may have arisen as salmon abundance in either current or previous years was not associated with the probability of producing a calf. We therefore demonstrate that being more social is positively associated with females' calving success in our study population, but social plasticity itself is not associated with fitness benefits, questioning whether this is likely to be a mechanism for this population of dolphins to cope with challenging environmental conditions.

Key words: dolphin, food abundance, environmental change, network, plasticity, social buffering, Tursiops

Introduction

Animals are frequently exposed to adverse environmental conditions, including extreme weather events or fluctuations in prey availability and predation risk, which can impact their fitness. To mitigate these factors, animals may change their traits (show phenotypic plasticity) to buffer any fitness costs that may otherwise be inevitable in adverse conditions (Blumstein et al., 2023; Candolin & Wong, 2011; López-Sepulcre & Kokko, 2012). For instance, brown trout *Salmo trutta* may decrease their metabolism at times of low food availability (Auer et al., 2015), while goldcrest *Regulus regulus* form larger groups to huddle and conserve heat in cold conditions (Hogstad, 1984). Behaviours are the type of trait that are often thought to be animals' first line of defence against adverse conditions, as they can change relatively quickly compared to morphological or even physiological traits (Sih, 2013; Sih et al., 2011). Consequently, changing behaviour to ameliorate the costs of environmental stressors is thought to be widespread (Tuomainen & Candolin, 2010; Wong & Candolin, 2015).

Many animals live in groups or near others, and so engage in social behaviours; interactions with conspecifics that can be cooperative or competitive in nature (Rubenstein & Abbot, 2017; Székely et al., 2010). Social behaviours are therefore a key mechanism through which animals may be able to buffer against environmental change (Komdeur & Ma, 2021). Global-scale comparative analyses have been used to test the general idea that social interactions with conspecifics helps animals cope with harsh environments. These relate aspects of a species' social structure, such as the presence or absence of cooperative breeding, to environmental parameters of the species' native range (e.g. variability in rainfall). For example, higher incidences of communal living are found in social spiders in areas with higher rain intensity which challenge the survival of lone females (Guevara & Avilés, 2015). These analyses have demonstrated a link between cooperative breeding systems and survival in harsh conditions, supporting the idea that social living helps animals cope with environmental stressors (Firman et al., 2020; Guevara & Avilés, 2015; Jetz & Rubenstein, 2011; Sheehan et al., 2015).

Comparative analyses, however, do not shed light on whether *plasticity* in behaviour helps animals survive and reproduce in adverse conditions. Such studies require

multiple measures of individual social behaviour across a range of environments and to associate variation in the social behaviours with a fitness component. Recent studies have demonstrated a clear interaction between social behaviour or social conditions (such as group size) and environmental factors in a regression on fitness components like survival or reproductive success (Borger et al., 2023; Guindre-Parker & Rubenstein, 2020). This suggests that animals can adjust their social behaviours to limit the harm caused by stressful environments, and the authors argue this provides evidence for adaptive social plasticity.

However, while the analyses conducted by Borger, Guindre-Parker, and colleagues shows whether particular behaviours of individuals bring benefits in certain conditions and not others, they do not explicitly test whether plasticity itself is beneficial. Distinct subsets of individuals could show different behaviours when environmental conditions are compared, which would still result in a clear statistical interaction. Instead, as proposed by Warrington et al. (2024), a more appropriate test for the adaptive value of social plasticity is to estimate the covariance between an individual's plasticity in social behaviour in response to some environment factor and a fitness component of that individual. This approach uses multivariate mixed-effect modelling techniques (Arnold et al., 2019; Houslay & Wilson, 2017), which specifically account for repeated measures of the behaviour but allow a single measure of the fitness component *and* estimate the covariance at the correct hierarchical level (the among-individual level). Such models estimate the covariances between fitness and both individual trait means and trait plasticities, testing the adaptive benefit of social behaviours overall (i.e., if being more gregarious brings fitness benefits) and the adaptive benefit of social plasticity itself (i.e., if being more flexible in connectedness brings fitness benefits). This approach has been used to show the benefits of plasticity in traits such as life-history and phenology, for instance female Ural owls *Strix uralensis* that show steeper declines in clutch size with earlier lay date have higher fitness (Brommer et al., 2012). However, this approach has not yet been used for social behaviours. We therefore have no current evidence testing the suggestion that animals have evolved to plasticly adjust their social behaviour to buffer against environmental stressors.

Here, we test the associations between a fitness component (calving success) and both mean and plasticity of individual social behaviours, in wild female bottlenose

dolphins (*Tursiops truncatus*). Bottlenose dolphins (*Tursiops* spp.) exhibit a fission-fusion grouping pattern where social interactions and relationships are critical components in their lives (Connor et al., 2000, 2019; Lusseau et al., 2006; Shane et al., 1986). Further, we have shown that dolphin gregariousness, quantified as the social network measure “strength”, increases in months of high salmon abundance (Fisher & Cheney, 2023, see also the correction: 2025), a key food source in this study population (Santos et al., 2001). This raises the question of whether this plasticity in response to salmon abundance is adaptive, i.e., does changing social behaviour enhance fitness. This would be expected if social associations influence the ability to acquire food (e.g., by cooperation or competition). Previous work has shown mean levels of social behaviour are associated with fitness components in toothed whales (Connor et al., 2022; Ellis et al., 2017; Gerber et al., 2022; Holmes et al., 2024) but the fitness benefits of plasticity itself are not quantified.

We directly tested for a possible adaptive function of social plasticity by fitting models that simultaneously estimate individual plasticity in social behaviours in response to salmon abundance and individual variance in a fitness component (calving success). Crucially, we estimate the covariance between calving success and both mean individual social behaviour (testing for benefits of mean behaviour) and plasticity in individual social behaviour in response to salmon abundance (testing for benefits of plasticity in behaviour). Since we previously looked at plasticity at both the monthly and yearly temporal scale (Fisher & Cheney, 2023), we repeat that two-scale approach to test whether responding to changes in monthly or yearly salmon abundance brings fitness benefits. Our aims are:

1. Determine if there are consequences for reproduction of changes in yearly salmon abundance.
2. Estimate plasticity in social behaviour in response to salmon abundance (as achieved by Fisher & Cheney, 2023 but with an updated dataset and with a slightly different modelling approach).
3. Estimate the association with fitness of individual variation in mean social behaviours.
4. Estimate the association with fitness of individual variation in plasticity in social behaviours.

Methods

Data collection

We used data from a long-term individual-based study of a population of over 220 bottlenose dolphins in the North Sea (Cheney et al., 2013, 2014, 2024). Boat-based photo-identification surveys have been carried out each year from May to September 1990 to 2022 within the Moray Firth Special Area of Conservation (SAC; 92/43/EEC). Upon encountering dolphins (an “encounter”), each group is carefully followed and photographs taken of both sides of as many of the dolphins’ dorsal fins as possible. Due to unique patterns of markings, scratches, and notches on each dolphin’s back and dorsal fin, individual dolphins are identified in these photographs and tracked through time. For this study, we used data from 14,614 sightings of individual dolphins across 2,368 encounters (average 70 groups per year, range 24 – 145, average group size 6.3, range 1 - 56).

Identifying individuals allows us to determine which dolphins are still alive, who is in the same group and so associating, and to identify new calves (Cheney et al., 2019). The year of birth and so age can be estimated for calves ≤ 2 years old, but ages are unknown for individuals first sighted as older calves, immature or adults. Mothers are assigned to calves based on repeat observations of the calf surfacing in echelon position next to the same adult female (Cheney et al., 2019), but paternity cannot be assigned as genetic data are not available. For more information on survey methods, see Cheney et al. (2014), while Fisher and Cheney (2023) provide information on using these survey records to construct social networks. Photographic survey work was conducted under NatureScot Animal Scientific Licence (number 93751) and all work was approved by the University of Aberdeen School of Biological Sciences ethics board (project ID SBSEC/01/2023/March).

Social trait and fitness component calculation

We defined reproductive output per year in a binary manner as whether the female was known to give birth or not (Cheney et al., 2019). Sightings records are then used

to determine whether the calf survived beyond one or two years. Calves are regularly observed with their mother in at least their first two years (Grellier et al., 2003) so repeat sightings the mother without the calf at that age is a reliable indicator of calf death rather than dispersal. We estimated a fitness component “calving success” as the number of calves produced by each female that survived more than two years divided by the number of years she lived as a reproductive individual (year last observed – year of first reproduction). For females of known ages, the start of their reproductive period was six years old (as this is the earliest known age a female has been observed with a calf in our population, with a median age of nine; Cheney et al., 2019), while for individuals of unknown age, it is from the year they were first observed with a calf.

We can measure social traits of individuals by using the repeated observations of individuals in groups to build social networks. In a social network, individuals who are observed in the same group (photographed during an encounter, within 100m, engaged in similar activities and if travelling moving in a single direction; Wells et al., 1987) are connected, while those who are never observed in the same group are not connected (the “gambit of the group”; Whitehead & Dufault, 1999). The relative frequency two individuals are seen together defines the strength of the association – precisely, the number of times two individuals were seen together in a given time period divided by the total number of times both individuals were seen, either together or alone (the “simple ratio index”), which ranges from 0 to 1 (Cairns & Schwager, 1987). We constructed a social network per month and per year, using observations of individuals of either unknown age or above three years old, i.e., excluding known calves. We used the whole network to calculate two measures of each individual’s social network position, representing two dimensions of social behaviour. However, we then excluded individuals observed fewer than three times in that month or year from any analysis, as their social network position would be based on very few observations, and we excluded entire months (i.e., all rows in that month) if there were fewer than five groups observed in that month.

For each individual in each month or year, we calculated “strength”, the sum of all an individual’s weighted connections, giving an estimate of overall gregariousness. We also calculated “closeness”, which is based on the path lengths from an individual to all others in the network, weighted by the inverse of association strengths,

representing connectedness to the entire population and has high values if an individual has strong connections linking them to all parts of the network (Opsahl et al., 2010). Both measures are therefore undirected and weighted. We use these measures as we have previously found they show some variation in individual change in response to measures of salmon abundance, which is necessary to then be linked to among-individual differences in fitness (Fisher & Cheney, 2023). Fisher & Cheney (2023) also found that dolphin social behaviour varies with salmon abundance only at the monthly scale, and therefore we expect any association between calving success and plasticity to be at this scale. We plot social networks in Fig. 1 for 2011 and 2021 as examples.

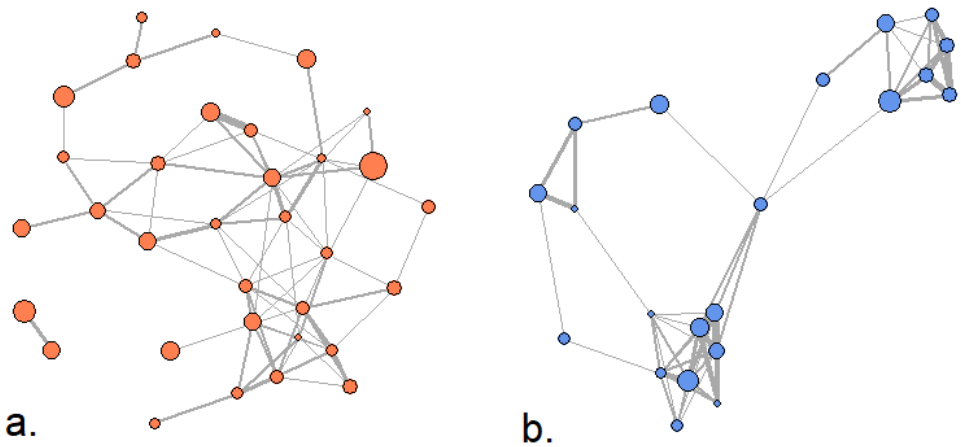

Figure 1. Plots of yearly social networks for 2011 (a.) and 2021 (b.). Points represent individual female dolphins and lines show associations between them. We have only plotted associations with a simple ratio index above 0.2 to reduce visual clutter. Line thickness is increased with stronger associations, and point size is increased if that individual had higher calving success in that year.

Salmon abundance estimate

We followed Fisher and Cheney (2023) and Lusseau *et al.* (2004) in using data on monthly catches by fishing rods (excluding nets) of Atlantic salmon (*Salmo salar*) from five rivers feeding into the Moray Firth (the Alness, Beauly, Canon, Ness, and Nairn) to quantify relative salmon abundance. These catch data are positively correlated among months and among rivers and with other data sources, suggesting

they accurately reflect abundance (Thorley et al., 2005; Youngson et al., 2002). Further, salmon abundance in the current year is positively associated with group size (Lusseau et al., 2004) and in the current month with individual dolphin gregariousness (Fisher & Cheney, 2023). We downloaded the data from https://marine.gov.scot/data/marine-scotland-salmon-and-sea-trout-catches-salmon-district-shinyapp, using “rod data”, both one sea winter and multiple sea winter adults and summing retained and released fish for a monthly index of salmon abundance. We summed monthly catches within a calendar year for an annual index of salmon abundance.

Data analysis

All models were fitted in MCMCglmm (v. 2.36) (Hadfield, 2010) in R (v. 4.4.1) (R Development Core Team & Team, 2016). To test the effect of salmon abundance on female reproduction (aim 1), we regressed the binary outcome of whether a female had a calf or not in that year on two variables: salmon abundance in the current year and salmon abundance in the previous year, as gestation in bottlenose dolphins is around 12 months and so could be affected by food availability in either calendar year. Both salmon abundances were z-transformed to a mean of zero and a standard deviation of one. In this analysis, we only included females who had been sighted a minimum of three times in that year, as we would otherwise be uncertain of their reproductive success. Note that for this and all other analyses increasing the minimum number of sightings per year decreases the number of observations and the number of unique females included: for the analysis of salmon abundance and reproductive success if we require a minimum of three encounters per individual per year we have 712 observations of 100 unique females, with four per year we have 612 observations of 94 unique females, and with five sightings per year we have 530 observations of 82 unique females. There is therefore an unavoidable trade-off between different aspects of statistical power. For this analysis the results are qualitatively the same with a threshold of three, four, or five sightings (Tables S1-3).

In our statistical models we included random effects of maternal ID and year to account for repeated observations of the same dolphins across years and for years that might have had higher or lower reproductive success on average. We also

included a binary fixed effect of whether the female had given birth in the last two years or not, as this would greatly reduce the chances of her reproducing in the current year and needs to be accounted for (Cheney et al., 2019). We used a categorical error structure, and uninformative priors with V = 1 and nu = 0.02 for both random effects and the residual variance fixed at 1 (as in a model with a binary response the residual variance is defined by the mean). We ran the model for 110,000 iterations, discarding the first 10,000 as the model would initially be far from convergence, and using 1 out of every 100 remaining iterations for the posterior distribution to minimise autocorrelation. We checked model trace plots for satisfactory convergence and tested three runs of this model with the Gelman and Rubin convergence diagnostic. All terms achieved satisfactory convergence (potential scale reduction factor [PSRF] very close to 1). We report the posterior distribution medians in the main text as they are likely the least biased (Pick et al., 2023), but include the modes and means in tables reporting full model results in the supplementary materials.

We then fitted four models to estimate mean and plasticity in social behaviour and testing for associations with calving success; aims 2-4, for all combinations of strength and closeness at monthly and yearly scales. All four models have an identical structure except that the monthly models also include a random effect of month, to account for seasonal variation in factors, aside from salmon abundance, that might influence social behaviour. For each model, we include a social network trait (either strength or closeness) and calving success as the two response variables. As before, we only included measures of social network traits where the female had been observed at least three times in a given month or year. Increasing this threshold to four or five approximately halves or quarters the dataset respectively for the monthly analyses, resulting in a dataset too small to fit our chosen models. The effect is less dramatic in the yearly analysis as relatively more females have at least four or five sightings per year, but we keep the same threshold for both temporal scales to allow comparisons of the results. We also only included females in these analyses that had been seen for at least five years as reproductive, as some individuals below that threshold had artificially high calving success due to having a surviving calf in one year and then not being seen again.

We used salmon abundance in that year or month (z-transformed) as a fixed effect for the social network trait only. We include the random effects of individual ID for both traits and year (and month for the monthly models) for the social network trait only. We include random intercepts for the social network trait and for calving success, and random slopes for the social network trait with salmon abundance. We estimate all pairwise covariances between social network trait intercepts (mean individual social behaviour), social network trait slopes (individual plasticity in social behaviour in response to salmon abundance), and individual calving success. These are estimated at the among-individual level, and so the covariance between the individual slopes and calving success specifically tests whether individual plasticity is associated with fitness (Houslay & Wilson, 2017). We used Gaussian error structures for both traits, uninformative priors with V = 1 and nu = 0.02 for the residual variance of the social network trait and the random effect of year. The residual variance for calving success was fixed at 0.0001 to aid estimation as the trait does not vary within individuals. Finally, for the variance-covariance matrix at the among-individual level, we used a parameter-expanded prior with V = 1, nu = 3, alpha.mu = 0, and alpha.V = 625 following Houslay and Wilson (2017). We checked the trace plots for all four models for satisfactory convergence and tested three runs of each model with the Gelman and Rubin convergence diagnostic. Terms in all models achieved satisfactory convergence (PSRF < 1.005), apart from the random effect of month in the model for monthly closeness (PSRF = 1.204) and to a lesser extent the same random effect in the model for monthly strength (PSRF = 1.055). Since these are control terms and not of specific interest we do not believe this is problematic.

Results

To test the effect of salmon abundance on yearly calf production and survival, we had 712 observations of known reproductive status across 100 different females. Salmon abundance in both current (posterior distribution median [PDM] = -0.218, 95% credible intervals [CIs] = -0.647 to 0.206) and previous years (PDM = -0.137, 95% CIs = -0.579 to 0.291) did not influence reproductive success. Having a calf in

the previous two years reduced the chance of a female producing a calf (PDM = -1.977, 95% CIs = -2.597 to -1.369; full model results in Table S1).

To test for the fitness associations between mean and plasticity in social behaviour at the monthly scale, we had 736 measures of social behaviour across 63 different females. For the yearly scale analysis, we had 602 measures of social behaviour across 66 different females.

At the monthly level, there were no covariances between calving success and plasticity in strength or closeness (Table 1). There were also no covariances between intercepts of strength or closeness and calving success (Figs. 2a & b & Table 1). There were no intercept-slope covariances for either trait (Table 1). Full model results are given in Tables S4 & 5.

Table 1. Estimates of the covariance parameters for the models with strength and closeness. In each cell are the posterior distribution median (and the 95% credible intervals in parentheses) for the covariance between the two terms shown. Above the diagonal (filled with Xs) are values for the monthly analyses, while below the diagonal are values for the yearly analyses. Covariances that do not overlap with zero are shown in bold.

	Strength		
	Individual intercepts	Individual slopes	Calving success
Individual intercepts	X	-0.250 (-0.964 to 0.123)	0.053 (-0.000 to 0.116)
Individual slopes	-0.034 (-0.289 to 0.138)	X	-0.015 (-0.048 to 0.008)
Calving success	**0.046 (0.005 to 0.091)**	0.000 (-0.015 to 0.017)	X
	Closeness		
Individual intercepts	X	-0.000 (-0.001 to 0.000)	0.001 (-0.001 to 0.003)
Individual slopes	-0.000 (-0.002 to 0.000)	X	-0.000 (-0.002 to 0.001)
Calving success	**0.003 (0.001 to 0.006)**	-0.000 (-0.002 to 0.001)	X

Figure 2. Plots of the relationship between monthly (a. & b.) and yearly (c. & d.) means of social network traits (a. & c show strength, b. & d. show closeness) and calving success. Each point represents an individual females' mean social network trait for a given month or year against that individual's calving success (one measure per individual). For both traits at the yearly level (c. and d.), there was a clear positive covariance, and so we show a trend line as a solid coloured line with the standard errors shown in grey (both calculated using the "stat_smooth" function in ggplot2; Wickham, 2009).

At the yearly level, there were no covariances between plasticity in strength and closeness (Table 2) and calving success. There were weak positive covariances between calving success and intercepts of both strength (Fig. 2c & Table 2, correlation median = 0.333, 95% CRIs = 0.106 to 0.548) and closeness (Fig. 2d & Table 2, correlation median = 0.345, 95% CRIs = 0.117 to 0.538). There were no intercept-slope covariances for either trait (Table 2). Full model results are given in Tables S6 & 7.

Discussion

We found that salmon abundance was not associated with female reproductive success (aim 1). We estimated both individual means and plasticities of social behaviour (aim 2) and demonstrated that there are positive covariances between individual means in strength and closeness and calving success, but only at the yearly timescale (aim 3). We found no evidence that social plasticity might be adaptive as there were no covariances between plasticity in strength or closeness in response to salmon abundance and calving success (aim 4).

Female dolphins who had high strength and closeness over an entire year had higher calving success. Positive associations between mean social behaviour and fitness components, such as longevity, has been reported multiple times in terrestrial mammals, such as rhesus macaques *Macaca mulatta* (Ellis et al., 2019), big horn sheep *Ovis canadensis* (Wal et al., 2015) and spotted hyenas *Crocuta crocuta* (Yoshida et al., 2016). Further, in a closely studied population of Indo-Pacific bottlenose dolphins *T. aduncus* (Allen et al., 2016), Stanton and Mann (2012) found that young males with higher eigenvector centrality (a social network measure of connectedness accounting for the connections possessed by one's social associates) had better survival from weaning to 10 years of age. More recent research on the same population showed that adult males with strong bonds and who are well integrated in their cooperative alliance sire more offspring (Gerber et al., 2022). However, females in Stanton and Mann's (2012) study, which is the sex we studied here, showed a non-significant negative relationship between eigenvector centrality and survival (although not directly tested for a difference from zero, it seems likely the relationship in females is at least not positive). Given that we studied different fitness components and a different species with a different ecology to Stanton and Mann, whether our results are truly in contrast is questionable. Clearly, further comparative work on associations between fitness components and social behaviour in both sexes and multiple populations of *Tursiops* spp. is warranted. Such work should take temporal scale into account, as we did not find a clear relationship between social network traits and calving success at the monthly scale. While we might expect the same animals to have high trait values in both the yearly and monthly analysis, the additional month-to-month variation in the monthly analysis may have made detecting the covariance more difficult. Additionally, the two

analyses had marginally different sets of females, which could have led to the slightly different results

In general, fitness benefits of sociality are thought to arise due to detection of and protection from predators, opportunities to share information, and the ability to complete tasks more efficiently compared to when alone (Rubenstein & Abbot, 2017). In this bottlenose dolphin population, social grouping is unlikely to function as protection from predators, as their natural predators are absent from these waters (Cheney et al., 2019). Additionally, while the dolphins in the Moray Firth SAC tend to be observed in groups (median size approximately 6-10 individuals; Cheney et al., 2024), they are generally observed hunting individually (B. Cheney, pers obs.), suggesting increased hunting efficiency may not be the key benefit. Instead, a possibility is that high gregariousness and being connected to all subgroups in the population may help adult female dolphins find food patches or maintain a larger number of female associates with whom to share calf care responsibilities, reducing the risk of infanticide by males and/or allowing mothers to spend more time foraging to provide energy for lactation (Methion et al., 2023). In the Indo-Pacific bottlenose dolphin, females tend to associate with conspecifics sharing similar reproductive state (Möller & Harcourt, 2008), and a female's reproductive success tends to be higher if she has successful female relatives or associates with other successful females (Frère et al., 2010). However, it is possible that the causality of the relationship between gregariousness and calving success could be in the opposite direction; regular presence of calves may make a female dolphin socially attractive (such an association in fact drove a spurious association between maternal social behaviour and offspring survival in Amboseli baboons Papio spp.; Creighton et al., 2025). Further, this relationship could be observed if female dolphins in poorer condition or those with adverse early life effects are less likely to have calves and spend more time alone hunting (Thompson, 2019). Since we analysed an association between repeated measures of social network traits and a single measure of reproductive success, confounding factors must act on a similar temporal scale. Fine scale data, such as those analysed by Creighton *et al*. (2025), and appropriate randomisations or experimental approaches, may be necessary to confirm causal relationships.

We did not detect any fitness benefits to plasticity. Female dolphins do not appear to adjust their social behaviour to buffer low salmon abundance or take advantage of high salmon abundance. This observational dataset has inherent limitations, for example, not all females are observed every year, not all calves are identified, and some calves may die before they are observed. These limitations add noise to the dataset and so prevent us detecting genuine relationships between fitness components and other traits. Also, as we did not manipulate social behaviour, we cannot be certain of the causal link to calving success. Nevertheless, given we show that salmon abundance is not related to calf production, it is perhaps not surprising that changes in social behaviour are not required to “buffer” low salmon numbers. This could indicate that the benefits of social behaviour identified here are not related to more effective salmon location and predation. Dolphins may switch to other prey when salmon are scarce, such as whiting *Merlangius merlangus*, saithe *Pollachius virens*, and cod *Gadus morhua* (Santos et al., 2001), instead of changing their social behaviour. Estimating the resource requirements of the population should be a priority in the face of a changing climate. Meanwhile, social behaviour, which shows considerable within-individual variation, may instead change in response to reproductive opportunities, to shifts in local currents and fronts, or other environmental factors such as anthropogenic disturbance, and the adaptive value of plasticity might show itself in any of these contexts.

Our study is the first to estimate the covariance between plasticity in social behaviour and a fitness component, but two previous studies on birds have tested whether different social behaviours yield fitness benefits in different conditions. In superb starlings *Lamprotornis superbus*, males have higher survival in larger groups only in wet years but the reverse is true in dry years (Guindre-Parker & Rubenstein, 2020). Interestingly, in females, larger groups are always associated with better survival, matching our result (although we looked at reproduction rather than survival). Meanwhile, in Seychelles warblers *Acrocephalus sechellensis*, low rainfall is associated with lower rates of reproduction but, in years of little rain, alloparenting was *less* common, in opposition to predictions that social behaviours help buffer harsh conditions (Borger et al., 2023). Therefore, while there is a range of evidence to show that social behaviour plastically varies with environmental conditions (Fisher

et al., 2021), there is currently no evidence that this plasticity buffers harsh environmental conditions.

In general, there is variable evidence for selection on plasticity. For example, Pelletier *et al*. (2007) found selection on seasonal plasticity in female bighorn sheep ewes, with more plastic individuals having higher reproduction. Meanwhile, female red deer *Cervus elaphus* that give birth early after dry autumns and late after wet autumns may have higher fitness, but this trend was marginally non-significant ($p = 0.06$) and only applied if those females were born in a high density period (Nussey et al., 2005). Meanwhile, female Ural owls show selection on quadratic reaction norms between laying date and clutch size, but no selection on the linear reaction norms (Brommer et al., 2012), which is what we evaluated here. These studies give an idea of the diversity of findings but we are not aware of any meta-analyses collecting selection estimates on plasticity in animals. Arnold et al. (2019) reviewed evidence for selection on thermal plasticity in plants and found it to be lacking, while Davidson et al. (2011) found that invasive plants were more plastic than non-invasive plants, but that this plasticity did not confer especial fitness benefits. Therefore, while we have spent much of the 21st century wondering what the costs of plasticity are (Pigliucci, 2005), the benefits might not be as empirically well-supported as expected.

Future studies on the benefits of social plasticity in bottlenose dolphins could focus on “developmental plasticity” – the ability of a genotype to produce different phenotypes over the course of development, which cannot be reversed (Taborsky, 2017). This is in contrast to “reversible plasticity”, where an adult individual changes its phenotype and can reverse the changes back (measured here). For example, stress exposure in juvenile rats *Rattus norvegicus* reduces sociality in later life (Toth et al., 2008). Evidence that developmental plasticity in social behaviour is adaptive, however, is inconclusive, with seemingly maladaptive changes often observed (Spencer, 2017). In Indo-Pacific bottlenose dolphins, juveniles can show considerable variation in social behaviour (Gibson & Mann, 2008), which persists into adulthood (Evans et al., 2021), and has fitness consequences (Gerber et al., 2022; Holmes et al., 2024; Stanton & Mann, 2012). Further work should therefore identify what factors drive early variation in social behaviour and the adaptive consequences of early-life effects.

Acknowledgements

We are forever grateful to Paul Thompson for conception and development of this long-term individual-based research study, and for commenting on this manuscript. We are especially thankful for our colleagues at the Lighthouse Field Station, past and present, who have contributed to and advanced this long-term study. Simon Allen and three anonymous reviewers made numerous useful comments and suggestions on an earlier draft. The contribution of numerous funders has been key for this long-term study, including University of Aberdeen, NatureScot, Beatrice Offshore Windfarm Ltd., Moray Offshore Renewables Ltd., Marine Scotland, the Crown Estate, Highlands and Islands Enterprise, the BES, ASAB, Greenpeace Environmental Trust, Whale and Dolphin Conservation, Talisman Energy (UK) Ltd., Department of Energy and Climate Change, Chevron and Natural Environment Research. Survey work was conducted under NatureScot Animal Scientific Licences.

Authors' contributions

BJC collects data on this long-term project and curates the database. DNF conceived the idea of this particular manuscript and conducted preliminary analyses. DNF and BJC discussed the ideas and the analysis before DNF finalised the analysis and wrote a draft. BJC edited the draft and together the authors revised the final version.

Conflict of interest declaration

We declare we have no competing interests.

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