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Individual flexibility in group foraging behaviour of reef manta rays (*Mobula alfredi*)

Annie Murray^{1,2,4} · Raphaël Royauté³ · Guy M. W. Stevens^{1,2,4} · Callum Roberts^{1,5} · Kathryn E. Arnold¹

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Abstract

Flexibility in animal foraging strategies can increase overall feeding efficiency for individuals. For example, group foraging can increase the efficiency of resource exploitation; conversely solo foraging can reduce intraspecific competition, particularly at low resource densities. The cost–benefit trade-off of such flexibility is likely to differ within and among individuals. Reef manta rays (*Mobula alfredi*) are large filter-feeding elasmobranchs that often aggregate to feed on ephemeral upwellings of zooplankton. Over three years in the Maldives, we free-dived to film 3106 foraging events involving 343 individually identifiable *M. alfredi*. Individuals fed either solo or in groups with a clear leader plus between one and eight followers. *M. alfredi* were significantly more likely to forage in groups than solo at high just prior to high tide and when aggregations were larger. Within aggregations, individuals foraged in larger groups when more food was available, and when the overall aggregations were relatively large suggesting that foraging in large groups was more beneficial when food is abundant, and the costs of intraspecific competition were outweighed by the efficiency resulting from group foraging strategies. Females, the larger sex, were more likely to lead foraging groups than males. The high within-individual variance (over 70%), suggested individuals were unpredictable across all foraging behaviours, thus individual *M. alfredi* cannot be classified into foraging types or specialists. Instead, each individual was capable of considerable behavioural flexibility, as predicted for a species reliant on spatially and temporally ephemeral resources.

Significance statement

Reef manta rays (*Mobula alfredi*), listed as “Vulnerable” on the IUCN Red List, are at risk from targeted and by-catch fisheries due to their slow life history and aggregative behaviour. *M. alfredi* feed together in aggregations on short-lived glut of microscopic zooplankton. Over three years in the Maldives, we filmed 3106 foraging events involving 343 individually identifiable *M. alfredi*. Manta rays were more likely to forage in groups than solo just prior to high tide and when aggregations were larger, attracted by the influx of zooplankton. Foraging groups included more individuals when plankton was more abundant. However, individuals flipped between solo and group foraging and did not specialise. Foraging groups were most often led by females, the larger sex. Individuals were very flexible in how they foraged, which makes sense for a species that relies on a food source that varies enormously in when, where and for how long it is available. Understanding manta ray foraging behaviour will help conservation management efforts and predict their responses to climate change.

Keywords Foraging specialists · Repeatability · Personality · Leaders · Plankton feeding

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Introduction

Within spatially and temporally dynamic environments, animals need to adjust their foraging strategies to increase feeding efficiency and reduce metabolic costs. Group living provides specific benefits by increasing foraging and movement efficiency, social information exchange and learning (e.g. regarding resource patches), and providing cooperative predator defence and reducing predator risk (Danchin et al. 2004; Kutsukake 2009; Marras et al. 2015; Meunier 2015; Ioannou et al. 2019). However, the costs of intraspecific competition in foraging can lead to groups splitting (Svanback and Bolnick 2007). These costs of group living include increased detection by predators and higher competition for resources, which is often more intense in larger groups, with individuals paying the consequences for reduced food intake (reviewed in Krause and Ruxton 2002; see also Fortin and Fortin 2009; Ioannou et al. 2019). This cost–benefit trade-off may differ dynamically within and among individuals reflecting energetic needs, relative position within feeding hierarchies, intraspecific competition, and food availability (Morrell and Romey 2008; Fortin and Fortin 2009; Marras et al. 2015; Seebacher and Krause 2017). For example, in three-spined sticklebacks (*Gasterosteus aculeatus*) bold individuals risked increased predation at the front of groups but benefited from increased growth rates (Ward et al. 2004; but see Jolles et al. 2017). Thus, foraging group membership can be fluid, with multiple options open to individuals, including whether to leave or stay in the group.

Amongst various species (including many marine animals), group structure is not necessarily fixed, i.e., it changes spatially and/or temporally. Individuals move within and between groups, leading to groups splitting (fission) and/or merging (fusion) (Aureli et al. 2008; Couzin and Laidre 2009; Lewis et al. 2011; Tsai and Mann 2013). Environmental factors (including resource abundance) can influence fission–fusion of groups; increasing or decreasing competition (Couzin and Laidre 2009; Silk et al. 2014). Thus, an individual's role (e.g., leader or follower) or position (e.g., at the edge or in the middle) within a group can alternate with the changing social, biotic and abiotic conditions (Lendvai et al. 2006; Fischhoff et al. 2007; Bonanni et al. 2010; David et al. 2011; Nakayama et al. 2013; but see (Georgopoulou et al. 2022)). Understanding how individuals assort within social foraging groups is vital because it gives a clearer understanding of the structuring within groups and the specific roles adopted by certain individuals or demographics (reviewed in Aureli et al. 2008).

Increasingly, studies are examining what influences the role or position that individuals adopt within a social

group, including knowledge, state dependence (nutritional or status), age (knowledge), or sex (body size) (Sueur 2011; Lee and Teichroeb 2016). State dependent leadership can indicate that the leadership role is not necessarily fixed, but will vary depending on the state of individuals. The ‘leading according to need’ theory proposes that food-deprived animals, or those with the highest nutritional needs, will adopt the front position and guide the direction of collective foraging to reap the benefits of leadership, including an increased net resource intake and potentially a better-quality diet (e.g., King and Cowlshaw 2009; Sueur 2011; Lee and Teichroeb 2016). Using dynamic modelling, Rands et al. (2008) found that individuals can predominantly act as a leader despite lacking specific leadership traits, including dominance or social abilities (King and Cowlshaw 2009). As such, hunger levels as opposed to dominance were shown to play a key role in determining which animal leads; the hungrier of the two becomes the decision-maker (Rands et al. 2008). These findings support the theory that leading and following may be state-dependent behaviours (Rands et al. 2003; Ward and Webster 2016). Thus, fringe positions might be adopted by hungrier individuals who travel further and faster, leaving the less hunger-driven and more cohesive group members positioned more safely, inside the group (Krause and Ruxton 2002; Ward and Webster 2016).

A non-exclusive alternative is that within-group biotic factors, such as sex, age, body size, aggressiveness and strength may influence leadership behaviour amongst individuals, although this will differ between species (Webster and Hixon 2000; Chase et al. 2002; Jolles et al. 2017). In groups of cleaning gobies (*Elacatinus prochilos*) in Barbados, the more dominant individuals, which were also larger, controlled optimal foraging areas with the highest food abundance, resulting in increased foraging success (Whiteman and Côté 2004). Age can be a proxy for other traits that determine leadership status such as dominance (e.g., Jacob et al. 2007), and also knowledge and experience (Frankish et al. 2020). Amongst killer whales (*Orcinus orca*), post-reproductively aged females led foraging in years of low food availability, which suggests a benefit of prior ecological knowledge which is key to reproductive success and survival (Brent et al. 2015). So, leadership status can be variable, but traits such as sex and age might be key in predicting which individuals become leaders (Ward and Webster 2016).

Many ecological studies treat conspecific individuals within groups as interchangeable, after accounting for biotic factors such as age, sex, and other group effects (Bolnick et al. 2003; Yamamoto et al. 2014; Wakefield et al. 2015). However, there is increasing evidence that individuals in many animal populations differ substantially in foraging behaviour (Araújo et al. 2011; Patrick and Weimerskirch

2014; Carneiro et al. 2017). Behavioural variation within populations can reduce the extent of intraspecific competition, as well as increasing individual foraging efficiency (Ceia and Ramos 2015; Carneiro et al. 2017). High repeatability of a behaviour (relatively low within-individual variance compared to high among-individual variance) is indicative of a personality trait or a foraging specialism (although a general consensus on repeatability or consistency is yet to be agreed (Cleasby et al. 2015)). Typically, the repeatability of behaviour is ~40–50% (Bell et al. 2009) which leaves much of the variation in behaviour explained by within-individual behavioural variance i.e. ‘behavioural plasticity’ or ‘flexibility’ (Alonzo 2015). The partitioning of variance in foraging strategies (flexible vs. consistent or repeatable) may be reflected in an individual's foraging preferences and behaviours, for example group vs. solo or the position they uphold within the group, for example leader or follower (Georgopoulou et al. 2022). Flexibility of strategies enables individuals to react differently, reducing pressure on a specific resource or habitat and altering a population's ability to cope with change (Masello et al. 2013; Maskrey et al. 2020). Fundamental is the realisation that residual within-individual variance in behaviour, which has previously been labelled ‘random’, in fact might indicate more adaptive phenotypic behaviour, which therefore should not be ignored (Westneat et al. 2015). A clearer understanding of individual flexibility enables us to better appreciate the ecological implications of changing environmental conditions, increased anthropogenic pressure and potentially how best to implement marine conservation measures to mitigate pressure on species (e.g., Belgrad and Griffen 2018; Maskrey et al. 2021).

Reef manta rays (*Mobula alfredi*) are slow-growing, large-bodied elasmobranchs. Manta rays are vulnerable to targeted and by-catch fisheries due to their ‘slow’ life history strategies, i.e. large body size, late maturity, low fecundity etc., and aggregating behaviour (Croll et al. 2016; Marshall et al. 2019). Consequently, *M. alfredi* is listed as “Vulnerable” to extinction on the IUCN Red List of Threatened Species (Marshall et al. 2019). Across global populations, manta rays are also impacted by natural predation, with individuals observed with tissue loss due to shark attacks (Marshall and Bennett 2010; McGregor et al. 2019), as well as anthropogenic threats, such as boat strikes and entanglement in fishing lines (O'Malley et al. 2013; Stewart et al. 2018; Strike et al. 2022). *M. alfredi* individuals are commonly observed associating in aggregations of varying sizes (Stevens 2016). The term “aggregation” in elasmobranch research is defined as ‘the co-occurrence of two or more individuals in space and time due to the deliberate use of a common driver’ (McInturf et al. 2023). In our study, the aggregations were driven by the need to forage on short lived food patches, but Mobulid aggregations often involve interactive behaviours

amongst individuals, including courtship displays and mating, or perhaps more complex, dynamic associative relationships (Guttridge et al. 2009; Jacoby et al. 2012; Mourier et al. 2012; Perryman et al. 2022; Sims et al. 2022; Palacios et al. 2023). There is evidence that *M. alfredi* in Raja Ampat, West Papua, showed social preferences within aggregations, with a study identifying some short-term non-random affiliations among mainly females, when accounting for a range of non-social potential sources of variation (Perryman et al. 2019). A further study of the same population using tracking devices suggested that some individuals showed differentiated relationships linked to strong spatial fidelity to certain sites (Perryman et al. 2022). The overall network structure of *M. alfredi* in that region seemed to be characteristic of a dynamic fission–fusion society (Aureli et al. 2008; Perryman et al. 2019), as has been suggested by other studies of this species' aggregations (Stevens 2016).

In our study, we investigated the pattern of individual variation in group foraging behaviour, and how this variation was affected by abiotic and biotic factors, within a wild population of *M. alfredi* in Baa Atoll in the Maldives. Overall, we test whether biotic factors (plankton density and number of manta rays in aggregation) or abiotic factors (site, time to high tide, current strength, year) or individual state (sex, age class and injury (shark bite or anthropogenic)) influenced different aspects of foraging behaviour. We addressed four specific questions; (1) What are the effects of abiotic and biotic factors on group and solo foraging behaviour? (2) What are the effects of abiotic and biotic factors on group size? (3) What are the effects of individual state on the probability to lead the group? (4) How much of the variation in group size and leadership behaviour was explained by among-individual, and within-individual differences? (5) How does within and among-individual variation differ depending on individual state (e.g. sex, maturity and injury)?

Methods

The Maldives Archipelago is home to the world's largest recorded population of *M. alfredi*, with over 5,200 identified individuals (Manta Trust 2023). This study was conducted on the sub-population of *M. alfredi* in eastern Baa Atoll (5.1569° N, 73.1335° E). Located 114 km northwest from Malé City, Baa Atoll was designated a UNESCO World Biosphere Reserve in 2011, in part due to the large number of *M. alfredi* which seasonally occur within the Atoll.

Manta ray feeding behaviour is distinctive and easily identified by researchers. Animals could be seen to be actively foraging with their cephalic fins unfurled in order to increase efficiency, opening their mouths to swallow

zooplankton rich water, then closing their mouths and gills to squeeze water out whilst filtering their zooplankton prey out (Stevens et al. 2018). We collected data on manta ray feeding behaviour at different times of day as part of the Manta Trust's Maldives Manta Conservation Programme (<https://www.mantatrust.org/maldives>) during the Southwest Monsoon (May through November) when the highest numbers of mantas are present. Data collection lasted for 160 days in 2014, 156 days in 2015, and 155 days in 2016. We identified five sites on the eastern side of Baa Atoll that served as the main monitoring spots: Dhigu Thila, Hanifaru Bay, Hurai Faru, Reethi Falhu and Veyofushi Falhu. Due to the restriction on SCUBA diving at the main study site, Hanifaru Bay, all foraging data was collected by free-diving. When we spotted foraging events, we free-dived beneath the animals to video their behaviour and record the unique identification spots on the ventral surface (Marshall and Pierce 2012), taking care not to impede or alter this behaviour. If, on entering the water, we observed more than one *M. alfredi* in the immediate vicinity, we dived in order to be in position before the first animal in the group swam overhead. If the animal was feeding, we filmed continuously until feeding stopped, until the last member of the group passed from sight, or we ran out of breath. We terminated filming once reaching the surface, and a clear view of the ventral markings was lost. Clips lasted between 30 and 180 s and were collected between depths of five and 16 m. As feeding events could last up to a few hours, video clips of individual feeding groups were recorded on a consecutive basis as they arose until the feeding event finished or until the weather or daylight deteriorated. We filmed using a GoPro Hero 3, or a Canon PowerShot S110 compact camera. It was not possible to record data blind because our study involved focal animals in the field.

The total number of *M. alfredi* was estimated visually in the field and confirmed by verifying identification photos. The number of *M. alfredi* references the total number of manta rays observed throughout the whole survey window, for example the total number of manta rays observed from the start to finish of the two-hour survey. Group size represents the number of manta rays in an individual feeding group, for example five manta rays feeding within two body lengths of each other. A description of type and visual estimation of plankton density was conducted at each site using a scale from zero to two representing low, medium, and high density (see Table S1 in Supplementary Information). Current strength was gauged using a scale from “no current” (0) to “strong” (3): (no current (0) – researcher able to hold position without finning; weak (1) – researcher able to hold position with little effort; medium (2) – researcher able to hold position with strong finning; Strong (3) – researcher unable to hold

position (Manta Trust, unpublished data). Time to high tide is defined as the number of minutes centred around high tide, either before (-) or after (+) high tide. Time to high tide was included as a test variable due to increased manta ray detection just after high tide (Harris and Stevens 2021).

Video Analysis

We only included *M. alfredi* that could be individually identified in analysis. Individuals were identified, aged and sexed by examining the unique spot-pattern on the ventral surface and matching this pattern with the categorised photographs in the regional database (Stevens 2016). Size estimation and visual maturity indicators are used to age manta rays (Marshall and Bennett 2010; Stevens 2016) (see Supplementary Information for details on ageing and sizing methods). Any injuries were also recorded (Fig. S1 in ESM) and noted as either ‘natural’ e.g. shark bites, or ‘anthropogenic’ e.g. made by fishing line. Unsexed individuals were excluded from analysis.

Only individuals observed actively feeding were included in analyses. Dataset includes manta rays exhibiting all eight of the foraging strategies described by Stevens et al. (2018); straight, surface, chain, piggyback, somersault, cyclone, sideways and bottom feeding. The most commonly observed strategies were somersault, straight and chain feeding (Stevens et al. 2018, see Fig. 1 and Fig. S1 in Supplementary Information). Foraging type was recorded as either ‘solo’ or ‘group’. We defined group feeding as two or more animals recorded feeding together within two body lengths (Mizumoto et al. 2019). We defined the leader as the individual *M. alfredi* positioned at the front of any group with individuals following directly behind them. Only one individual could lead a group at any one time. Each clip did not necessarily focus on a single group. Where it did, if the leadership changed then this was noted. We also recorded all manta rays solo foraging, i.e., more than two body lengths away from another individual. Whole clips were analysed which often contained multiple examples of foraging groups and singletons. We measured the number of *M. alfredi* in the aggregation as the total number of individuals observed across a full survey, while group size referenced the number of individuals involved in an individual feeding group, for example those *M. alfredi* observed feeding in an individual chain.

Statistical Analysis

We conducted analysis using R 4.3.2 Statistics Package (R Core Team 2024), aiming to answer these specific study questions. Full models are outlined in Table 1.

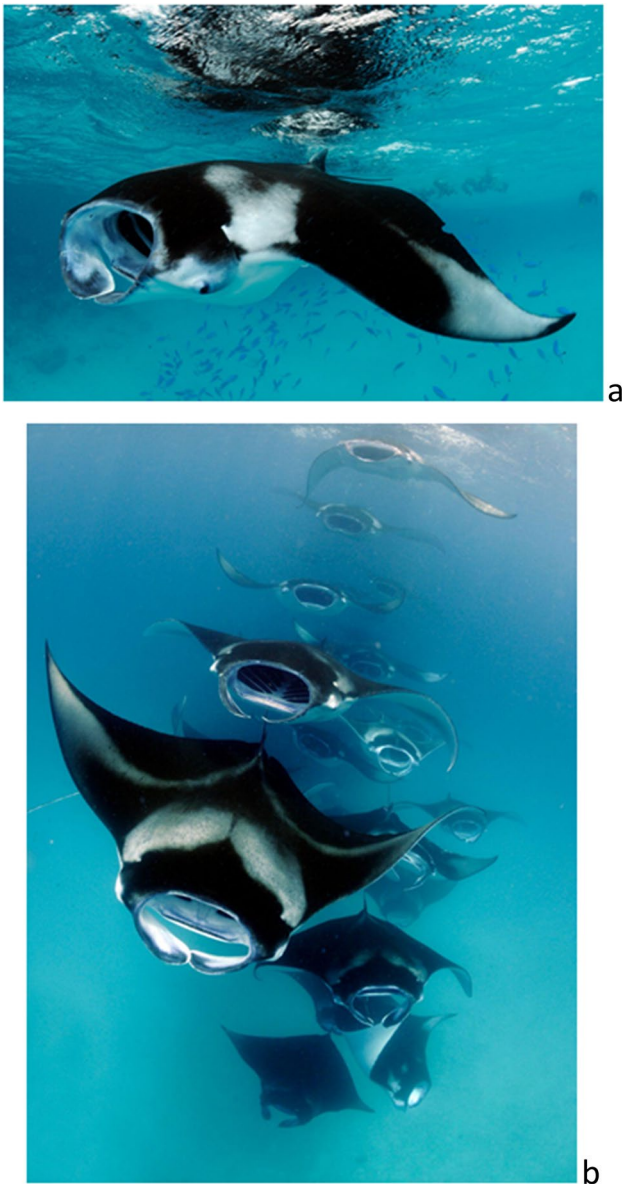


Fig. 1 a) Manta ray solo feeding at the surface at Hanifaru Bay; b) Manta rays chain feeding at Hanifaru bay. More than one chain is visible in the photo. © Guy Stevens | Manta Trust

What are the effects of abiotic and biotic factors on group and solo foraging behaviour?

We ran candidate generalised linear mixed models (GLMMs) with grouping behaviour as the response variable (whether the manta ray was observed foraging in a group, defined as within two body lengths of another manta ray or solo) against all abiotic and biotic fixed effects (Table 1), using a Binomial error distribution. Within the study population, individual manta rays differed in their re-sighting rates across the full study period. To account for this variation, individual animal identity was used as the random effect

throughout the analysis. Due to problems with convergence, the factor “site” was included as a random rather than fixed effect. We applied the Akaike Information Criterion (AIC) function to find the model of best fit and ΔAIC tested the degree of model(s) best fit. We considered the model with the lowest AIC value the best model and models with $\Delta\text{AIC} > 2$ a significantly poorer fit. We considered models with $\Delta\text{AIC} < 2$ as having equivalent support compared to the best model (Burnham and Anderson 2004).

What are the effects of abiotic and biotic factors on group size? What are the effects of individual state on the probability to lead the group?

Variables tested for each behaviour trait (group size, and leadership) differed due to the intrinsic nature of the behaviour. Candidate models tested the effect of abiotic and biotic factors by fitting GLMMs in the package lme4 (Bates et al. 2015), for each behavioural trait, group size (Table 1a), and leadership (Table 1b) as predictor variable and individual animal identification as a random effect. We applied the AIC function to find the model of best fit and ΔAIC tested the degree of model(s) best fit for each behavioural trait. For this study, biotic factors were plankton density or the number of manta rays in aggregation. The ordinal variable “number of mantas”, defined as the total number of mantas observed feeding in an aggregation at a given site on a given day, was scaled for control in analysis. ‘Individual state’ referred to sex or age class. Due to problems with convergence, the factor “site” was included as a random rather than fixed effect in the group size model.

How much of the variation in group foraging, group size and leadership behaviour was explained by among-individual, fixed effects and within-individual differences?

For each behaviour, we calculated ratios of variation explained by fixed effects (V_{fe}), individual identity (V_i) and residuals (V_R , i.e. the within-individual variance) using the rptR package (Nakagawa and Schielzeth 2010; Stoffel et al. 2017). We estimated the residual variance on the latent (link) scale given that the considered behaviours do not follow Gaussian distributions. We included all fixed effects considered in the models and used Binomial and Poisson error distributions depending on the behaviour considered (Binomial: group vs. solo foraging and group leadership, Poisson: group size).

We tested for the significance of the among-individual random effect using a permutation test ($n_{\text{permutations}} = 1000$) i. Next, we calculated the proportion of variance explained by each variance component relative to the total variation: $R^2_i = V_i / (V_i + V_{fe} + V_R)$; $R^2_{fe} = V_{fe} / (V_i + V_{fe} + V_R)$ as well as the conditional R^2 , $R^2_{\text{cond}} = (V_i + V_{fe}) / (V_i + V_{fe} + V_R)$ (Schielzeth and Nakagawa 2013).

Table 1 Models tested to explain a) Group versus solo foraging, b) group size, c) leadership (not including interactions). Variables tested for each behaviour trait differed due to the intrinsic nature of the behaviour. The number of *M. alfredi* is defined as the number of individuals observed in the aggregation across the whole survey. Group size is defined as the number of individuals observed per foraging group

Models	Variables tested
a) Solo versus group foraging	-
Null	
Abiotic	Site, current, time to high tide
Biotic	Plankton, number of mantas (scaled)
Abiotic + Biotic	Site (random factor), current, time to high tide, plankton, number of mantas (scaled)
b) Group Size	-
Null	
Abiotic	Site (random factor), current, time to high tide
Biotic	Plankton, number of mantas (scaled)
Abiotic + Biotic	Site, current, time to high tide, plankton, number of mantas (scaled)
c) Group leadership	Sex, age class
Null	
Individual state	
Individual state + injury	Sex, age class, shark bite, anthropogenic injury
Injury	Shark bite, anthropogenic injury

How does within and among-individual variation differ depending on individual state factors?

To estimate how the influence of an individual's state (sex, maturity) and injury state affected the expression of variation in group leadership, we compared the distribution of the among-, within- and fixed effect variance between each group considered. To do so we estimated mixed effect models for each subset of the data with rptR and computed the difference between bootstrap values for each variance component and ratios (ΔV , ΔR^2), similarly to Royauté and Dochtermann (2021). From that distribution, we calculated 95% confidence intervals to assess the precision of the estimate. We also report the probability of effect direction (pd) corresponding to the proportion of estimates of the same sign as the median using the bayestestR package (Makowski et al. 2019a). Values of pd close to 1 indicate a higher plausibility of a difference between two variance components, with pd > 0.975 being equivalent to a statistically significant difference at $\alpha = 0.05$ for a two-tailed test (Makowski et al. 2019b).

Results

A total of 854 observations were made in 2014, 1,075 in 2015, and 1,177 in 2016. In 2014, 185 individuals, 196 individuals in 2015, and 209 individuals in 2016 were included in the study database. Individuals had a median of 37.5 observations across all study years. In 2014, 119 females and 66 males were recorded, 132 females and 64 males in 2015, and 133 females and 76 males in 2016. Based on the photo ID database, the sex ratio of the whole

population in the area was approximately 50/50 (Stevens 2016). A total of 114 juveniles and 71 adults were recorded in 2014, 101 juveniles and 95 adults in 2015, and 80 juveniles and 129 adults in 2016.

What are the effects of abiotic and biotic factors on group and solo foraging behaviour?

Mixed models highlighted the significance of abiotic and biotic factors in determining group foraging behaviour amongst *M. alfredi* (see Table S3 in Supplementary Information for AIC comparisons). In the final GLMM investigating group vs. solo foraging, *M. alfredi* were more likely to forage in groups in 2015 and 2016 compared with 2014 (Table 2a; Fig. 2a). Current strength (no current, weak, medium, strong) was not statistically significant but remained in the final model. *M. alfredi* were significantly more likely to feed in groups in the three hours prior to high tide than after high tide (Table 2a; Fig. 2a). Plankton density did not predict group or solo foraging. Group foraging was more likely than solo foraging when the numbers of mantas in the aggregations were larger (Table 2; Fig. 2a).

What are the effects of abiotic and biotic factors on group size?

In group size analysis, smaller group sizes were recorded in 2015 than 2014 Table 2b; see AIC and deltaAIC values in Table S3). Groups were smallest when plankton density was medium compared with low (Table 2; Fig. 3b). The largest group sizes were recorded three hours before high tide,

Table 2 Model coefficients for Generalized Linear Mixed Models of environmental covariates influence on group foraging (a), group size (b) and group leadership (c). Group foraging and group leadership were fitted with Binomial error and Poisson error for group size. P-values for each fixed effect term were calculated using type III sums of squares. For random effects (site and/or ID), R^2 and P-values were calculated using 1000 bootstraps and permutation tests respectively. Significant P-values are bolded

Trait	Term	N	Estimate	95% CI	P	R^2
a) Group vs. solo foraging						
Fixed effects						0.03
	(Intercept)	3,010	-0.53	-1.1, 0.05	0.073	
	Year				< 0.001	
	2014	758	—	—		
	2015	1,075	0.60	0.26, 0.94	< 0.001	
	2016	1,177	0.60	0.27, 0.93	< 0.001	
	Current	3,010	0.19	-0.01, 0.38	0.058	
	Time to high tide	3,010	-0.24	-0.35, -0.12	< 0.001	
	Plankton				0.55	
	Low	431	—	—		
	Medium	990	-0.16	-0.45, 0.13	0.27	
	High	1,589	-0.14	-0.45, 0.18	0.39	
	No. of mantas	3,010	0.23	0.11, 0.36	< 0.001	
Random effects						
	sd_{ID}	3,010	0.73		< 0.005	0.11
	sd_{site}	3,010	0.34		< 0.01	0.02
b) Group size						
Fixed effects						0.05
	(Intercept)	1,727	1.6	1.4, 1.9	< 0.001	
	Year				< 0.001	
	2014	406	—	—		
	2015	658	-0.33	-0.43, -0.22	< 0.001	
	2016	663	0.01	-0.09, 0.11	0.84	
	Current	1,727	-0.14	-0.20, -0.08	< 0.001	
	Time to high tide	1,727	-0.01	-0.04, 0.03	0.70	
	Plankton				< 0.001	
	Low	230	—	—		
	Medium	522	-0.19	-0.28, -0.10	< 0.001	
	High	975	0.00	-0.10, 0.09	0.92	
	No. of mantas	1,727	0.13	0.09, 0.16	< 0.001	
Random effects						
	sd_{ID}	1,727	0.22		< 0.05	0.06
	sd_{site}	1,727	0.24		< 0.005	0.09
c) Group leadership						
Fixed effects						0.01
	(Intercept)	1,760	-0.78	-0.97, -0.59	< 0.001	
	Sex				0.016	
	Female	1,215	—	—		
	Male	545	-0.36	-0.65, -0.07	< 0.05	
	Maturity				0.57	
	Juvenile	1,115	—	—		
	Adult	645	0.08	-0.19, 0.35	0.57	
	Shark bites				0.54	
	No injury	1,557	—	—		
	Injured	203	0.13	-0.27, 0.52	0.54	
	Anthropogenic injury				0.39	
	No injury	1,392	—	—		
	Injured	368	-0.15	-0.48, 0.19	0.39	
Random effects						
	sd_{ID}	1,760	0.52		< 0.005	0.05

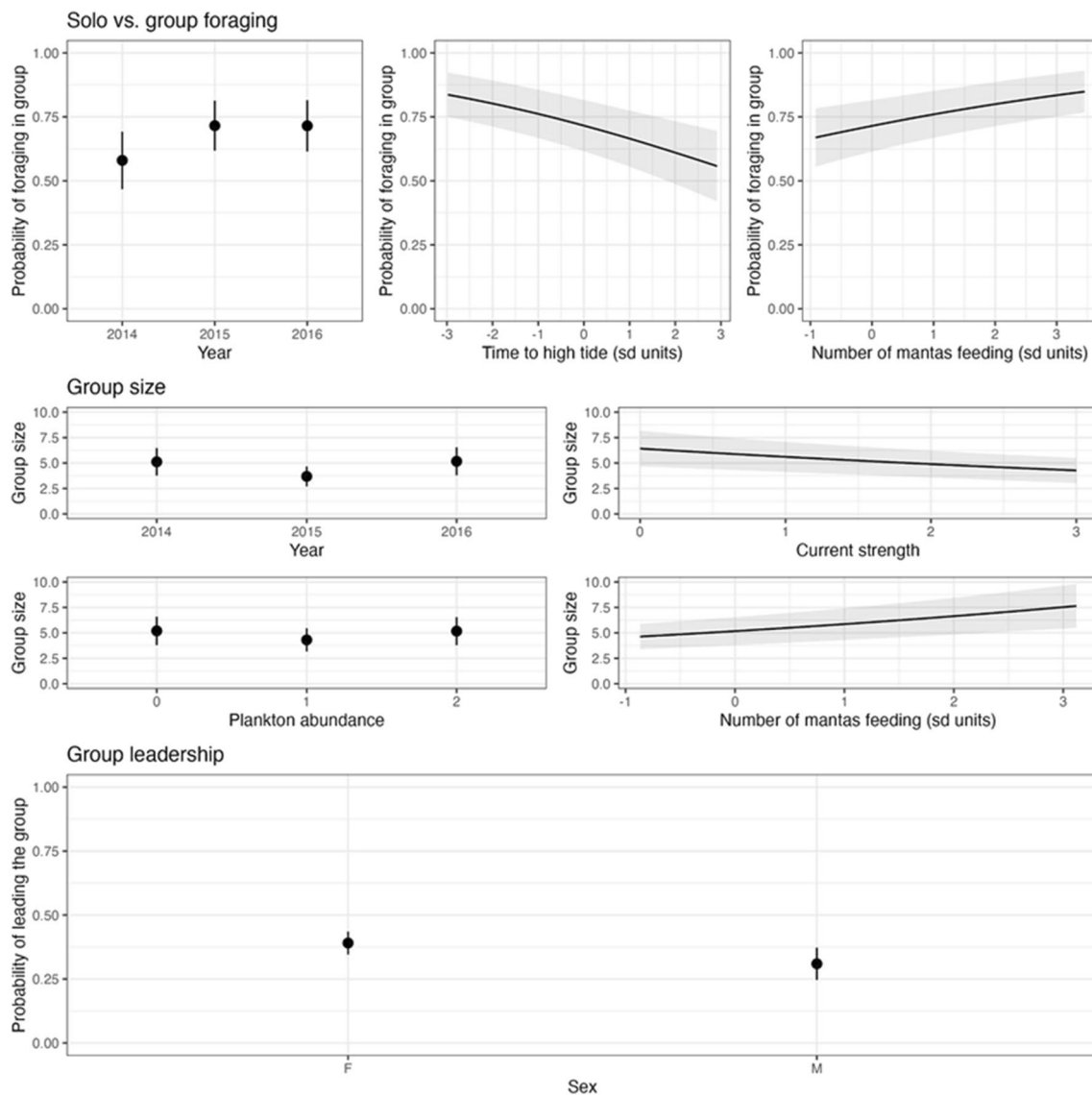


Fig. 2 Fixed effects significantly predicting the probability of **a**) Solo versus group foraging; **b**) Foraging group size and **c**) Leadership of a foraging group. Error bars and shaded areas represent 95% confidence intervals based on GLMM of behavioural traits

steadily decreasing in size thereafter (Table 2b; Fig. 2b). Larger general aggregations resulted in larger individual foraging groups (see test statistics in Table 2b; Fig. 2b).

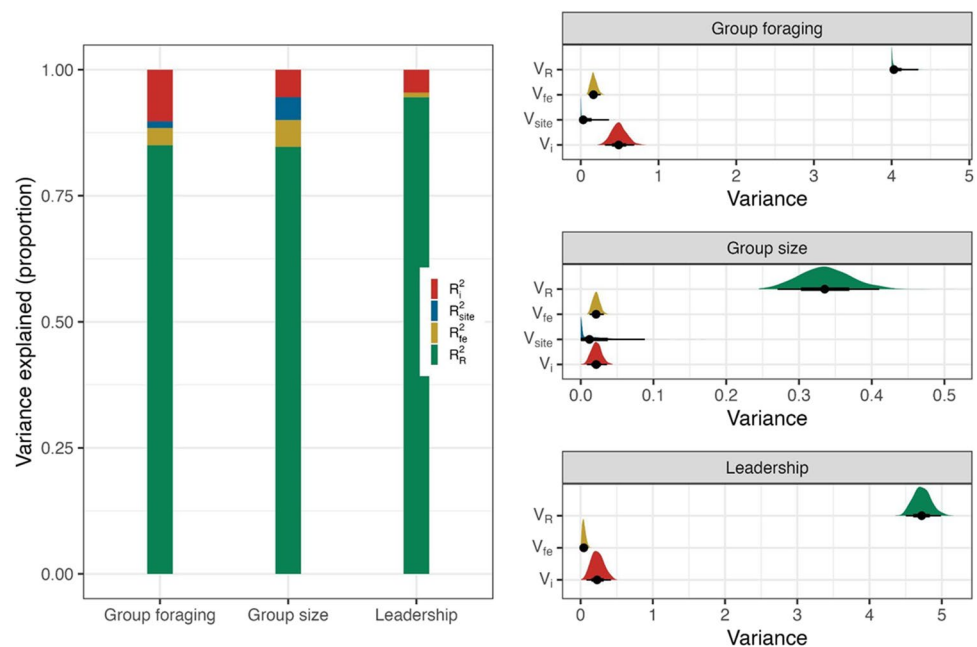
What are the effects of individual state on the probability to lead the group?

Leadership behaviour was most influenced by individual state model (see Table S3 in Supplementary Information for full AIC comparisons and R^2). Females were significantly more likely to adopt the leader position than males) (Table 2c, S3; Fig. 2c). Age class and presence of injury did not predict leadership behaviour.

How much of the variation in group foraging preference, group size and leadership behaviour was explained by among-individual, and within-individual differences?

Environmental variables, individual state and individual identity consistently explained <20% of the variation in foraging for all behaviours considered (R^2_{cond} [95% confidence interval], group vs. solo foraging: $R^2_{\text{cond}} = 16.19\%$ [10.80, 20.72]; group size: $R^2_{\text{cond}} = 19.74\%$ [7.65, 29.23]; leadership: $R^2_{\text{cond}} = 6.02\%$ [4.80, 6.84]). While we found statistical evidence for among-individual differences in all behaviours (all p -values <0.05, Table 2), the variance explained by individuals

Fig. 3 Individual identity and environmental variables explained < 25% of the variation in group foraging, group size and probability of leading the foraging group. Plots represent the proportion of variance explained by fixed effect (red; R^2_{fe}), individual identity (blue; R^2_{i}) and residuals (yellow; R^2_R) (left-hand size) along with the distribution of variance components on the latent scale (right-hand size). Variance distributions were estimated through 1000 bootstraps using a binomial GLMMs for the probability of foraging in a group or leading the group and a Poisson GLMM for group size. Error bars represent 95% (thin bars) and 66% (thick bars) confidence intervals based on bootstrap values



remained small. Preferences for foraging in group vs. solo had the highest signature for among-individual differences, yet still explained < 10% of the total variation (group vs. solo foraging: $R^2_i = 10.00\%$ [7.00; 14.00]; group size: $R^2_i = 5.00\%$ [2.00; 9.00]; group leadership: $R^2_i = 5.00\%$ [1.00; 8.00], Table S4). Fixed effects explained equally little variation, leaving the > 80% of variation was explained by unmeasured, within-individual sources of variation (Fig. 4). This means that while there are some individual preferences for foraging strategies, individuals tend to be very flexible in their foraging styles.

How does within and among-individual variation differ depending on individual state?

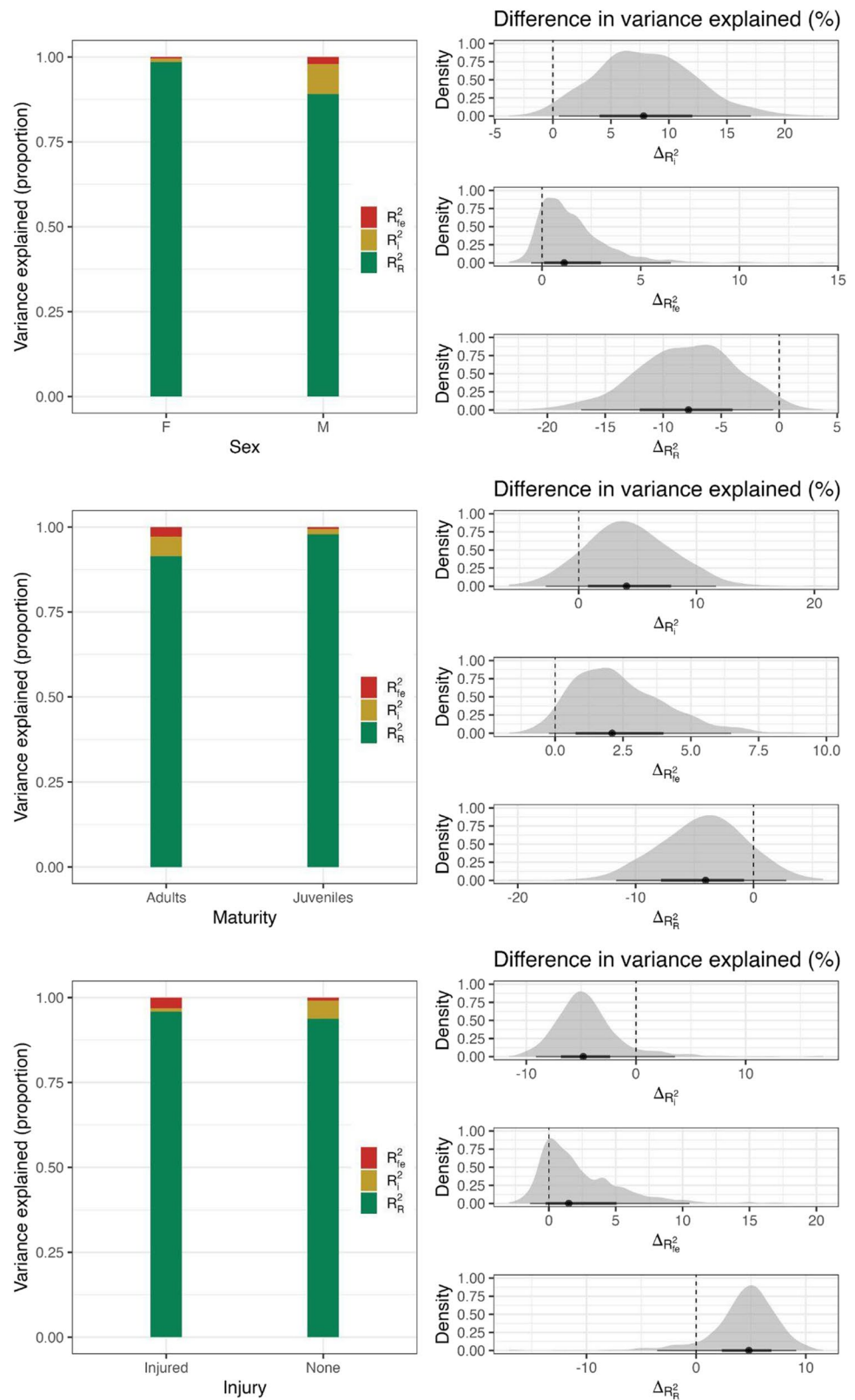
Using variance partitioning models, we showed that the majority of the variation explained was found in the residuals, which consistently explained > 80% of the variation regardless of the behavioural category considered. This means that there is overall very little evidence for among-individual differences in group leadership and all individuals were relatively equally likely to lead or follow the group in turn. We did find evidence for males being significantly more repeatable in their leadership preferences than females (Fig. 3). Male among-individual variance explained ~ 9.0% more of the total variation compared to females individuals (percent of variance explained, males: 8.69% [95% CI, [1.39, 17.82]; females: 0.54% [0.00, 3.38]; $\Delta R^2_i = 7.83\%$ [0.24, 16.99], $pd = 0.98$; Fig. 3). All other categories (juveniles vs. adults, injured vs. non-injured) showed no evidence of differences in variance components ($pd < 0.95$, See Supplementary Table S5).

Discussion

Mobula alfredi demonstrated considerable flexibility in individual foraging behaviour. Both solo and group feeding behaviour were frequent, with group feeding behaviour significantly influenced by the tide, year and aggregation size. Foraging group sizes were smallest when there was a strong current and there were moderate plankton densities. The largest groups formed three hours before high tide and gradually decreased in size. Larger overall aggregations resulted in larger foraging groups. Our study also showed that neither shark bites nor anthropogenic injuries were significant in explaining leadership position in the group. Leadership was influenced by sex, with females significantly more likely to lead than males, although a significant proportion of variance remained unexplained by fixed effects. Variation in group size and leadership behaviour were both shown to be strongly influenced by residual within-individual factors, explaining over half of variation in each trait, along with low repeatability scores, which indicated that *M. alfredi* were highly flexible in their foraging behaviour. All individuals were relatively equally likely to feed in groups or solo, as well as lead or follow the group. The repeatability of leadership behaviour was very low (< 10%), especially compared to published values for behavioural repeatability ($R \sim 47\%$, Bell et al. 2009), highlighting a flexibility in individual positioning and indicating that the majority of the variation in leadership was influenced by behavioural plasticity.

Our study shows a high level of within-individual variation, and little among-individual variance in group size, indicating no evidence of individual preference for small

Fig. 4 Males had stronger among-individual differences in leadership preferences compared to females, while maturity and injury status had no effect on among-individual differences. Bar plots show the proportion of variance in group leadership explained by all sources of variation (fixed effects, individual identity and residuals) compared among **a**) males and females along with the distribution for the difference in variance explained ($\Delta R^2 = (R^2_{\text{males}} - R^2_{\text{females}}) \times 100$); **b**) Adults and juveniles along with the distribution for the difference in variance explained ($\Delta R^2 = R^2_{\text{adult}} - R^2_{\text{juvenile}}$) and **c**) Injured and non-injured individuals along with the distribution for the difference in variance explained ($\Delta R^2 = R^2_{\text{injured}} - R^2_{\text{non-injured}}$). Variance explained was calculated with 1000 bootstraps by fitting a binomial GLMM to males and females, adults and juveniles and injured and non-injured separately. ΔR^2 was calculated as the difference in bootstrap values, e.g. $\Delta R^2 = 10$ indicates individual differences among males explain 10% more of the total variation compared to females. Error bars represent 95% (thin bars) and 66% (thick bars) confidence intervals based on bootstrap values



or large feeding groups. In the Maldives, monsoonal currents influence the abundance of zooplankton around the archipelago, with periods of increased food availability in

specific areas, thus driving seasonal movements of *M. alfredi* (Anderson et al. 2011; Harris et al. 2020). Specifically, Hanifaru Bay, where we record the largest aggregations and

group sizes, attracts *M. alfredi* due to the strong lunar currents drawing seasonally large volumes of zooplankton from the deeper waters outside the atoll into the shallower inner channel where it concentrates (Harris and Stevens 2021). The ephemeral nature of the dense food availability means that *M. alfredi* feeding aggregations can be large in size, but are quick to disperse (Harris et al. 2021). Hence, we found that group sizes were largest around the high tide dwindling rapidly thereafter. This lack of consistent food availability and its patchy distribution supports the suggestion that *M. alfredi* must be flexible, travelling to productive areas and associating with conspecifics potentially in order to gain information about these ephemeral patches (Buckley 1997) and increase feeding efficiency (Sueur et al. 2011; Jaïne et al. 2012). In a study using acoustic telemetry, individual *M. alfredi* in West Papua varied strongly in levels of regional residency, site fidelity and number of transitions between aggregation areas, again suggesting flexible and responsive foraging movements (Perryman et al. 2022).

The grouping behaviour of *M. alfredi* seemed sensitive to diurnal and annual variations in biotic and abiotic conditions, indicating both costs and benefits to social foraging. Group leaders often have optimal access to prey, but will experience the greatest energy expenditure, while animals positioned behind benefit from energy saving while compromising on food intake (Couzin et al. 2002; Krause and Ruxton 2002). In this study, for example, we observed ‘chain feeding’ in which followers are not directly behind one another, but slightly offset either to the side, or above or below each other like of flock of birds in flight (see Fig. S3 in Supplementary Information). In *M. alfredi*, the benefits of group feeding strategies, e.g. chain feeding, are suggested to be twofold, firstly reducing the rate of collision between manta rays and secondly, increasing the feeding efficiency of following manta rays (Stevens 2016; Liao 2022). This could explain the increased group foraging observed in larger aggregations, but also in 2015 and particularly 2016 in which El Nino caused significant disruption to marine ecosystems and severe coral bleaching in the Maldives (Monte-falcone et al. 2020). This indicates that group foraging was most beneficial, e.g. by reducing energy expenditure, when intraspecific competition for food was highest.

A key motivator to leadership behaviour is individual state, either stemming from a dominant personality or the need to optimise one's position, for example, to increase nutritional intake, movement capabilities, foraging strategies or reduce predation risk (Jacobs et al. 2008; Hodgkin et al. 2014). Our study also showed that injuries had little influence on leadership behaviours which suggests there is a low cost to adopting the leader position, but this remains to be tested (Ioannou et al. 2019). For future study, we could examine the effects of injuries on individuals, for example with our long-term dataset, we could examine the

repeatability of these individuals to establish how consistent they are in their foraging behaviour before and after injury (Bell and Sih 2007).

Our study did find sex to be the most important factor in predicting the probability of leading the group, with females dominantly leading the foraging groups. Female leadership is evident in other species, for example, adult females act as leaders within the southern population of killer whales (*Orcinus orca*) (Brent et al. 2015) and amongst prides of lions (Smith et al. 2019). Consistent leadership can be beneficial to groups; pods of foraging bottlenose dolphins (*Tursiops truncatus*) in the Lower Florida Keys led by consistent leaders were more frequently recorded in areas of higher fish biomass, travelled more direct paths, experienced less leader switches, and had more complex home ranges than groups with non-consistent leaders (Heithaus et al. 2013). Followers, in the dolphin study, benefited from the prior ecological knowledge of the leaders, but remains to be tested in Mobulids. Leadership need not be reliant on complex social information transfer between individuals, but can arise from simple mechanisms for spatiotemporal coordination (e.g. female leadership in grey reef sharks (*Carcharhinus amblyrhynchus*; Jacoby et al. 2016). Our observed bias in female leadership within foraging groups could reflect the higher food requirements of the larger sex and the nutritional demands of pregnancy.

Using a repeated measures analysis, the residual variance in our models included both the unobserved sources of variation, as well as within-individual variance. One explanation could be that most of the contribution to the phenotypic variation came from unmeasured sources of variation (residual variance), i.e., our model was incomplete. The second, non-exclusive, explanation is that the residual variance consisted largely of individual variance that does hold strong biological importance (Westneat et al. 2015). This would support the null hypothesis that individual *M. alfredi* are flexible in their foraging behavioural traits. There has been increased interest in how flexible foraging behaviour emerges as a result of the spatial and temporal availability and predictability of prey; Behavioural variation may be affected by physical processes leading to ‘passive’ plasticity in individuals (Scheiner 2006), for example fluctuations in prey density could lead to passive plasticity in an animal's foraging success (Westneat et al. 2015). Moreover, female *M. alfredi* could become passive leaders if males choose to follow them whether that be for foraging or courtship reasons. Foraging flexibility can also be selective or future-dependent, for example, in anticipation of the predictability of resource availability (Billard et al. 2020). Finally, trial-and-error learning may be present in which ‘learning rules’ as opposed to evolutionary change, influence phenotypic variation within a population (Franks et al. 2010).

In our study, both adaptive plasticity and residual within-individual variance arising through other stochastic processes were likely influential in explaining *M. alfredi* foraging behaviour. There was little evidence of individuals in our study population specialising in either leader or follower phenotypes. *M. alfredi* acting as leaders likely differ in their energy output, nutritional intake and predation risk compared to those following, but we suggest that this trade-off will vary dynamically within- and among-individuals as environmental and social conditions change (Lendvai et al. 2006; Fischhoff et al. 2007; Bonanni et al. 2010; David et al. 2011; Nakayama et al. 2013; but see Georgopoulou et al. 2022). The ephemeral nature of zooplankton upwellings, which can quickly disperse with the changing currents (Jaime et al. 2012; Stevens 2016), seems to lead to flexibility in individuals' foraging. Our results have implications for understanding how *M. alfredi* could respond to environmental change; manta rays were found to switch to group foraging strategies in response to increased food availability, a food source which is already ephemeral and highly vulnerable to decline in tropical waters in response to climate change (Stewart et al. 2018; Farmer et al. 2022). Future conservation efforts should focus on how the likely changes in zooplankton distribution and availability could shift the distributions and foraging behaviour of *M. alfredi* aggregations (Stewart et al. 2018). Understanding individuals' behaviours within feeding aggregations allows us to begin to understand the network of social interactions and relationships amongst wild populations of animals, particularly those demonstrating fission–fusion dynamics (Aureli et al. 2008). Behavioural flexibility in foraging behaviour could be key to a species' continued survival in light of changing environmental conditions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-024-03489-w>.

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Author contributions KEA and AM contributed to the study conception and design. Material preparation and data collection were performed by AM and GS. Data analyses were performed by AM and RR. The first draft of the manuscript was written by AM and KEA. All authors commented on previous versions of the manuscript, and read and approved the final manuscript.

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Data availability The data that support the findings of this study are available in the Dryad Repository <https://doi.org/10.5061/dryad.8cz8w9gxd>

Code availability All code for reproducing the statistical analyses and results is available on github: <https://github.com/rroyaute/mantarays-iiv-analysis>

Declarations

Ethics approval The research activities were approved by the Animal Welfare and Ethics Board at the University of York (ref. CR321) and adhered to the Manta Trust's code of conduct for minimising disturbance when interacting with Manta Rays (<https://swimwithmantas.org/>) (see Murray et al. 2019 which provides an evidence base for this code of conduct). Field research was approved by the Maldives' Environmental Protection Agency (EPA) permits EPA/RP/2015/01, EPA/2016/RP-01 and EPA/2016/RP-02.

Conflict of interests Authors declare no competing interests related to the work submitted for publication.

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