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Eat-clean-repeat: reef manta rays (*Mobula alfredi*) undertake repetitive feeding-cleaning cycles at an aggregation site in Seychelles

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To maximise energy efficiency, manta ray (*Mobula alfredi*, *M. birostris*) foraging and cleaning behaviours are thought to often be mutually exclusive, whereby individuals will only forage when prey density thresholds are met and will only clean when foraging is too energetically costly (i.e., thresholds are not met). Here, snorkel surveys and remote camera cleaning station footage show reef manta rays (*M. alfredi*) undertaking repetitive and short-term movements between surface-feeding and cleaning station visits around D'Arros Island, Seychelles. These observations demonstrate that foraging and cleaning behaviours are not mutually exclusive even when prey densities are high. At D'Arros Island, the proximity of cleaning stations to highly productive foraging areas may afford individuals the opportunity to undertake non-foraging activity without incurring significant energy loss from the shifts in behaviour. These data inform a more nuanced understanding of this species' use of key habitats.

KEYWORDS

energy expenditure, behaviour, manta ray, activity regime, habitat use

1 Introduction

Manta rays (Myliobatidae, Bonaparte 1838) (*Mobula alfredi*, *M. birostris*) are planktivorous ectotherms with a circum-global distribution in tropical and sub-tropical waters (Lawson et al., 2019). As planktivorous species, manta rays must often cope with the boom-and-bust characteristic nature of oligotrophic environments (i.e., Papastamatiou and Lowe, 2005; Papastamatiou et al., 2007), whereby sporadic foraging opportunities may be followed by periods of starvation (Rohner et al., 2017). In response to their patchily

distributed prey resource (Folt and Burns, 1999; Srokosz et al., 2003), manta rays often form predictable aggregations at known locations (“aggregation sites”) often associated with high prey availability (Couturier et al., 2011; Armstrong et al., 2016; Harris et al., 2020; Harris and Stevens, 2021). Understanding the function of these aggregation sites is important for mobulid conservation (Palacios et al., 2023). Importantly, foraging opportunities are not wholly responsible for animal presence, with cleaning station visitation (O’Shea et al., 2010; Jaine et al., 2012), socialisation and/or mating opportunities (Stevens et al., 2018) and predator avoidance (Germanov et al., 2019) also known to be drivers.

Different behaviours have different energetic consequences to the individual (e.g., Kacelnik and Houston, 1984; Houston, 1995; Christian et al., 1997; Williams et al., 2006) and current understanding suggests that, in response to this, different behaviours (particularly foraging and cleaning) are often mutually exclusive, triggered by differing conditions and generally occurring at different times (O’Shea et al., 2010; Barr and Abelson, 2019; Weeks et al., 2015). For example, the slow swimming speed associated with filter-feeding is thought to be energetically costly (Alexander, 1990; but see Paig-Tran et al., 2011), and as a result, it is only energetically efficient for manta rays to forage when prey densities reach a threshold that outweighs the energetic costs of filter-feeding (Armstrong et al., 2016; Armstrong et al. 2021b). It even appears that different fine-scale local environmental conditions preferentially drive foraging behaviour and cleaning station visitation within aggregation sites around the world (e.g., Dewar et al., 2008; Jaine et al., 2012; Couturier et al., 2018; Harris and Stevens, 2021). While specific local conditions, such as tidal height and range, may be strongly associated with certain behaviours (e.g., foraging, cleaning), it does not restrict these behaviours from being undertaken under other conditions and cleaning and/or foraging may very well occur outside of these constraints within the same aggregation site, albeit less-frequently (e.g., Jaine et al., 2012; Harris and Stevens, 2021; Harris et al. 2021).

The way an animal uses energy in its environment and how conditions influence the energetic costs of foraging and locomotion can be reconstructed from an animal’s energy landscape (Shepard and Lambertucci, 2013). Requirements modulated through energy landscapes can provide explanation to an individual’s habitat use, distribution, and migration pathways (Wilson et al., 2012; Shepard and Lambertucci, 2013). Given the disproportionate risk of extinction in large elasmobranchs and shifting global conditions affecting energy balance (Lawson et al., 2019), it is therefore increasingly relevant to develop a more nuanced understanding of energetics and habitat use in these species.

Here, observations are reported of reef manta rays (*M. alfredi*) around D’Arros Island, Seychelles undertaking frequent cycles between surface foraging and cleaning behaviours. To the best of our knowledge, these data suggest definitively for the first time that foraging and cleaning behaviours are not always mutually exclusive in reef manta rays. This has implications for our understanding of reef manta energetics as well as the functioning of key reef manta ray aggregation sites.

2 Methods

D’Arros Island (5°24.9’S, 53°17.9’E) is a 2 km long by 1 km wide coral sand cay, situated within the Amirantes Island Group, Seychelles (Figure 1). D’Arros is encompassed by a recently gazetted ‘Zone 1’ marine protected area (MPA) that affords the site “high biodiversity protection” (Official Gazette No 34 – Ministry of Agriculture, Climate Change and Environment, 2020). The surrounding reefs provide habitat for over 400 individual reef manta rays (Grimmel, *unpublished data*) that make use of productive foraging areas and cleaning stations year-round with seasonally driven peaks in their presence around the island (Peel et al., 2019, 2020).

2.1 Cleaning stations

The coastal reefs north of D’Arros Island host several cleaning stations, two of which have been identified and are monitored with stationary cameras set at fixed locations at ~ 20 m depth (“MantaCam”). These two stations are situated to the north of D’Arros Island approximately 150 m apart along a west-east axis and are located within 10 meters from the start of the reef crest, where the reef steeply slopes from ~3 m to ~ 20 m depth. As individual manta rays can be identified from unique ventral markings (Beebe and Tee-Van, 1941; Marshall et al., 2008), cameras face upwards to capture images of the ventral surface of reef manta rays as they use the cleaning site. GoPro Hero 8 and 9 cameras (GoPro Incorporation, California, United States of America) with Voltaic 75V always-on external batteries (Voltaic Systems, New York, United States of America) are housed inside waterproof casings and take pictures on timelapse every 10 seconds during daylight hours (0630-1830 or 0600-1800, depending on season). Cameras are changed regularly to ensure near continuous coverage of the sites. Data from each station is downloaded and processed by identifying individual mantas using the station against an ID database of all known individuals within the wider Seychelles archipelago (Seychelles Manta Ray Project). To distinguish between cleaning behaviours and cleaning station visitation for socialization (or other behaviours), cleaning was identified when cleaner wrasse were observed interacting with the individual. Date and timestamps for each sighting are recorded. Any individual that stayed at the station for a prolonged period had the entire duration of that visit noted down.

2.2 Surface-feeding

Reef manta ray surface-feeding behaviour was monitored via survey, whereby a small vessel patrolled the coastal areas (within 1 km from shore) of D’Arros, completing a full circumference of the island. During these surveys, the vessel completed a distance of approximately 7 km around the island at a maximum speed of 8 knots, with the skipper and at least two snorkelers locating manta

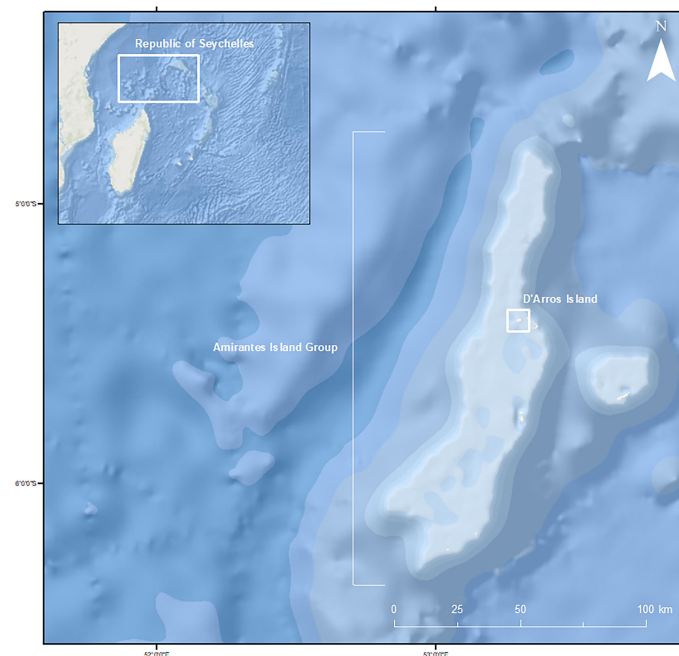


FIGURE 1

D'Arros Island (5°24.9'S, 53°17.9'E) situated within the Amirantes island group of the Seychelles archipelago. Manta survey efforts contained to shallower water depths around the perimeter of the island (within 1 km). Two cleaning stations are situated along the northern edge of the island. Exact locations are not disclosed to protect key habitats of the species. Basemap source: Esri®.

rays. On survey days described here, surveys were undertaken by three or four snorkelers (excluding the skipper) for a duration of approximately three hours. While individuals may be located along the entire survey area, during the surveys identified here individuals were predominantly located along the 2 km stretch north of D'Arros, intersecting where the two cleaning stations are located. The closest proximity of surface-feeding individuals to cleaning stations was approximately 20 m, when individuals were located directly above the cleaning stations. Manta rays located from aboard the vessel were followed via snorkel to collect photo identification of their ventral surface using GoPro Hero 9, 11 or 12. Footage was cross-referenced with the ID database to identify and pinpoint timestamps for each individual when they were surface-feeding. Surface-feeding was identified as when cephalic lobes unfurled and individuals' mouth was open.

2.3 Feeding-cleaning cycles

Repetitive movements, grouped as total numbers of behavioural transits (one-way movements from surface-feeding to cleaning station use or vice versa) as well as feeding-cleaning cycles (feeding, cleaning and back to feeding or vice versa), were quantified from survey and camera data. Behavioural transits were quantified over a maximum of 1-hour periods whereby an individual that was observed surface-feeding (or cleaning) must be observed undertaking the other behaviour within 1-hour of the initial observation. Feeding-cleaning cycles were quantified over a maximum of 2-hour periods whereby an individual had to be observed surface-feeding (or cleaning), transit to

the other behaviour, and then return to the original behaviour within the 2-hour period. This timeframe was based on survey duration and the time-period over which the majority of reef manta rays were observed surface-feeding. Individuals that cycled or transitioned between behaviours but outside of these parameters were not included.

3 Results

Across four survey days during November and December 2023, 11 identified individual reef manta rays undertook repetitive behavioural transits and feeding-cleaning cycles (Table 1). A total of 27 transits ($\mu = 2.45 \pm 0.78$ S.D) and 15 cycles (1.36 ± 0.5) were undertaken, with cycles ranging from 11 to 102 min (66 ± 29) in duration (Table 1). Here, duration of cycles is the total time taken for the individual to move from one behaviour (e.g., cleaning) to another (e.g., feeding) and then return again to the original behaviour (e.g., cleaning). Median time taken for an individual to transit between behaviours was 28 minutes ($\mu = 29.48 \pm 17.75$ S.D). SC-MA-0014 undertook the quickest transits between behaviours with a mean of 8.33 ± 5.44 minutes. SC-MA-0101 undertook the longest transits with a mean of 48.5 ± 2.5 minutes (Table 1).

Cleaning-only behaviour was the most commonly seen behaviour across the four survey days. The second most common behaviour was feeding-cleaning cycles except on 18 December where feeding-only was the second most common behaviour. The 21 November ($n=23$) had the highest proportion of individuals undertaking both feeding and cleaning behaviours (56.5%) and

TABLE 1 Metadata table of individual reef manta rays (*Mobula alfredi*) that undertook movements between surface-feeding and cleaning behaviours.

Date	Individual ID	Sex	Maturity	Size class	Surface-feeding (timeframes)	MantaCam West (timeframes)	MantaCam East (timeframes)	Behavioural Transits	Feeding-Cleaning Cycles
14-Nov-23	SC-MA-0298	M	Immature	2	1009-1017, 1140-1144, 1232-1235	–	1104-1112, 1341	2	1
21-Nov-23	SC-MA-0006	M	Mature	3	0900-0901, 1056-1058	1009-1011	1014, 1033-1047, 1126	2	1
21-Nov-23	SC-MA-0100	F	Mature	4	0917-0921, 0928-0929, 1054	0929-0931, 1043-1047	0847-0849, 0941, 1126	4	2
21-Nov-23	SC-MA-0101	F	Mature	4	916	0824-0825, 1009-1011, 1028-1042, 1135-1139, 1306	1002-1009, 1011-1013, 1015-1023, 1141-1154, 1221-1230, 1253-1303	2	1
21-Nov-23	SC-MA-0092	M	Mature	3	0821-0843, 0903-0905, 1026	–	0642-0639, 0938, 0956—0959	2	1
21-Nov-23	SC-MA-0014	F	Mature	3	0842-0846, 0857-0905, 0914	0931-0952	0851-0853, 1427-1430	3	2
21-Nov-23	SC-MA-0321	F	Immature	2	0820-0840, 1056-1057	–	0956-0959, 1121-1125	2	1
21-Nov-23	SC-MA-0281	M	Immature	2	0920, 1055-1058	1135, 1154	0832-0837, 1008, 1154-1158, 1612-1638	4	2
21-Nov-23	SC-MA-0267	F	Immature	1	0905-0916, 1058-1106	1034, 1154, 1434, 1539	1154-1158, 1318-1322, 1434-1442, 1526-1539	2	2
18-Dec-23	SC-MA-0007	F	Mature	4	0824, 0909-0912, 0915-0916, 0947, 1046-1052	–	0916-0920	2	1
19-Dec-23	SC-MA-00461	M	NA	NA	0928-0930, 0936-0943, 1100-1112, 1130-1136, 1148-1157	1002	0955-0958	2	1

Surface-feeding timeframes are based on how long the individual is in one video. MantaCam timeframes are based on the first and last timestamp for individuals photographed at that cleaning station. Where timeframes consist of a single time, the individual was at the cleaning station or video footage from snorkel surveys were of the individual < 1 minute. This does not necessarily represent the amount of time the individual was feeding or cleaning in the area but instead reflects either the snorkeller moving to a different individual or limitations in MantaCam camera angle. To account for variability in individual wingspan (wingtip to wingtip) estimation based off stereo video, individuals were classed into binned estimates of their wingspan: (1) 2-2.5 m, (2) 2.6-3 m, (3) 3-3.5 m, (4) 3.6-4 m and (5) 4+ m.

feeding-cleaning cycles (34.8%). The 18 December (n=10) had the lowest proportion of individuals exhibiting both behaviours (14.3%) and feeding-cleaning cycles (7%), with an equal representation of cleaning-only and feeding-only behaviours (42.9% for both). Most individuals (excluding SC-MA-0298, -0092, -0321 and -0007), not only undertook repetitive movements between surface-feeding and cleaning behaviours but also repetitively moved between visiting each of the two cleaning stations (Table 1).

4 Discussion

An individual’s capacity to minimise energy expenditure (i.e. cost of locomotion) and maximise energy gain through foraging has

direct (e.g., body condition, mortality) (du Plessis et al., 2012; Giles et al., 2020) and indirect (e.g., reproductive success) (Ballard et al., 2010; Jeanniard-du-Dot et al., 2017; Jeanniard du Dot et al., 2018) consequences on fitness and survival. According to optimal foraging theory, animals must maximise energy acquisition by obtaining as much energy as possible through foraging in a given period of time (Schoener, 1971; Norberg, 1977, 2021). Under this assumption, when conditions favour foraging (e.g., plankton densities exceed a threshold), manta rays will exclusively forage in order to meet energetic demands and will not expend energy undertaking other behaviours elsewhere (see O’Shea et al., 2010; Barr and Abelson, 2019). Findings here, however, demonstrate short-term cycles between surface-feeding and cleaning station use in reef manta rays at a Seychelles aggregation site for the first

time. At D'Arros, high-use cleaning stations adjacent to the northern reef slopes coincide with areas of preferred feeding (Peel et al., 2024). The reefs on the northern shores have a steeper topographic relief relative to the south, potentially driving greater upwellings of plankton and influencing observed spatial patterns in feeding at the site. Similarly, the steeper reef slopes around the north of D'Arros make for more pronounced deep reef patches that act as quality cleaning stations. The proximity of these cleaning stations to highly productive foraging areas may mean that cleaning activity can be undertaken without significant loss of energy or that intermittent cleaning confers other benefits to the individual. Cleaning stations play an important role in manta ray fitness, offering an important location for socialisation and potentially improving social learning, predator avoidance and contribute to foraging efficiency through collective feeding events (Perryman et al., 2019). As a result, manta rays are thought to preferentially select cleaning stations with hard coral substrate and specific cleaner wrasse species with these 'quality' cleaning stations contributing to a spatial map the individuals possess of their landscape (Armstrong et al. 2021a). Here, reef manta rays most commonly exhibited cleaning behaviours, whether these were cleaning-only or cleaning alongside feeding behaviours. While cleaning may very well be the most common behaviour over surveyed days, cleaning stations are consistently monitored by remote camera across the entire day whereas surveys are limited to the survey period (~3 hours). Therefore, it is possible that an animal that was only observed cleaning also surface-fed but was not identified during the survey. Regardless, functional cleaning and foraging habitat in close proximity may benefit not just foraging success but also sociability in this population whereby interrupted or unsuccessful cleaning events can be returned to after a brief foraging 'break'. Such quality cleaning sites occurring in concert with productive foraging areas may play an important role in selection of key high-use habitats.

Observations here offer a unique perspective into the energy landscape of D'Arros Island reef manta rays where the seascape hosts opportunities to undertake multiple behaviours simultaneously without suffering an apparent net energy loss through reduced foraging opportunities. Energy landscapes are dynamic, varying in space and time (Masello et al., 2017) and so these observations may be situational even within the D'Arros Island aggregation site as both localised and broad-scale environmental conditions influence energetic costs of behaviour for the population. It should be noted that the need to maximize foraging activity, as according to optimal foraging theory, may not be applicable to all populations of manta ray. Some populations live in highly productive environments where they do not suffer the energetic knife edge associated with oligotrophic conditions (see Papastamatiou and Lowe, 2005; Papastamatiou et al., 2007). For populations where feeding to satiation is not favoured, repetitive and simultaneous cycles between foraging and cleaning events may offer a unique opportunity to undertake a multitude of behaviours

without a net energy loss. Regardless of the potential circumstantial nature of these feeding-cleaning cycles, the data presented here offers important consideration for conservation of key aggregation sites of vulnerable species.

While other aggregation sites suggest feeding and cleaning behaviours may present closer to mutual exclusivity in manta rays (O'Shea et al., 2010; Barr and Abelson, 2019), specific habitats, such as D'Arros, may provide for alternative energetic strategies. D'Arros is not the only site that may offer habitat characteristics that afford multiple behaviours occurring simultaneously. Manta rays in aggregation sites within Raja Ampat, Indonesia, use the habitat for foraging and cleaning, though repetitive feeding-cleaning cycles have not been formally identified at these sites (Setyawan et al., 2020). Areas such as these may be important for both social behaviour and energy acquisition through foraging. Continuous effort should be made into identifying habitat where individuals undertake multiple key behaviours simultaneously and can be done using non-invasive techniques (e.g., remote camera as used in this study, drones as discussed in Setyawan et al., 2020). Increasing anthropogenic pressure at manta ray aggregation sites, particularly cleaning stations (Tratalos and Austin, 2001; Murray et al., 2020), could have ongoing consequences for the capacity of individuals to meet their energy demands if these areas coincide with highly productive foraging areas. Defining the function and overlap in important cleaning, feeding or socialisation areas is therefore imperative to the long-term conservation of these species.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was approved by Seychelles Bureau of Standard, Seychelles Government. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

RN: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. HG: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Writing – review & editing. DP: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. EM: Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. AA: Data curation, Formal analysis,

Investigation, Methodology, Writing – review & editing. RB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing, Supervision.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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