Insight into manta ray behaviour using animal-borne Crittercams

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Abstract
Animal-borne video cameras equipped with depth and temperature sensors were deployed on 16 reef manta rays (*Mobula alfredi*) in Raa Atoll, Maldives and 12 oceanic manta rays (*Mobula birostris*) in the Revillagigedo Archipelago, Mexico. These deployments provided descriptive behavioural data that give vital context to existing biotelemetry data and enabled a comparison of the social dynamics between the two manta ray species. Overall, cruising was the most dominant daytime behaviour recorded for both species. For *M. alfredi*, cleaning was the second most common behaviour, followed by courtship and feeding. No courtship behaviour was recorded for *M. birostris*. Across *M. alfredi* and *M. birostris* deployments, individuals spent an average of 43 and 8% of recorded time interacting with conspecifics, respectively. Sociability was higher in *M. alfredi* than *M. birostris*, however the findings should be interpreted with caution beyond the two deployment populations and times. Crittercams captured multiple courtship events of *M. alfredi* at depths greater than recreational scuba diving limits and captured previously undocumented interspecific interactions with *M. mobular*. Crittercam deployments also recorded *M. alfredi* travelling in groups and hugging the contours of the ocean floor, possibly as a tactic to reduce predation risk and/or improve swimming efficiency, enforcing the importance of this novel technology as a valuable tool to gain new insight into the ecological drivers of habitat use by these species. Lastly, these quantitative and descriptive results provide context for future hypothesis-driven research questions using animal-borne video cameras for mobulid rays.

Keywords

1. Introduction
Understanding the behavioural ecology of a species (Cooke, 2008), the full range of their habitat use (Costa et al., 2012; Graham et al., 2012), and drivers of spatial distribution in natural habitats (Jaine et al., 2012) are important for developing effective conservation strategies (Cooke, 2008). In the case of migratory marine species, it can be particularly challenging to research behaviour in the species’ natural environment (Costa et al., 2012; Graham et al., 2012; Hays et al., 2016). Direct observations of highly mobile marine species are often brief and discontinuous across their full range of available marine habitats (Jaine et al., 2012; Graham et al., 2012; Armstrong et al., 2021). Advances in biotelemetry technology have revealed insights into marine animals’ movement ecology and diving behaviour (Costa et al., 2012; Graham et al., 2012; Hays et al., 2016); however, these tags cannot discern behaviour states without validation through an accompanying video component (Marshall et al., 2007; Moll et al., 2007).

Crittercams are small, animal-borne video cameras equipped with data-logging devices designed to document habitat use and fine-scale behaviour of marine and terrestrial species (Calambokidis et al., 2007; Heithaus et al.,...
The device records video from the animal’s perspective and monitors depth and temperature metadata at set intervals (Marshall et al., 2007; Moll et al., 2007). The video component allows researchers to have a view comparable to that of the subject species and record fine-scale movements and information about habitat choice from a behavioural perspective. Crittercams and other such animal-borne video camera systems have been deployed on several marine taxa, including seabirds (Ponganis et al., 2000; Tremblay et al., 2014), marine turtles (Thomson et al., 2011), marine mammals (Yoshino et al., 2020), and elasmobranchs (Nakamura et al., 2011) to investigate foraging rates and predator searching behaviour. For example, animal-borne cameras deployed on seabird species have recorded these animals using the presence of congeners or fishing vessels as visual cues to indicate the presence of prey (local-enhancement; Tremblay et al., 2014). These inferences would not have been reached without this visual data. Elsewhere, Crittercams have been used to identify the negative impacts of handline capture and release for grey reef sharks (*Carcharhinus amblyrhynchos*), demonstrating the potential implications of this video data in conservation planning and environmental management initiatives (Skomal et al., 2007).

Oceanic manta rays (*Mobula birostris*) and reef manta rays (*Mobula alfredi*) are large migratory elasmobranchs that consume zooplankton and small fishes throughout their circumglobal range (Kashiwagi et al., 2011; Stewart et al., 2016a, 2017). Photo-identification studies capitalising on the unique ventral markings of manta rays and biotelemetry studies have shown that both manta ray species are highly mobile (Armstrong et al., 2019; Knochel et al., 2022), seasonally migratory (Harris et al., 2020), exhibit site affinity (Couturier et al., 2014; Braun et al., 2015; Harty et al., 2022), are long-lived (Dulvy et al., 2014), and slow to reproduce (Marshall & Bennett, 2010; Deakos, 2012; Stevens, 2016). Biotelemetry studies have also shown that both species utilise coastal and offshore habitats (Jaine et al., 2014; Stewart et al., 2016a) and exhibit reverse diel vertical migration behaviour (Braun et al., 2014; Andrzejaczek et al., 2021). While both species are sympatric across much of their range, *M. birostris* are more likely observed in sub-tropical waters or at offshore islands or seamounts and in fewer numbers than their *M. alfredi* counterparts (Kashiwagi et al., 2011; Nicholson-Jack et al., 2021; Strike et al., 2022). These differences in habitat use and observed aggregation sizes have led observers to hypothesise that *M. birostris* may be
more solitary than *M. alfredi* (Kashiwagi et al., 2011; Palacios et al., 2023). However, formal comparisons between the gregariousness of both species have yet to be conducted.

Manta rays aggregate at predictable locations worldwide to feed (Harris & Stevens, 2021), engage in courtship behaviour (Stevens et al., 2018a), and be cleaned by reef fishes (O’Shea et al., 2010; Jaine et al., 2012; Harris & Stevens, 2021). However, studies at these locations are spatially and temporally restricted due to observer limitations and ocean conditions (Jaine et al., 2012; Graham et al., 2012). Sightings of individual animals are often brief, influenced by human observers, and limited to recreational diving depths (<40 m). Natural behaviours have been catalogued and described through photographic and video capture (Stewart et al., 2018), but the extent and vertical distribution of behaviours often remain unknown. Satellite telemetry has increased knowledge of manta ray migration and depth stratification outside the vicinity of human observer presence (Stewart et al., 2018; Lassauce et al., 2020) but cannot discern behaviours across space and time (Graham et al., 2012; Stewart et al., 2016a). Opportunistically recorded feeding behaviour of *M. birostris* within the deep scattering layer between 130–140 m highlights that functionally important behaviours are occurring across a wide range of depths (Stewart et al., 2016b).

While increased research focus over the past two decades has vastly improved our understanding of manta ray ecology, research comparing the behaviour of the two species in their natural environment (Stevens et al., 2018), particularly outside the direct range of human observation (Stewart et al., 2019) has remained limited. Therefore, *in situ* research under natural conditions, and without the influence of human observers, is necessary to begin understanding socialisation and drivers of habitat use away from shallow observable reef systems. Through several Crittercam deployments, we aimed to provide additional context to behaviours that cannot be ascertained from traditional biotelemetry data and to compare the social activity of *M. birostris* to *M. alfredi*.

### 2. Methods

#### 2.1. Study sites

Crittercams were deployed on *M. birostris* at the Revillagigedo Archipelago, Mexico, in December 2015 (Figure 1) at dive sites ‘El Boiler’ in San Benedicto and at ‘Cabo Pearce’ at Isla Socorro, located approximately 400 km
southwest of the Baja California Peninsula. *Mobula birostris* frequent the shallow volcanic topography of this archipelago to take advantage of cleaning stations and to socialise (Stewart et al., 2019). Researchers deployed the Crittercams on *M. birostris* in Revillagigedo Archipelago by hand pressing a 20 cm suction cup attached the Crittercam unit onto the dorsal surface of the manta, described as passive suction in Stewart et al. (2019).

Located approximately 150 km north of the capital city of Malé, Raa Atoll was chosen as a study location because of the high concentration of *M. alfredi*, which frequent cleaning stations on the eastern edge of the atoll during the Southwest Monsoon (May–November) to clean, engage in courtship, and other social behaviours (Stevens, 2016; Stevens et al., 2018a). Deployments occurred in October 2016 on shallow coral reefs deemed suitable for freediving at Kottefaru Beyru and Neyo Beyru (Stewart et al., 2019). The deployment method (passive suction) was tested on *M. alfredi* but found to be ineffective as the Crittercams quickly slid off after deployment. Crittercam attachments were modified for use on *M. alfredi* in Raa Atoll, Maldives, to include a J-shaped Plexiglass hook with a blunt tip (to prevent injury) for use with the suction cup (Stewart et al., 2019). (Figure 1.)

Manta rays were selected opportunistically at a cleaning station or while cruising along the reef at both sites. During each deployment, we photographed the ventral patterns of individuals for identification, confirmed sex based on the presence or absence of claspers, and recorded the maturity status of the individuals (Stevens, 2016). The Crittercam collected high-resolution (1280 × 720 pixels, 30 frames/s) video and using a Star-Oddi DST milli-TD, recorded temperature every 15 s and depth every 5 s (Stewart et al., 2019).

Videos were downloaded from the Crittercams, and times were synced to the depth and temperature data recorded by the environmental data loggers. Data was sorted into deployments for each individual and viewed to classify behaviours. Videos were not recorded during two deployments on *M. birostris* therefore, the deployments could not be synced to the depth loggers and were discarded from analyses.

2.2. Behavioural classification

The footage collected from the deployments was categorised based on the manta’s actions and activities, as described in the following sections.
2.2.1. Cruising

Manta rays are constantly in motion; thus, cruising behaviour included all swimming that could not be linked to courtship, feeding, or cleaning. In *M. alfredi*, due to this species’ smaller head width and body size, the cephalic lobes were not always visible in the video footage (Figure 2a–b); thus, cruising was selected when criteria-based behaviours were not recognizable for this species. In *M. birostris*, cruising was only recorded if the cephalic lobes were visible and furled while the animal moved forward (Figure 2c).

2.2.2. Feeding

Eight distinct feeding strategies have been described for *M. alfredi* (Stevens, 2016; Stevens et al., 2018b): straight, surface, somersault, chain, piggy-back, sideways, cyclone and bottom. Fewer of these foraging strategies have been observed in *M. birostris* and only include the following: straight, somersault,
Figure 2. Representative visual examples of behaviour captured on Crittercam footage: *Mobula alfredi* cruising along the seabed with cephalic lobes visible (a) and not visible in the frame (b), and *Mobula birostris* cruising mid-water (c). *M. alfredi* feeding at depth (d) and at the surface (e–f). *M. alfredi* engaged in courtship evasion and avoidance behaviours (g–i). *M. alfredi* (j–k) and *M. birostris* (l) engaged in cleaning behaviour.
surface, and sideways. However, all instances of foraging include unfurling the cephalic lobes and widening the mouth to facilitate filter feeding on zooplankton prey.

For *M. birostris*, observations in the video where particulate density increased, swimming speed of the manta ray increased, and cephalic lobes were unfurled would have been classified as feeding behaviour. The forward-facing positioning of the Crittercam and limited view of the cephalic lobes in *M. alfredi* deployments made it difficult to discern when foraging behaviour was occurring in the smaller species. Therefore, feeding behaviour in *M. alfredi* was only classified when other manta rays were also visible within view of the video with their cephalic lobes unfurled and mouths open (Figure 2d–f).

### 2.2.3. Courtship

During courtship, female manta rays lead males in synchronised courtship trains to test their suitability as a potential mate (Stevens et al., 2018a). Swimming speed and positioning of the individuals engaged in the courtship train is often highly variable, with the animals chasing one another, displaying forward somersault and close following behaviours (Stevens et al., 2018a). Manta rays also sometimes engage in close following behaviour when not courting, most likely to increase hydrodynamic efficiency or reduce the risk of predation. Therefore, courtship was only classified when close following behaviour also encompassed forward somersault behaviour or above-average swimming speeds (Figure 2g–i).

### 2.2.4. Cleaning

Manta rays utilise cleaning stations to allow themselves to be cleaned, often unfurling their cephalic lobes during this process (O’Shea et al., 2010; Jaine et al., 2012). From the camera’s viewpoint, the cephalic lobes were not always visible in the video footage of *M. alfredi*; therefore, cleaning behaviour was determined by the manta ray’s very slow swimming movements around coral reef structures. Cleaner wrasse (*Labroides dimidiatus, Thalassoma amblycephalum, Thalassoma lunare*) and other cleaning manta rays were often visible in the Crittercam footage (Figure 2j–k). Cleaning was more difficult to distinguish for *M. birostris* as cleaner species were not often visible. To avoid over-classifying cleaning based on swimming patterns, the behaviour was only recorded if Clarion Angelfish (*Holacanthus clarionensis*) were recorded in the footage and the animal appeared to be swimming slowly or hovering within a cleaning station habitat (Figure 2l).
2.2.5. Unknown behaviour
An additional category of ‘unknown behaviour’ was used if the behaviour could not be attributed to one of the other categories. When the cephalic lobes of *M. alfredi* were visible in the camera footage, individuals were occasionally observed unfurling and flinching their cephalic lobes between periods of cruising behaviour. The reason for this could not be determined, thus these durations were recorded as unknown. For *M. birostris*, it was more challenging to definitively determine behaviour, particularly when an animal’s cephalic lobes were unrolled, and there were no other indicators of a behaviour (i.e., cleaner species, high prey concentrations, or courtship behaviours). At depths below 90–120 m, light depletion restricted our ability to determine behaviour; therefore, the behaviour was considered unknown.

2.2.6. Diver-influenced behaviour
For *M. alfredi* in Raa Atoll, video footage was recorded from locations away from tourists; therefore, individual manta rays spent very little time in the presence of researchers underwater. In the Revillagigedo Archipelago, the Crittercams were deployed in the presence of tourists and recorded numerous interactions with divers. Divers can alter natural behaviour (Gómez-García et al., 2021), therefore, time spent in the presence of divers (or diver bubbles on the camera) was not included as natural behaviour.

2.2.7. Crittercam reaction
An additional category was also used to signify behaviours (rapid swimming on deployment, attempting to remove/shake off the Crittercam) or agitation that appeared to be a reaction to the Crittercam attachment.

2.3. Determining interaction
In this study, the level of every interaction was determined throughout the Crittercam deployments based on criteria outlined in Figure 3. For example, every individual behaviour recorded also carried an interaction classification based on the presence of conspecifics within the video frame during that behaviour. When an interaction between the manta ray fitted with the Crittercam and another individual ended, a ten-second grace period was given, when a manta ray could return to the video before the interaction was designated as solitary during the video’s annotation. Due to the nature of courtship, all courtship was regarded as social, while cleaning and cruising could be social, solitary, or passive. Because of the need to view other individuals to confirm feeding behaviour in *M. alfredi*, feeding was recorded only...
Figure 3. Summary of social interaction criteria based on observed behaviour of *Mobula alfredi* in Raa Atoll, Maldives and *Mobula birostris* Revillagigedo Archipelago, Mexico as recorded by Crittercams.

as social or passive. An unknown level of interaction was only recorded if light depletion was such that the footage was completely indiscernible. Reactions to the Crittercam and interactions with divers in *M. birostris* deployments were not considered natural behaviour; thus, a level of interaction was not determined during these periods.

2.4. Quantifying social behaviours

Deployments less than 15 min in length were removed from further analyses. We defined this 15-minute cut-off period post-hoc to allow for a degree of standardisation between deployments and to ensure sufficient sampling time. This method removed four *M. alfredi* deployments but retained all *M. birostris* deployments. We compared the proportion of intervals spent engaged in social and solitary behaviour between *M. alfredi* and *M. birostris* using a two-sample *t*-test, with a Welch correction for unequal variances. Proportion data for each species’ measured interactions were normally distributed.

3. Results

Crittercams deployed on *M. alfredi* in Raa Atoll, Maldives recorded 1404.63 min (mean ± SD = 87.78 ± 96.02 min, range 3–302.5 min) of data from 11 females, three males and two individuals of undetermined sex between
Figure 4. Crittercam deployment times for *Mobula alfredi* in Raa Atoll, Maldives, and *M. birostris* in Revillagigedo Archipelago, Mexico. Each segment indicates the length of the Crittercam deployment. Non-shaded areas indicate daytime while shaded areas indicate night-time. Dashed lines indicate the approximate time of sunrise and sunset for each respective location.

08:17 to 18:00 local time, which corresponds with approximately two hours post sunrise and five minutes after sunset (Figure 4). Crittercams deployed on seven male and five female *M. birostris* in the Revillagigedo Archipelago recorded 946.18 min (mean = 78.94 ± 43.22 min, range 19.75–171 min) of data, from 10:06 to 15:07 local time (Figure 4), which corresponds to two hours post sunrise and three hours before sunset. All but one individual across both species included in the study were considered adults, with one sub-adult female *M. alfredi* accounting for 32 min of footage recorded in Raa Atoll (Table 1).

Reactions to the camera deployment accounted for a total of 41.89 min (1.78%). *Mobula birostris* reacted to the deployment of Crittercams for 4.6 min (0.5% of footage recorded in Revillagigedo), while *M. alfredi* reacted for 37.3 min (2.66% of footage recorded for Raa Atoll) (Table 1). No breaching behaviour was recorded in Revillagigedo Archipelago, however three individuals equipped with the Crittercam using a J-hook attachment in Raa Atoll breached (Video 1 at 10.6084/m9.figshare.24203817). Breaching may
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<th>Deployment time</th>
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<th>Diver influenced behaviour (min)</th>
<th>Total deployment duration (min)</th>
<th>Total duration of natural behaviour (min)</th>
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*Subtotal: 947 deployments, 263 deployment days, 102 reactions to deployment.*
Table 1. (Continued.)

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<th>Camera malfunctions (min)</th>
<th>Reactions to deployment (min)</th>
<th>Diver influenced behaviour (min)</th>
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<td>0.6</td>
<td>0.0</td>
<td>5</td>
</tr>
<tr>
<td>MDV-15</td>
<td></td>
<td>M</td>
<td>12 October 2016</td>
<td>12:57–17:59</td>
<td>303</td>
<td>9.4</td>
<td>3.8</td>
<td>0.0</td>
<td>289</td>
</tr>
<tr>
<td>MDV-16</td>
<td></td>
<td>?</td>
<td>12 October 2016</td>
<td>14:03–17:19</td>
<td>197</td>
<td>8.5</td>
<td>5.2</td>
<td>0.0</td>
<td>183</td>
</tr>
</tbody>
</table>

Subtotal 1405 54 37 0 1313
Total 2352 317 42 102 1890

Total deployment durations are rounded to the nearest quarter minute. *Indicates entire deployment was not recorded due to a malfunction. Dates are given as Month/Day/Year.
have been an attempt by the individuals to shed the Crittercam which is further discussed in Stewart et al. (2019). Diver-influenced behaviour was only recorded in the Revillagigedo Archipelago and accounted for 101.78 min (15%) of the footage for that study site (Table 1). This behaviour was not recorded in Raa Atoll as the Crittercams were deployed in locations away from tourists. Four recordings were interrupted by malfunctions, three in Raa Atoll ($N = 53.73$ min) and one in Revillagigedo Archipelago ($N = 1.47$ min). Reactions to the deployment, camera malfunctions, and diver influenced behaviour were classified as unnatural behaviour (Table 1).

The total duration of natural behaviours (cleaning, feeding, cruising, and courtship, and unspecified) for both species observed was 1889.71 min (80.35%) of all deployments (Table 1). Feeding was recorded by *M. alfredi* during two deployments (Table 2) and lasted a mean ± SD of 36.6 ± 24.71 min (range 19.12–54.07 min). Both events occurred between the hours of 15:00–17:00. However, the events differed in that the first (MDV-09) happened while the individual was at the surface (Figure 5a). MDV-09 actively chain and straight surface fed for approximately 54 min. MDV-16 fed much deeper, at an depth of 52.48 ± 14.67 m (average ± SD; range 13–69.9 m) (Figure 5b). During the period of deeper feeding, swimming speed appeared to be slower than surface feeding, with increased somersault and vertical straight feeding behaviours. The total feeding duration was 73.19 min, 6% of the natural behaviours recorded in Raa Atoll (Video 2 at 10.6084/m9.figshare.24203817). For *M. birostris*, feeding behaviour was not recorded. Additional information on the feeding behaviours recorded by the Crittercams is detailed by Stewart et al. (2019).

Crittercams recorded courtship behaviour in five deployments on *M. alfredi* for a cumulative duration of 83.18 min (6.3% of natural behaviour recorded in Raa Atoll) (Table 2: Video 3 at 10.6084/m9.figshare.24203817). More than 80% ($N = 69$ min) of the courtship observed occurred during two of the deployments, MDV-09 and MDV-15. Continuous durations of courtship lasted a mean ± SD of 4.35 ± 5.37 min (range 0.17–16.25 min). During the longest continuous recording of courtship (MDV-09: 16.25 min), four (including the individual with the Crittercam) *M. alfredi* were recorded in a courtship train between depths of 25.3 and 66.9 m (Figure 5a). For MDV-15: the maximum period of courtship was 9.25 min with three individuals; however, the depth range for courtship was more variable in this deployment, occurring between 4.1 and 86.3 m (Figure 5c). While the authors briefly
### Table 2.
Depths, temperatures and percentages of behaviour recorded by Crittercams on manta rays in Raa Atoll, Maldives and Revillagigedo Archipelago, Mexico.

<table>
<thead>
<tr>
<th>Species ID</th>
<th>Time of day</th>
<th>Max depth (m)</th>
<th>Average depth (m)</th>
<th>Temp range (°C)</th>
<th>% Time cruising</th>
<th>% Time cleaning</th>
<th>% Time courtship</th>
<th>% Time feeding</th>
<th>% Time unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td>REV-01</td>
<td>13:45–14:06</td>
<td>21.6</td>
<td>12.8</td>
<td>27.9–28</td>
<td>78%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>22%</td>
</tr>
<tr>
<td>REV-02</td>
<td>14:08–15:06</td>
<td>83.5</td>
<td>33.9</td>
<td>23.2–28.0</td>
<td>55%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>45%</td>
</tr>
<tr>
<td>REV-03</td>
<td>10:10–12:08</td>
<td>85.0</td>
<td>28.7</td>
<td>21.7–28.1</td>
<td>47%</td>
<td>2%</td>
<td>0%</td>
<td>0%</td>
<td>51%</td>
</tr>
<tr>
<td>REV-04</td>
<td>12:21–13:50</td>
<td>31.0</td>
<td>10.0</td>
<td>27.8–28.0</td>
<td>62%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>38%</td>
</tr>
<tr>
<td>REV-05</td>
<td>11:36–12:33</td>
<td>40.9</td>
<td>13.7</td>
<td>28.0–28.1</td>
<td>54%</td>
<td>2%</td>
<td>0%</td>
<td>0%</td>
<td>45%</td>
</tr>
<tr>
<td>REV-06</td>
<td>13:24–13:44</td>
<td>30.8</td>
<td>22.1</td>
<td>28.0–28.5</td>
<td>71%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>29%</td>
</tr>
<tr>
<td>REV-07</td>
<td>14:04–15:07</td>
<td>118.0</td>
<td>68.3</td>
<td>18.4–28.0</td>
<td>55%</td>
<td>8%</td>
<td>0%</td>
<td>0%</td>
<td>37%</td>
</tr>
<tr>
<td>REV-08</td>
<td>14:40–15:31</td>
<td>117.3</td>
<td>61.4</td>
<td>18.8–28.5</td>
<td>62%</td>
<td>2%</td>
<td>0%</td>
<td>0%</td>
<td>36%</td>
</tr>
<tr>
<td>REV-09</td>
<td>10:06–11:46</td>
<td>26.3</td>
<td>14.8</td>
<td>27.5–27.8</td>
<td>37%</td>
<td>26%</td>
<td>0%</td>
<td>0%</td>
<td>38%</td>
</tr>
<tr>
<td>REV-12</td>
<td>12:15–14:40</td>
<td>47.5</td>
<td>26.4</td>
<td>27.5–27.7</td>
<td>27%</td>
<td>10%</td>
<td>0%</td>
<td>0%</td>
<td>63%</td>
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</tbody>
</table>
Table 2.
(Continued.)

<table>
<thead>
<tr>
<th>Species ID</th>
<th>Time of day</th>
<th>Max depth (m)</th>
<th>Average depth (m)</th>
<th>Temp range (°C)</th>
<th>% Time cruising</th>
<th>% Time cleaning</th>
<th>% Time courtship</th>
<th>% Time feeding</th>
<th>% Time unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td>MDV-01</td>
<td>14:30–14:44</td>
<td>19.1</td>
<td>7.4</td>
<td>28.3–29.0</td>
<td>8%</td>
<td>90%</td>
<td>0%</td>
<td>0%</td>
<td>1%</td>
</tr>
<tr>
<td>MDV-02</td>
<td>11:04–13:40</td>
<td>93.6</td>
<td>39.1</td>
<td>24.6–28.8</td>
<td>61%</td>
<td>29%</td>
<td>3%</td>
<td>0%</td>
<td>6%</td>
</tr>
<tr>
<td>MDV-03</td>
<td>11:20–11:24</td>
<td>42.2</td>
<td>34.8</td>
<td>28.4–28.5</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>MDV-04</td>
<td>80:17–08:51</td>
<td>41.5</td>
<td>16.0</td>
<td>28.2–29.5</td>
<td>95%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>5%</td>
</tr>
<tr>
<td>MDV-05</td>
<td>08:24–09:00</td>
<td>69.6</td>
<td>38.0</td>
<td>28.1–28.5</td>
<td>98%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>2%</td>
</tr>
<tr>
<td>MDV-06</td>
<td>09:55–09:59</td>
<td>23.6</td>
<td>12.7</td>
<td>28.4–28.6</td>
<td>36%</td>
<td>59%</td>
<td>0%</td>
<td>0%</td>
<td>5%</td>
</tr>
<tr>
<td>MDV-07</td>
<td>10:39–11:20</td>
<td>68.5</td>
<td>19.5</td>
<td>28.0–28.6</td>
<td>15%</td>
<td>74%</td>
<td>0%</td>
<td>0%</td>
<td>12%</td>
</tr>
<tr>
<td>MDV-08</td>
<td>10:51–11:39</td>
<td>98.5</td>
<td>66.6</td>
<td>21.9–28.6</td>
<td>86%</td>
<td>0%</td>
<td>13%</td>
<td>0%</td>
<td>1%</td>
</tr>
<tr>
<td>MDV-09</td>
<td>13:26–17:36</td>
<td>91.4</td>
<td>34.7</td>
<td>20.5–29.0</td>
<td>44%</td>
<td>1%</td>
<td>21%</td>
<td>25%</td>
<td>9%</td>
</tr>
<tr>
<td>MDV-10</td>
<td>13:23–14:07</td>
<td>82.4</td>
<td>44.6</td>
<td>23.8–28.7</td>
<td>62%</td>
<td>35%</td>
<td>0%</td>
<td>0%</td>
<td>3%</td>
</tr>
<tr>
<td>MDV-11</td>
<td>08:30–11:26</td>
<td>95.0</td>
<td>49.1</td>
<td>21.7–28.6</td>
<td>81%</td>
<td>8%</td>
<td>0%</td>
<td>0%</td>
<td>11%</td>
</tr>
<tr>
<td>MDV-12</td>
<td>08:42–09:14</td>
<td>81.2</td>
<td>34.2</td>
<td>23.8–28.6</td>
<td>62%</td>
<td>33%</td>
<td>0%</td>
<td>0%</td>
<td>5%</td>
</tr>
<tr>
<td>MDV-13</td>
<td>11:18–12:19</td>
<td>92.8</td>
<td>43.9</td>
<td>24.3–28.8</td>
<td>76%</td>
<td>23%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>MDV-14</td>
<td>12:54–13:00</td>
<td>45.6</td>
<td>20.6</td>
<td>27.5–28.7</td>
<td>54%</td>
<td>46%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>MDV-15</td>
<td>12:57–17:59</td>
<td>336.0</td>
<td>46.1</td>
<td>12.7–29.0</td>
<td>83%</td>
<td>3%</td>
<td>9%</td>
<td>0%</td>
<td>5%</td>
</tr>
<tr>
<td>MDV-16</td>
<td>14:03–17:19</td>
<td>87.4</td>
<td>47.1</td>
<td>21.0–28.9</td>
<td>73%</td>
<td>5%</td>
<td>1%</td>
<td>10%</td>
<td>11%</td>
</tr>
</tbody>
</table>

Percentages of time are of the natural behaviour recorded. Deployments where no video was recorded (REV10 and REV11) are not included in the table.
Figure 5. Time series graphs for *M. alfredi* individuals MDV-09: MDV-16: and MDV-15. (a) MDV-09 depicts courtship behaviour to a maximum depth of 86.3 m. (b) MDV-16 was recorded feeding at a maximum depth of 68.9 m. (c) MDV-15 engaged in courtship behaviour in shallow warm water before diving to approximately 300 m with a temperature of 13 degrees. Colours in the legend indicate the length of the track attributed to a specified behaviour. Parts of the track with no colour indicate cruising behaviour.
observed courtship activity while deploying the Crittercams on *M. birostris*, no individuals equipped with a Crittercam recorded courtship behaviour.

In Raa Atoll, all 16 Crittercam deployments occurred when *M. alfredi* were cleaning, and 12 individuals resumed cleaning during their deployment for 162.1 min (12.34% of natural behaviour recorded for *M. alfredi*) (Table 2; Video 4 at 10.6084/m9.figshare.24203817). The mean ± SD continuous duration of cleaning behaviour in Raa Atoll was 7.04 ± 5.61 min, range 0.25–22.08 min. Two female *M. alfredi* accounted for the most considerable amount of time at cleaning stations, totalling 45.0 min of cleaning behaviour within a 156.25 min deployment, and 29.0 min of cleaning within a deployment of 40.5 min, for MDV-02 and MDV-07 respectively.

The majority of *M. alfredi* cleaning observed was solitary (*N* = 63.22 min, 39.74%); however, social (*N* = 49.02 min) and passive interactions (*N* = 46.85 min) each accounted for approximately 30% of the footage (Table 3). Cleaning was the only behaviour where passive interaction was prevalent (47.0 min), and multiple *M. alfredi* appeared to utilise the same cleaning station without engaging in social interactions. The average depth of cleaning behaviour was 13.15 m ± SD 5.66 m, range 1.3–37.1 m.

*Mobula birostris* were observed cleaning for 35.02 min throughout six deployments (6.08% of natural behaviour recorded for *M. birostris*) (Table 2; Video 5 at 10.6084/m9.figshare.24203817). The mean ± SD continuous duration was shorter for *M. birostris*, with periods of cleaning lasting on average 1.26 ± 1.09 min, range 0.32–4.78 min. Solitary cleaning was observed most often, accounting for 70% (*N* = 24.42 min) of the observed behaviour (Table 3). Only a small percentage was recorded as social (*N* = 3.35 min, 10%) or passive (*N* = 7.24 min, 21%). Deployment REV-09 had the overall longest duration of cleaning recorded (*N* = 15.2 min, with a continuous duration of 4.78 min). The mean ± SD depth of cleaning in the Revillagigedo Archipelago was 18.67 ± 6.69 m, range 6.4–42.01 m. During three deployments (REV-03, REV-09 and REV-12), *M. birostris* were recorded passing by divers or through diver bubbles between cleaning periods which shortened the continuous durations recorded. If the cleaning was recorded with divers or bubbles present, it was recorded as diver-influenced and not counted as natural behaviour (see interspecies interactions). All the deployments were conducted at cleaning stations but given the requirement to see cleaner species in the footage, cleaning was not recorded for all *M. birostris*. 
Table 3.
Comparison of gregariousness by type of behaviour for *M. alfredi* and *M. birostris* as recorded by Crittercams in Raa Atoll, Maldives and Revillagigedo Archipelago, Mexico.

| Behaviour | *Mobula alfredi* | | | *Mobula birostris* | | |
|-----------|--------|--------|--------|--------|--------|
|           | Min.   | % of duration (unweighted) | % of duration (weighted) | Min.   | % of duration (unweighted) | % of duration (weighted) |
| Total*    |        |        |        |        |        |        |
| Social    | 549.7  | 43%    | 39%    | 56.1   | 10%    | 8%     |
| Passive   | 79.5   | 6%     | 8%     | 56.7   | 10%    | 7%     |
| Solitary  | 658.0  | 51%    | 53%    | 463.6  | 80%    | 85%    |
| Unknown   | 1.4    | 0%     | 0%     | N/A    | 0%     | 0%     |
| Cruising  |        |        |        |        |        |        |
| Social    | 333.0  | 37%    | 38%    | 13.1   | 5%     | 4%     |
| Passive   | 16.5   | 2%     | 2%     | 25.3   | 9%     | 9%     |
| Solitary  | 548.7  | 61%    | 60%    | 245.0  | 86%    | 87%    |
| Cleaning  |        |        |        |        |        |        |
| Social    | 49.0   | 34%    | 34%    | 3.4    | 10%    | 5%     |
| Passive   | 43.5   | 31%    | 29%    | 7.2    | 21%    | 18%    |
| Solitary  | 49.7   | 35%    | 37%    | 24.4   | 70%    | 77%    |
| Feeding   |        |        |        |        |        |        |
| Social    | 65.0   | 89%    | 92%    | N/A    | 0%     | 0%     |
| Passive   | 8.2    | 11%    | 8%     | N/A    | 0%     | 0%     |
| Courtship |        |        |        |        |        |        |
| Social    | 83.2   | 100%   | 100%   | N/A    | 0%     | 0%     |
| Unknown   |        |        |        |        |        |        |
| Social    | 19.5   | 21%    | 22%    | 39.64  | 15%    | 12%    |
| Passive   | 11.3   | 12%    | 9%     | 24.13  | 9%     | 7%     |
| Solitary  | 59.6   | 65%    | 68%    | 194.18 | 75%    | 81%    |
| Unknown   | 1.4    | 2%     | 0%     | N/A    | N/A    | N/A    |

*The total duration presented is the natural duration excluding deployments <15 min. Unweighted averages were calculated by summing the minutes of observed interactions for each behaviour across all individuals and dividing by the total sum. Weighted averages accounted for individual variation by computing the proportion of deployment time for each individual before calculating the mean ± SD.

In Raa Atoll, cruising accounted for 69.0% (*N* = 902.73 min) of the natural behaviour recorded, with more than nine hours (i.e., 559 min) recorded as solitary cruising for *M. alfredi* (Table 3). The *M. alfredi* (MDV-15) that reached the deepest depth in Raa Atoll registered approximately 90 m before the light was lost and 230 m before the Crittercam video malfunctioned (Figure 6). However, the depth sensor recorded a dive to 336 m, where the water...
temperature was 12.7°C. This individual (MDV-15) made two deep dives, both in the afternoon hours, between 13:00 and 17:30 (Figure 5c). After reaching the deepest part of the dives (294.6 m and 336 m), MDV-15 quickly
returned to the surface. The purpose of this rapid dive was not discernible from the Crittercam footage due to lack of light; therefore, it was classified as unknown behaviour until the camera malfunctioned. Despite the high level of solitary cruising reported, a considerable duration of social cruising behaviour (333 min) was also observed for *M. alfredi*. *Mobula alfredi* were highly social during cruising, shown with shadowing behaviours and reactions to passing *M. alfredi*. On multiple occasions, *M. alfredi* were observed changing their swimming pattern to interact with other *M. alfredi* socially (Video 6 at 10.6084/m9.figshare.24203817).

In Revillagigedo Archipelago, *M. birostris* cruised for 283.35 min (49% of the natural duration recorded), 84% (= 245 min) of which was solitary. The deepest depth recorded by *M. birostris* was 118 m during deployment REV-07. During REV-07: there were two deep dives to the seabed at approximately 118 m (Video 7 at 10.6084/m9.figshare.24203817), but the reason for the deep dive could not be discerned from the footage. REV-08 was the only other deployment in the Revillagigedo Archipelago to record a depth greater than 100 metres (max 117.27 m). This individual spent 14 consecutive minutes below 100 metres, which ended only when the Crittercam was released from the manta. Both individuals recorded dives exceeding 100 metres in the afternoon hours (between 14:30 and 15:30) (Figure 6). Social cruising was recorded at a minimal level (= 13.08 min), only 5% of the cruising behaviour observed. The majority (86%; 244.95 min) of cruising behaviour by *M. birostris* was solitary in nature.

*Mobula alfredi* spent an average of 38.6% (= 549.67 min) of recorded time engaged in social interactions, 8.5% (*N* = 79.49 min) in passive interactions, and 52.9% (= 658 min) in solitude (weighted, Table 3). In contrast, *M. birostris* spent 8.0% (= 56.07 min) of recorded time in social interactions, 7.4% (*N* = 56.69 min) in passive interactions, and 84.5% (= 463.55 min) in solitude (weighted, Table 3). A simple two sample *t*-test with a Welch correction for unequal variance indicated that the mean ± SD proportion of time *M. alfredi* spent in social interactions was higher than that for *M. birostris* (*t* = −3.8003; *df* = 13.085; *p* = 0.002182; Figure 7). The same test suggested the mean ± SD proportion of time spent in solitude was also higher for *M. birostris* than *M. alfredi* (*t* = 3.3283; *df* = 15.93; *p* = 0.004279). Differences between sex and maturity status were not investigated due to the skewness of sampling towards females and adults.
Figure 7. (A) Crittercam deployment times for *Mobula birostris* in Revillagigedo Archipelago, Mexico and *M. alfredi* in Raa Atoll, Maldives. Each segment indicates the length of the Crittercam deployment. Levels of socialisation between manta rays and conspecifics throughout the duration of the deployments are coded by colour. (B) The proportion of time spent engaged in social, passive, or solitary behaviour across 12 deployments of *Mobula alfredi* in Raa Atoll, Maldives and ten deployments of *Mobula birostris* in the Revillagigedo Archipelago, Mexico. The coloured bars indicate the median, the boxes encompass the first and third quartile, while the whiskers indicate minimum and maximum values for each group. Red dots indicate the group’s mean ± SD.
In Raa Atoll, *M. alfredi* were recorded interacting with a school of five feeding spinetail devil rays (*Mobula mobular*) during one deployment for 3.5 min, between 33.1–41.0 m in open-water away from the reef (Figure 8a–d; Video 8 at 10.6084/m9.figshare.24203817). Before the interaction, the female *M. alfredi* (MDV-02) rapidly followed a male *M. alfredi* upwards from 70–36 m. At 36 m, the *M. mobular* suddenly came into view, and the female swam in their direction while the male manta ray was no longer visible in the Crittercam footage. Having approached within a metre of the schooling rays, MDV-02 followed closely as the *M. mobular* swam in front, evading the manta with quick turns whenever it approached to less than approximately one metre from their tails. Crittercams also captured nine different interactions between *M. alfredi* and giant trevallies (*Caranx ignobilis*) swimming underneath the manta (Figure 8d–g). One *C. ignobilis* was observed rubbing itself on the ventral side of *M. alfredi* (Video 9 at 10.6084/m9.figshare.24203817). On two occasions, these large piscivores were recorded swimming directly in front of the *M. alfredi* equipped with the Crittercam. A small piece of string (part of the Crittercam release mechanism) was visible in both instances and may have been mistaken for a prey species. Interactions between *M. alfredi* and *C. ignobilis* were recorded between 37 and 81 m, and all interspecies interactions (aside from cleaning behaviour) occurred when manta rays were engaged in cruising behaviour. The crittercams recorded grey reef sharks (*Carcharhinus amblyrhynchos*), whitetip reef sharks (*Triaenodon obesus*), and blotched fantail rays (*Taeniura meyeni*). One grey reef shark approached a *M. alfredi* from the front, but the manta ray recorded no significant changes in behaviour. Interactions between *M. alfredi* and humans were limited after the deployment of the Crittercam, with the devices recording five brief encounters (<10 s) with researchers and no noticeable changes in natural behaviour.

*Mobula birostris* were not recorded interacting with other ray species but were recorded in association with black trevally (*Caranx lugubris*) during nine deployments (Figure 2l). More than fifty interactions were recorded, but the exact number could not be quantified as the trevally were frequently observed going in and out of the camera’s view. *Caranx lugubris* were observed swimming under and in front of the manta rays, once crossing between two individuals (the individual with the Crittercam (REV-04) and another manta ray in front. During six deployments, common remoras (*Remora remora*) were recorded travelling on the Crittercam manta rays.
Figure 8. Interspecies interactions captured on Crittercam footage: A female *Mobula alfredi* approached and closely followed a school of five feeding spinetail devil rays (*Mobula mobular*) in Raa Atoll, Maldives (a–d). Giant trevallies (*Caranx ignobilis*) swimming in front of and underneath cruising *M. alfredi* and rubbing on the ventral surface of the manta ray (e–i).
The remoras were recorded above the eye of the individuals with the Crittercam and travelling on the underside of manta rays in the camera’s view. During two deployments (REV-05 and REV-12), common remoras were recorded detaching from the Crittercam manta and swimming, one changing manta ray hosts. The remora in REV-05 was also observed opening and closing its mouth, potentially feeding while attached to the Crittercam manta. Of note, one Crittercam ascended through schools of black trevally and silky sharks (*Carcharhinus falciformis*) that approached the camera in the 4.23 min it took to float to the surface.

Divers were present during the deployments in the Revillagigedo Archipelago. *M. birostris* swam toward divers, through their exhaust bubbles and around divers. These interactions were recorded in eight of the ten deployments, accounting for 101.78 min (15%) of the footage, which was not considered natural behaviour.

4. Discussion

4.1. Comparing and contrasting associations between conspecifics of *Mobula alfredi* and *M. birostris*

Our results provide a quantifiable comparison of *M. birostris* and *M. alfredi* socialisation outside the limits of traditional methods (i.e., SCUBA and snorkelling). The mean in the proportion of time spent engaged in social behaviours in *M. alfredi* was higher than for *M. birostris*. However, these results should be interpreted with caution as these data were sampled over approximately a week at one location for each species on opposite sides of the world. Despite these limitations, deployments occurred during the day at cleaning stations commonly used by each species in their respective habitat. The results suggest that there may be a difference in the degree of sociality between these two closely related species. Outside this study, *M. alfredi* appear overall to be more gregarious than their larger counterparts and have been recorded feeding in groups of up to 250 individuals (Stevens et al. 2018b, GMW Stevens, pers. obs.). *Mobula birostris* have never been recorded in feeding aggregations of similar magnitude. At cleaning stations, the number of individuals observed is generally less than what is observed in a feeding aggregation (GMW Stevens, pers. obs.); however, high numbers of both *M. birostris* and *M. alfredi* have been reported on occasion. The highest reported number of *M. birostris* seen within one day consisted of
a stream of 60 individuals at a cleaning station in Isla de La Plata, Ecuador (Harty et al., 2022) while the max number of *M. alfredi* reported was 53 individuals at a cleaning station in Baa Atoll, Maldives (GMW Stevens, pers. obs.). Aggregative behaviour may be driven by mutual preference for the same patch of interactions rather than intentionally sought out interactions but can lead to opportunities for social dynamics to take place. Since larger-bodied species generally have lower population densities (Damuth, 1987), and smaller-bodied mobula ray species tend to aggregate in larger group sizes (Palacios et al., 2023), the potential differences in levels of gregariousness between the two species could be explained by higher population densities of *M. alfredi* than *M. birostris*, and therefore greater opportunities for interactions with conspecifics. These results suggest that *M. birostris* is more solitary than *M. alfredi*, at least over this study’s short time sampling scale (i.e., days) and at the two aggregations sampled.

4.2. Associative cruising observed in Mobula alfredi

Crittercams recorded *M. alfredi* cruising together in groups, often while hugging the contours of the seabed and engaging in following behaviour. These behaviours could represent attempts to improve travelling efficiency (i.e., improved hydrodynamics) (Ma et al., 2022) or might be a response to predation risk as these animals pass through risky habitats (Palacios et al., 2023). While Crittercam deployments occurred over peak courtship and mating season in the Maldives, and this grouping behaviour could be attributed to reproductive behaviour, it does appear that some of these grouping dynamics were unrelated to courtship. The close shadowing behaviour observed may be representative of drafting, a technique used to increase movement efficiency, whereby one animal following another benefits from the displacement in the water caused by the forward motion of the lead animal (Weihs, 2004). Travelling in chains likely reduces costs associated with moving between foraging grounds and cleaning stations, with the added benefit of reducing predation risk. Prey exhibit risk-induced trait responses to the presence of predators, causing shifts in both the prey’s habitat use and foraging strategies (Peacor et al., 2020). Many animal species respond to predation risk by forming groups; for example, certain dolphin species form mixed-species groups, likely in response to increased predation risk (Norris & Dohl, 1980; Syme et al., 2021). Elephant seals (*Mirounga angustirostris*) are also known to swim close to the seabed while entering and exiting coastal haul out sites.
to avoid white sharks (*Carcharodon carcharias*; Le Boeuf & Crocker, 1996). Similarly, *M. alfredi* are likely to be most vulnerable to predation in Raa Atoll when entering and exiting atolls through channels or travelling along the outer reefs of the atoll systems, where they are more likely to encounter large predatory shark species. The fear of predation is known to influence the movement and behaviours of batoid species; for example, southern stingrays (*Hypanus americanus*) were less likely to forage in deeper forereef zones in Belize, where risk of predation by reef sharks was higher and instead remained in the safer sand flats (Bond et al., 2019). There is evidence that smaller, younger, and therefore more vulnerable manta rays skew their habitat use towards shallow lagoons (Stevens 2016; Peel et al., 2019; Setyawan et al., 2022), possibly to avoid predators lurking in deep channels or the forereef (Stevens, 2016). Predator avoidance, in addition to patchiness of prey sources and cleaning behaviour, could be an important driver of grouping behaviour and 3D distribution in the water column for manta rays.

### 4.3. Behavioural observations outside the limits of recreational dive depths

Until now, courtship behaviour in manta rays and other mobulid species has only been studied through direct observation (Yano et al., 1999; Stevens et al., 2018a; Duffy & Tindale, 2018; Carpenter & Griffiths, 2023). Courtship was the deepest criteria-based behaviour other than cruising recorded by Crittercams to a maximum depth of 86.3 m, over 45 m beyond recreational diving limits. Observational and telemetry limitations would not have allowed this behaviour to be described without an observable video component. Indeed, the new insight into *M. alfredi* courtship behaviour observed here is particularly interesting as it confirms that courtship events often last at varying intensity for extended periods away from cleaning stations and outside the viewing vicinity of underwater observers. Courtship was not observed in video components for *M. birostris*, but this could be attributable to the low sample size of deployments with restricted temporal resolution. Sampling for *M. alfredi* in Raa Atoll may have contributed to the observed instances of courtship behaviour because this study occurred during the peak courtship and mating season (Stevens et al., 2018a).

Vertical diving behaviour in elasmobranchs is hypothesised to be driven by foraging opportunities, thermoregulation, predator avoidance, or increased energy efficiency (Stewart et al., 2018; Andrzejaczek et al., 2019). One individual (MDV-15), an adult female *M. alfredi*, was observed engaging in courtship behaviour for approximately one hour between depths of
25–86.3 m. After breaking off from courtship behaviour, the individual made a dive to 324 m and began returning to the surface immediately after reaching depth, forming a V-shaped dive. No length of time was spent at depth, nor were any behaviours indicative of foraging observed, so feeding behaviour was unlikely to be the driver for this dive. Instead, this dive profile is consistent with research on diving and subsequent thermoregulation in elasmobranchs (Thums et al., 2013), including other mobula species (Thorrold et al., 2014). It is possible the individual dove to escape pursuing male suitors or to cool down after increased courtship activity in shallow, warm water. V-shaped dives have also been recorded for tagged *M. alfredi* in Saudi Arabia (Braun et al., 2014). The authors hypothesise that *M. alfredi* were not feeding at depth but taking advantage of their negative buoyancy to implement energy-saving gliding behaviour. The malfunctioning of the Crittercam video component during the deepest dive negated our ability to determine whether the animal had reached the ocean floor or was swimming in the middle of the water column; however, the seabed only reaches a maximum depth of 350 m between Lhaviyani Atoll to the east and Raa Atoll (Rasheed et al., 2021).

Satellite and acoustic tags have provided insight into late afternoon dives and evening movements offshore for *M. birostris* in Revillagigedo Archipelago, Mexico, and Northern Peru (Stewart et al., 2016b; Andrzejaczek et al., 2021). Two *M. birostris* individuals (REV07 and REV08) exceeded 100 metres in the afternoon and remained deeper than average until the crittercams were released. These dives were unlikely indicative of foraging as the Crittercam did not record feeding. The timing of the dives suggest they may have been moving offshore for the evening hours, potentially to feed away from shallower habitats. These individuals were also hugging the seabed during the dives, which may have been a tactic for predator avoidance (Stewart et al., 2018; Andrzejaczek et al., 2019). Alternatively, both species could be using the dives to access geomagnetic and bathymetric cues. These cues can help the species orient themselves and navigate as has been observed in scalloped hammerheads (*Sphyrna lewini*) (Klimley, 1993; Howey et al., 2016).

Of all behaviour categories, feeding only occurred during 5% (73.9 min) of recorded time for *M. alfredi* in Raa Atoll and 0% for *M. birostris* in Revillagigedo. Given the estimated large metabolic demands of both species, this was unexpected. However, camera deployments in Raa Atoll took place...
at a well-known cleaning aggregation site and were temporally inconsistent. As such, individuals that came here may have already fed earlier and arrived at the cleaning station afterwards. Furthermore, Crittercams were only deployed on three animals during the afternoon, two of which were recorded feeding during their track. Additionally, the view of the Crittercam must be addressed in this study as a potential limitation to observing feeding behaviour in *M. alfredi* as cephalic fins were only sometimes visible in the footage, making it difficult to confirm foraging.

There is also evidence from stable isotope analyses that a substantial portion of dietary intake for both species of manta ray is mesopelagic in origin (Burgess et al., 2016; Peel et al., 2019). Foraging on mesopelagic zooplankton is hypothesised to take place at night when this prey vertically migrates towards the surface. Since our deployments were limited to daylight hours for logistical reasons, any insights into night-time foraging behaviour could not be gathered. Stewart et al. (2016b) highlighted similar challenges and could only confirm feeding at depth (130–140 m) in Revillagigedo for *M. birostris* using opportunistic sightings from manned submersibles. In Papua New Guinea, groups of *M. alfredi* have also been repeatedly observed from a manned submersible feeding on mysid shrimp at a depth between 190–200 m (M. Erdmann, pers. comm.). Crittercam data from the Maldives confirmed social feeding to a depth of 69.8 m and confirmed that Maldivian *M. alfredi* are not solely reliant on surface prey patches. Exploitation of deeper sourced prey could explain why surface sightings of *M. alfredi* drop during the months of monsoonal transitions, when patches of surface prey are less predictable and sought out by these animals. Capturing foraging events in the future, especially at night, will likely require the addition of infrared light sources and increased camera retention.

### 4.4. Interspecific interactions and cognition

*Caranx* species employ several feeding strategies facilitated by the foraging behaviour or large body size of marine megafauna species (Parrish et al., 2008; Auster et al., 2016; Knochel et al., 2023). For example, *Caranx spp.* have been observed following foraging monk seals (*Monachus schauinslandi*) in the Hawaiian Islands and ingesting prey dislodged from the sediments due to the rooting behaviour of the seal (Parrish et al., 2008). *Caranx spp.* have also been observed following stingrays in shallow areas waiting to consume any prey flushed from the benthos by the bioturbation caused...
by the foraging ray (Kiszka et al., 2015). Trevally have been observed to use marine megaplanktivores like whale sharks (*Rhincodon typus*) and *M. birostris* to ambush unsuspecting prey (Auster et al., 2016; Nicholson-Jack et al., 2021) and to attack smaller commensal teleosts that live in association with these larger species (Knochel et al., 2023). In the *M. alfredi* Crittercam footage, giant trevally (*Caranx ignobilis*) can repeatedly be seen biting the release string of the hook attachment from the Crittercam, which may have been confused for prey. The observations provide further evidence that large predatory piscivorous teleost species may opportunistically forage on other teleosts associated with manta rays.

Manta and devil rays possess enlarged telencephalon regions in their brains, which is generally associated with higher sensory processing, memory, learning, and the potential for complex social behaviour (Ari, 2011). Curiosity and exploratory behaviours are also good indicators of higher brain function (Berlyne et al., 1965), and manta rays are well known by divers to be inquisitive of humans (O’Malley et al., 2013). *Mobula birostris* have been incidentally photographed following sicklefin devil rays (*Mobula tarapacana*) (Stevens et al., 2018b), but the interaction in this study between the female *M. alfredi* and the *M. mobular* is the first time these inter-mobulid species interactions have been documented. Although the motivation for this interaction cannot be known, the footage showed that the manta ray was exhibiting the same curiosity it showed to other manta rays it encountered during the deployment. Further deployments will hopefully shed more light on the social behaviours of these rays.

4.5. Limitations and future work

Advancements are needed to ensure longer-term retention and improve the angle of the video frame. While most Crittercam deployments on other species involve capture in their application, there are logistical constraints to capturing manta ray species, so any camera deployment would likely need to be performed on free-swimming animals. However, adjustments to the Crittercam body could provide a better viewing angle of the cephalic lobes, including altering the pitch lengthwise to give the camera a more ‘downward’ view. The use of animal-borne cameras in combination with a suite of sensors (accelerometer, temperature, depth, oxygen) would also enable better categorization of behaviours. Indeed, in this study we used the apparent slowing of swimming speed of *M. alfredi* in addition to other parameters (i.e.,
the presence of cleaner fish in the video frame) to deduce that cleaning had occurred. Adding a tri-axial accelerometer component would provide data useful in categorising and confirming behaviours observed in the video. The application of these bio loggers will be instrumental in developing bioenergetic models for these large epipelagic rays and confirming prey species identity and foraging rates. Delayed start recordings, recordings at set intervals to prolong battery life, sampling over multiple days, and adding a light source to the camera body are techniques that can be used to capture nighttime behaviours, where foraging on vertically migrating prey is hypothesised to take place.

The drivers of behaviour can be multi-faceted and complex, making behavioural studies challenging to conduct in the wild. Criteria were used to classify behaviour; however, some behaviours may have been misidentified, which needs to be considered a limitation. Early stages of courtship behaviour in adult rays may have been misidentified as social cruising; therefore, increased sampling of immature individuals may widen understanding of socialisation unrelated to reproductive behaviour. With a more consistent viewing angle, an analysis of cephalic lobe movements may reveal better insights into feeding and social behaviour (Perryman et al., 2021). Despite the limitations, the video recorded by the Crittercams increases the data available over extended periods for both *M. alfredi* and *M. birostris*.

4.6. Conclusions

Most studies using animal-borne video cameras remain descriptive instead of hypothesis driven. Nonetheless, the observations made here provide behavioural context that can be used to fuel hypothesis-driven research questions. Crittercams revealed associative cruising behaviour in *M. alfredi*, confirmed courtship behaviour in *M. alfredi* depths of at least 86.3 m, and provided a quantifiable estimate of gregariousness between the *M. birostris* and *M. alfredi* populations sampled in this study. Observations of investigative behaviour towards human SCUBA divers and other mobula ray species highlight the inquisitive nature of these rays. Future work should sample behaviours at other times of the year and away from divers (particularly for *M. birostris*) and widen the demographics of the sampled population to include juveniles.
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References


**Appendix**

**Video 1.** Breaching behaviour by *Mobula alfredi* equipped with a Crittercam in Raa Atoll, Maldives. This video can be accessed at 10.6084/m9.figshare.24203817.

**Video 2.** Surface feeding behaviour by *Mobula alfredi* equipped with a Crittercam in Raa Atoll, Maldives. This video can be accessed at 10.6084/m9.figshare.24203817.

**Video 3.** Courtship behaviour as recorded *Mobula alfredi* equipped with a Crittercam in Raa Atoll, Maldives. This video can be accessed at 10.6084/m9.figshare.24203817.

**Video 4.** A reef manta ray (*Mobula alfredi*) equipped with a Crittercam approaches a cleaning station. Species of cleaner wrasse (*Labroides dimidiatus, Thalassoma amblycephalum, Thalassoma Lunare*) can be observed cleaning the mantas. This video can be accessed at 10.6084/m9.figshare.24203817.

**Video 5.** Cleaning behaviour by Clarion Angelfish (*Holacanthus claronensis*) as recorded by *Mobula birostris* equipped with a Crittercam in Revillagigedo Archipelago, Mexico. This video can be accessed at 10.6084/m9.figshare.24203817.

**Video 6.** Social cruising behaviour as recorded by *Mobula alfredi* in Raa Atoll, Maldives. This video can be accessed at 10.6084/m9.figshare.24203817.

**Video 7.** Solitary cruising along the seabed by *Mobula birostris* in Revillagigedo Archipelago, Mexico. This video can be accessed at 10.6084/m9.figshare.24203817.
**Video 8.** Crittercam recording of spinetail devil rays (*Mobula mobular*) interacting with *Mobula alfredi* in Raa Atoll, Maldives. This video can be accessed at 10.6084/m9.figshare.24203817.

**Video 9.** A crittercam recording of trevally (*Caranx ignobilis*) interacting with *Mobula alfredi* in Raa Atoll, Maldives, possibly as an abrasive surface to scratch themselves to remove parasites. This video can be accessed at 10.6084/m9.figshare.24203817.