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Current strength, temperature, and bodyscape modulate cleaning services for giant manta rays

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Abstract

The cleaner-client system among reef teleosts has received considerable attention in both wild and captive environments, but the spatially and taxonomically diverse associations between cleaner fish and elasmobranchs are less understood. Using remote video, we investigated interactions between giant manta rays *(Mobula birostris*) and cleaner wrasse at a seamount in the Philippines. Cleaning events occurred between 11:00 and 16:00 hours on a seasonal basis and were constrained by current strengths and ambient water temperatures. The frequency with which giant manta rays interacted with cleaner fish varied on an individual basis. Blue streaked cleaner wrasse (*Labroides dimidiatus*) and moon wrasse (*Thalassoma lunare*) selectively foraged on manta rays' gills and pelvis, with *L. dimidiatus* also demonstrating slight preferences for the pectoral fins. Cleaners' foraging preferences may indicate ectoparasitic infections in specific areas of a manta ray's body. The exclusivity with which giant manta rays visited a particular cleaning station on the seamount may be a response to the quality of services that cleaners provide there. Giant mantas' fidelity to this site may also be attributed to localised concentrations of food that are available nearby. The seamount provides habitat that appears to be important to the life history strategies of the region's giant manta rays.

Key Words: cleaner fish, mutualism, ectoparasite, elasmobranch, seamount, giant manta ray

Introduction

Seamounts are widely regarded as hotspots of biodiversity due to the unique oceanographic conditions that they generate (Morato et al. 2010, Clark et al. 2010), and have been identified as important staging areas for migrant marine megafauna (Worm et al. 2003, Pitcher et al. 2010). While the ecological mechanisms that attract elasmobranchs to seamounts are poorly understood, it has been suggested that they provide refuge, represent social convergence points, act as navigational waypoints, and function as mating, feeding, and nursery grounds for a variety of pelagic species (Worm et al. 2003, Pitcher et al. 2010, Oliver & Bicskos 2014, Wells et al. 2018).

The giant manta ray (*Mobula birostris*) is one of two recognised manta ray species (Marshall et al. 2009). Reaching 6.70 m in total (disc) width, the ray is popular among tourists for its size and approachable behaviour. Recognised from fisheries and by-catch to frequent tropical and subtropical offshore waters circumglobally, giant manta rays mature late, have low fecundity, and are classified as Vulnerable to Extinction by the International Union for the Conservation of Nature and Natural Resources' (IUCN) Red List of Species (Marshall et al. 2018). For the past two decades, giant manta rays have been observed by SCUBA divers on Monad Shoal, which is a shallow coastal seamount in the Central Visayas of the Philippines, where they interact with blue streaked cleaner and moon wrasse (*Labroides dimidiatus* and *Thalassoma lunare*) (Acebes et al. 2016). Rays, including giant manta rays, are known to host metazoan parasites (Caira and Healy 2004), and it is proposed that they visit a cleaning station at this site to control infection.

Batoid rays infected with parasites suffer a variety of health consequences. These include skin lesions, necrosis, anaemia, respiratory disease, and chronic bacterial and viral infections that have been reported as lethal in some species (Caira and Healy 2004, Garner 2013). Ectoparasitic infections in captive elasmobranchs cause behavioural modifications such as rubbing against the

structures of enclosures and interacting with cleaner fish (Keyes 1982, Reed et al. 2009).

The cleaning system is a classic model of cooperative behaviour among species in which cleaner fish remove ectoparasites and dead or infected tissue from the surface, gills and sometimes the mouth of client fish (Soares 2017). Interactions with cleaner fish appear to improve the health of teleost clients by reducing their ectoparasite loads, but the benefit of these interactions is less understood amongst elasmobranchs (Grutter 1996, Grutter and Lester 2002, Waldie et al. 2011, Soares et al. 2011, Ros et al. 2011). Clients will often 'pose' near cleaning stations to solicit 'services' from cleaner fish (Bshary and Côté 2008, Oliver 2012). There are approximately 130 species of marine cleaners, with ectoparasitic infection being the most likely proximate cue for clients seeking their services (Keys 1982, Sikkel et al. 2004, Oliver et al. 2011). The blue streaked cleaner wrasse, *Labroides dimidiatus,* is an obligate cleaner that preferentially feeds on gnathiid isopod larvae that are known to infect the gills of reef manta rays (*Mobula alfredi*) (Grutter 1996, Grutter and Bshary 2004, Marshall 2009, O'Shea et al. 2010). *L. dimidiatus* prefer large clients and interact with manta rays at spatially diverse locations across the globe (Grutter 1996, Grutter et al. 2005, Marshall 2009, Kitchen-Wheeler 2010, Germanov et al. 2019). The moon wrasse, *Thalassoma lunare*, which is less understood as a cleaner species, also provides cleaning services for manta rays (Kitchen-Wheeler 2010, Barbu et al. 2011, Germanov et al. 2019). Moon wrasse are facultative cleaners wherein only juveniles clean whilst contemporaneously exploiting alternative food sources (Côte 2000).

Cleaners may maximize the profitability of their energy return by selectively foraging on areas of clients where specific types of parasites can be found (Rohde 2005). When investigating how cleaners forage on elasmobranchs, Oliver et al. (2011) showed that *L. dimidiatus* and *T. lunare* spent more time inspecting areas of thresher sharks (*Alopias pelagicus*) that were infected by

ectoparasitic digeneans (*Paronatrema spp*) compared to areas that are known to harbour other types of parasites (Cadwallader et al. 2015). They concluded that cleaners may optimise their foraging by selecting areas of a client's body that are most likely to produce the highest energy reward per unit effort (Rohde 2005, Oliver et al. 2011). A cleaner's foraging behaviour is therefore likely to be driven by the quality of the food patch in relation to the ease with which food may be obtained there (Oliver et al. 2011). Since specific types of parasites infect specific patches of an elasmobranch's body (Caira and Healy 2004, Rohde 2005), it can be predicted that cleaners will show preferences for foraging in some patches over others.

In this paper we show that giant manta rays (*M. birostris*) interact with cleaners at a seamount in the Philippines and investigate the cleaner-client association. We quantified behavioural interactions between giant manta rays and cleaner wrasse from remote video observations to address the following hypotheses: (1) the dynamics of the cleaner-manta system are driven by environmental factors; and (2) cleaner wrasse preferentially forage on specific areas of a manta ray's body. The cleaner-manta association is discussed in relation to other known cleaner-client systems in the marine environment.

Method

Location

Monad Shoal (N 11° 19' 06.7", E 124° 11' 31.9") is a seamount in the Central Visayan Sea, near Malapascua Island, Cebu, the Philippines (Oliver et al. 2011). The top of the mount (15 – 25 m) is formed by a shallow plateau of low-profile *Acropora* that is fringed on all sides by a coral reef which crests and sheers down 250 m to the valley below. An array of cleaning stations lines the southern face of the mount, one of which (Station A) is frequented by giant manta rays (Oliver et al. 2011).

101 *Sampling*

102 SCUBA divers initially deployed remote video cameras using protocols described by Oliver et al.
103 (2011) at five cleaning stations (A - E) on Monad Shoal during a pilot study which ascertained that
104 Station A was the only location on the seamount where giant manta rays could be observed
105 interacting with cleaner fish. A total of 1,171.45 hours of video observations were subsequently
106 recorded from a fixed point on Station A between April 2011 and June 2013, during three field
107 expeditions spanning 262 days over 20 months. A Sony Handycam® HDR-SR8, housed in an
108 Amphibico Elite housing and fitted with a 120° wide-angle lens, with focal range locked to 0.3 m,
109 was pre-set to record for 360 continuous minutes for all camera deployments. The camera was
110 retrieved at the end of each deployment period, and the video data downloaded for analysis.
111
112 Environmental data including tidal conditions, water temperature, and the *in situ* current strength
113 were documented for each camera deployment. Temperature was measured *in situ* to the nearest
114 degree Celsius using the readouts of a dive computer at the time of the camera deployment. Current
115 strength was measured from a submerged windsock that was fixed to the substrate in the camera's
116 field of view. Tides were estimated from Admiralty predictions for Bogo Bay, the Philippines
117 (EasyTide 2011-2013).
118
119 *Analysis of video recordings*

120 Video observations of giant manta rays were analysed in 29.97 frames s^{-1} resolution using Final
121 Cut Pro 7 (Apple Inc. CA). Sequences documenting interactions between manta rays and wrasse
122 were classified as cleaning 'events'. These began when a manta ray entered the camera's field of
123 view and ended after it left and did not return for ≥ 5 minutes. If an individually identified manta
124 (see section below) returned during this time period it was considered to be a continuation of the
125 cleaning event. Because it was not possible to scale a manta ray from its distance to the camera,

size was not considered in the analyses. Sex was determined through the presence or absence of claspers.

Identification of individual manta rays

We took still images of the video recordings when a manta ray was positioned directly above the camera to capture its ventral surface. We then entered the still images into a photo bank that considered patterning in the manta's ventral markings to identify a new individual, or a match to an individual that had been previously observed at Station A following Marshall et al. (2011) and Town et al. (2013). Due to the camera's field of view, it was not always possible to capture the entire ventral surface for each manta ray so some mantas could not be individually identified.

Cleaning interactions

To investigate whether cleaners forage selectively on giant manta rays, it was assumed that different areas of a client's bodyscape host different types of parasites (Caira and Healy 2004, Rohde 2005), and that some areas represent higher quality food patches for cleaners than others (Bshary and Grutter 2002, Oliver et al. 2011). Eight food patches were outlined on a sketch of a giant manta ray and categorised as 'gills', 'pelvis', 'dorsal head', 'ventral head', 'pectoral', 'ventral body', 'dorsal body', and tail (Fig. 1). These were then used to document cleaner interactions for each event. The pelvic and tail patches included the cloaca and tail respectively, the pectoral patch incorporated both pectoral fins, the gill patch included both sets of gill openings, and the head patch consisted of the cephalic lobes, the eyes, and the mouth. The ray's dorsal surface was split into two patches, the boundary of which followed the underside of the ray's superbranchial region (Fig. 1).

Cleaning interactions were characterised by a cleaner's mouth making discernible physical contact

151 with a manta ray and were termed 'bites'. Bite locations were individually mapped onto the sketch
152 according to their associated cleaner species (*Labroides dimidiatus* or *Thalassoma lunare*) and
153 treated separately in the analyses. Bites were used as a proxy for parasite removal following Oliver
154 et al. (2011). The number of cleaning inspections may be underestimated because cleaner fish
155 activity behind a manta ray could not be observed on the video recordings.
156
157 *Statistical Analyses*
158 To investigate variation in the distribution of manta ray visits to the cleaning station, a generalized
159 additive model was fitted with a binomial error distribution. The response variable was manta ray
160 presence, or absence, in any given minute during which the camera was recording. The effects of
161 the explanatory variables day of the year, minutes after high tide, minutes after 05:00 and current
162 strength (m/s) were modelled by thin-plate cubic splines. Knots were conservatively set to three
163 unless we believed there to be more degrees of freedom in the relationship, in which case knots
164 were increased until no further changes were visible when plotting the output (Wood 2017), which
165 occurred in the cases of day of the year (k = 12), and minutes after high tide (k = 4). Temperature
166 (°C), and minutes observed, were also included as explanatory variables, but with only a linear
167 effect since they took too few distinct values to allow a more complex approach.
168
169 To investigate variation in the rate of cleaning interactions, a hierarchical Poisson regression model
170 was fitted. The number of interactions observed in a cleaning event was the response variable, with
171 day of the year, minutes after high tide, temperature (°C), minutes after 05:00, manta ray identity
172 term, and current strength (m/s) as quantitative explanatory variables. We included an offset term
173 representing the natural log of event time in seconds, under the assumption that the expected
174 number of interactions over the duration of an event was the product of the rate of interactions per
175 second, and the total event time. Event number was included as a normally-distributed random

intercept term with a mean of zero and an unknown standard deviation, to account for differences between events in the rate of interactions.

To determine how cleaner wrasse foraging differed between patches on a manta ray, another hierarchical Poisson regression model was fitted. The number of cleaning interactions on a given patch of a given manta ray by a given cleaner species was modelled as a random variable with a Poisson distribution. The natural log of the expected number of interactions per unit area (where the unit is the entire surface area of a manta) was modelled as a linear function of patch, cleaner species, and the interaction between patch and cleaner species. To control for differences in patch size, the expected number of interactions per unit area was multiplied by the proportion of body surface area that each patch represents. These area proportions were estimated by counting pixels in each patch on a perpendicular image of a manta ray's dorsal and ventral surfaces in Adobe Photoshop (Adobe Inc, San Jose, California). The effects of event number on the natural log number of inspections were assumed to be drawn from a normal distribution with mean zero and an unknown standard deviation. To examine whether each species of cleaner wrasse preferred specific patches after controlling for patch area, back-transformed patch effects with central 95% credible intervals were calculated for each cleaner species. These estimates were expressed graphically relative to the preference for the dorsal head patch, with overlapping credible intervals between species indicating that there was not a clear difference in preference.

All analyses were completed in the R statistical environment (R Core Team, 2019), using the rstanarm package (Goodrich et al. 2018), which implements the NUTS algorithm for Bayesian inference (Gelman et al. 2013). Generic weakly informative priors (independent normal (0, 1)) (Gelman et al. 2015) were used for all parameters. For each model, four Monte Carlo chains were run for 2500 warmup iterations followed by 2500 sampling iterations. Potential scale reduction

201 factors ($\hat{R}$) were < 1.1 for all parameters and effective sample sizes (n_{eff}) were greater than 2500,
202 indicating no problems with model convergence. To assess model fits, PSIS-LOO values were
203 computed in the loo package (Vehtari et al. 2017). Pareto *k* diagnostics and marginal posterior
204 predictive checks were undertaken using the bayesplot package (Gabry et al. 2018) which did not
205 reveal any obvious issues (PSIS $\hat{k} < 0.7$ and no evidence of overdispersion). Initial models were
206 simplified through term by term deletions, operating under the assumption that a negative
207 difference in ELPD values of more than 2 estimated standard deviations indicated a worse model.
208
209 **Results**
210 *Event Frequency*
211 We identified 15 individual manta rays from 154 cleaning events that were recorded over 60 days
212 during 15 of the study months (April 2011 - June 2013). Individual mantas were observed
213 interacting with cleaners for a mean (± SE) of 4.4 ± 0.22 events (95% CI: 4.18-4.62), and events
214 lasted 5.23 ± 0.97 minutes (95% CI: 5.06-5.56 minutes).
215
216 Nine mantas (M2 - M10) were first recorded in 2011, four of which were observed revisiting the
217 site in 2012 (M5, M7, M8, M9). Six mantas (M11 - M16) were first observed in 2012, two of
218 which (M12, M13) were observed revisiting the site in 2013. One manta (M9) was observed every
219 year (2011 - 2013). Across all observations four manta rays were only seen on a single occasion.
220 The remaining eleven (± SE) had a return rate of 5.64 ± 0.27 (95% CI: 5.10 - 6.18) across the three
221 observation years.
222
223 Comparisons between models of giant manta ray visits showed that the minutes observed, and the
224 minutes after the high tide explanatory variables should be omitted from the final model (Table 1).
225 Manta ray visits to the cleaning station varied throughout the year, occurring most frequently

between April and September, with visits rare during March and July (Fig. 2(a), Table 2). Visits were most likely to occur during warmer temperatures (Fig. 2(b) and in the afternoon (Fig. 2(c), Table 2). Visits were also most likely to occur when the current was strong (> 1.5 m/s) or weak (~ 0.2 m/s - 0.4 m/s), but they were rare when the current was mild (~ 1 m/s) (Fig. 2(d), Table 2).

Cleaning Interactions

There were 32 recorded cleaning events by 11 identifiable mantas for which all data was available. These events lasted between 41 and 2976 seconds (mean: 1087 seconds) and involved between 1 and 22 discernible cleaning interactions (mean: 4.91). Comparisons between single term deletions of the model for cleaning interactions indicated that all of the explanatory variables should remain in the final model (Table 3).

The rate of interactions varied between individual manta rays (Fig. 3(b); Table 4), with some (for example M8) receiving much more attention from cleaners than others. The current strength was found to constrain the number of interactions a manta ray received (Fig. 3(d)), and higher water temperatures had a weakly positive effect (Fig. 3(e) Table 4). The minute after 05:00 had a weak negative effect (Fig. 3(a), and the day of the year had a weakly positive effect (Fig. 3(f); Table 4).

Patch Preference

Single term deletions of the model for patch preferences by cleaner species indicated that the interaction between the patch and species should be omitted from the final fitted model (Table 5). After controlling for differences in patch area and comparing each patch to the 'dorsal head', cleaners showed preferences for certain patches (Fig. 4, Table 6). Both species targeted the gills, which received the largest absolute number of cleaning interactions, with both cleaner species also showing a preference for the pelvis (Fig. 4; Table 6). The pectoral fins received large absolute

numbers of cleaning interactions by *L. dimidiatus*, which resulted in a slight preference for this patch by this species despite its large value for patch proportion (Fig. 4; Table 6). *T. lunare*'s preference for the ventral body could not be estimated since no cleaning interactions were recorded in this patch for this species, even though this parameter was structurally identifiable in the analysis (Table 7).

Discussion

While the cleaner-client system amongst reef teleosts has received considerable attention, the spatially and taxonomically diverse associations between cleaners and elasmobranchs are less understood (Couturier et al. 2018, Grutter et al. 2018). This study represents the first attempt to quantify interactions between giant manta rays and cleaner wrasse in the natural environment and supports knowledge of the importance of cleaning stations to marine ecosystems.

Visit Frequency

Our observations of giant manta rays were most likely to occur in the afternoon on a seasonal basis between the months of April and September. Giant manta rays' large body size and planktivorous diet make ocean productivity a key factor in determining their movements (Papastamatiou et al. 2012, Braun et al. 2014, Burgess et al. 2016), and seasonal shifts in food availability encourage them to undertake substantial migrations (Dewar et al. 2008, Papastatamatiou et al. 2012, Burgess et al. 2016). Giant manta rays are known to frequent cleaning stations in Mozambique, Ecuador, and Indonesia during the austral winter (Dewar et al. 2008, Rohner et al. 2013, Burgess et al. 2016), and their seasonal fidelity to these sites has largely been attributed to increases in local productivity (Carleton et al. 2001, Pitcher et al. 2008) that is driven by oceanographic processes, including currents (Dewar et al. 2008, O'Shea et al. 2010, Jaine et al. 2012, Rohner et al. 2013, Burgess et al. 2016). It is possible that giant manta rays have limited movements on a regional scale in our

study area and that they are only in the vicinity of Monad Shoal when seasonal oceanographic processes promote shifts in productivity and the consequent availability of food (Stewart et al. 2016). They may partition their time to converge on Station A during the afternoon when food is scarce and/or when hydrodynamic conditions facilitate cleaning (see below) (Johansen et al. 2008, Marshall et al. 2011). Similar temporal trends for giant manta rays visiting cleaning stations have been observed in Indonesia where they are known to move offshore to forage nocturnally in deep waters after they clean (Dewar et al. 2008). Mantas' movements and use of our study area may be part of a strategy that considers both temporal variations in food availability and cleaner services without being mutually exclusive (Burgess et al. 2016, Oliver et al. 2019).

The overall occurrence of giant manta ray cleaning events was strongly influenced by the state of the current on the seamount. Certain hydrodynamic conditions may generate sufficient water flow and lift for giant mantas to 'hover' over specific topographical features (Johansen et al. 2008, Marshall et al. 2011). In Mozambique reef manta rays are known to clean during moderate strength currents because these conditions are favourable for hovering over cleaning stations (Rohner et al. 2013). Hovering may facilitate giant mantas' interactions with cleaners since cleaning typically occurs near spatially finite structures that are known as 'focal points' (Acebes et al. 2016, Stevens et al. 2018). Hovering is also likely to be an energetically efficient strategy that makes giant manta rays more accessible to cleaners and therefore more attractive as clients (Acebes et al. 2016, Fish et al. 2018). However, even though hydrodynamic flow may provide lift and facilitate a giant manta's hovering behaviour over a cleaning station, cleaning events were not observed on Monad Shoal when the current was strong. Cleaners are known to seek refuge and conserve their energy during strong currents, which stalls the provision of cleaning services for their clients (Johansen et al. 2008, Eggersten et al. 2016). The reduced availability of cleaners may have decreased the likelihood of a giant manta ray visiting the site during these periods in spite of the energetic

benefits provided by strong currents (Tebbich et al. 2002, Johansen et al. 2008, Fish et al. 2018).

Cleaning Interactions

Reef teleost clients are known to show preferences for specific services that are offered by specific cleaners at specific stations (Bshary and Grutter 2006, Pinto et al. 2011). A client's fidelity to individual cleaners may be driven by the type and quality of service on offer (parasite removal, wound healing, tactile stimulation), or other clients competing for the same resources (Bshary and Grutter 2006, Bshary et al. 2008, Adam 2010). Many of the individual mantas that we observed on Station A had open wounds from bite marks and dismembered cephalic lobes, presumably from encounters with predators and/or fishing gear (Oliver 2012). Giant manta rays' fidelity to this site may be indicative of a lack of competition from other elasmobranch clients, and/or specialist wound healing and parasite removal services that are on offer at this particular location.

Higher temperatures were found to influence the frequency with which giant manta rays visited Station A and were also associated with an increase in the frequency of their interactions with cleaners. Digenean flatworms (Phylum Platyhelminthes) that are known to infect the cloacas of elasmobranchs on Monad Shoal (Caira and Healy 2004, Oliver et al. 2011, Cadwallader et al. 2015) are typically dioxenous, parasitising two hosts during their life cycle (Mills 1979). During reproduction, oviparous digeneans release their fertilised eggs into the water column where they hatch to produce miracidia. The miracidia swim to find an intermediate mollusc host where they grow through several life stages until they eventually emerge as cercaria larvae (Gibson et al. 2002). Larvae live freely in the water column before they attach to their terminal host, which they locate from host-derived chemical or mechanical cues, or shadows (Whittington et al. 2000). Attachment typically occurs during seasonal epizootic events, which are characterised by cool (~ 25 °C) or warm (~ 32 °C) water conditions (Whitfield et al. 1977) and may coincide with a time

when hosts are particularly vulnerable to infection (Möller 1978, Silan et al. 1985, Tubbs et al. 2005, Rückert et al. 2008). We conjecture for further study that the seasonality with which giant manta rays visit Monad Shoal might coincide with ectoparasite attachment events in the area, leading to heightened parasitism and a greater need for interacting with cleaners.

Since cleaner fish tend to modify their foraging patterns in response to variations in the quantity and quality of a food resource, giant manta rays with the highest parasite loads are more likely to be attractive clients (Oliver et al. 2011, Pinto et al. 2011). *L. dimidiatus* typically favours larger clients with high ectoparasite infections, and a client's body size has been positively correlated with ectoparasite abundance (Barber et al. 2000, Sikkel et al. 2000, Grutter and Bshary 2003, Caira and Healy 2004). The number of cleaning interactions (per unit time) varied substantially among individual mantas across our observations. Although we were not able to quantify body size, it is possible that larger mantas received more attention from cleaners than smaller ones (Sikkel et al. 2000, Grutter and Bshary 2003, Oliver et al. 2011).

Cleaning interactions were patch-specific, suggesting that the cleaners forage selectively across a giant manta ray's bodyscape. Ectoparasites that attach to elasmobranchs are site specific and typically infect the same sites across different host species (Littlewood et al. 1997, Henderson et al. 2002, Caira and Healy 2004, Dippenaar et al. 2008). Platyhelminthes parasitise most elasmobranchs (Caira and Healy 2004), and *Paronatrema spp* found in and around the cloaca of pelagic thresher sharks (*Alopias pelagicus*) that regularly visit our study site are thought to be the primary driver for cleaners preferentially foraging on their pelvis (Oliver et al. 2011, Cadwallader et al. 2015). Monogenean flatworms are similarly known to infect the cloaca of manta rays in Mozambique (Marshall 2009), and gnathiid isopods, which are a primary food source for the blue streaked cleaner wrasse, infect their buccal cavities (Grutter and Poulin 1998, Marshall 2009).

While it was not possible to verify whether manta rays visiting Monad Shoal are infected by gnathiids, digeneans, or monogeneans, our observations suggest that either parasitic abundance is highest in and around the cloaca and gills, or that cleaner fish are selecting parasites, mucus, and/or dead tissue there because they are accessible.

Concluding remarks

Many large marine organisms visit cleaning stations to have parasites removed and giant manta rays appear to regularly visit cleaning stations on inshore reefs. The rays may visit cleaning stations to benefit from feeding opportunities nearby or they may migrate inshore to clean after they forage in deep-water (Burgess et al. 2016, Stewart et al. 2016). Giant manta rays are thought to have limited regional connectivity and so the low number of absolute visits that we recorded either suggests that the habitat no longer supports their requirements, or that they are in regional decline (Stewart et al. 2016). Cleaning interactions are both spatially and taxonomically diverse and cleaners' selective foraging on giant manta ray clients demonstrates a level of preference for areas of a manta's body where specific types of parasites might be found. Future identification and quantification of parasite loads on giant manta rays would offer further evidence that elasmobranch clients provide high quality food patches for cleaners at seamounts. Cleaning stations are key points of convergence for giant manta rays and they may only frequent specific cleaning stations so these spatially finite habitats should be carefully managed.

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Author contributions

SO conceived and performed the experiments. CM and MS analysed the data. CM wrote the first draft as part of his undergraduate dissertation. SO, CM and MS wrote the final manuscript. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Compliance with ethical standards

Conflicts of interest

The authors declare that they have no conflicts of interests.

Ethical standards

The research presented in this paper complies with the guidelines from the directives 2010/63/EU of the European parliament and of the Council of 22nd September 2010 on the protection of animals used for scientific purposes. All of the fieldwork was undertaken with the permission of the Governor of the Province of Cebu and adhered to the Philippine 'Wildlife Resources Conservation and Protection Act'.

Data Availability

The datasets generated and/or analysed during the study are available from the corresponding author on reasonable request.

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Tables

Table 1. Comparisons between models of manta ray visits with single term deletions. "ELPD Difference" refers to the computed differences in the model's ELPD values (each model compared to the model described in row 1), and SE difference is the estimated standard error of the difference.

	ELPD Difference	SE Difference
Day of Year + Minutes after High Tide + Minutes after 05:00 + Current Strength	0	0
- Minutes Observed	- 0.7	0.7
- Minutes After High Tide	- 0.9	0.5
- Temperature	- 1.1	0.2
- Current Strength	- 2.1	0.8
- Minutes After 05:00	- 8.6	4.2
- Day of the Year	- 15.3	5.5

663 **Table 2.** The posterior mean, the 0.025- and 0.975-quantiles of the posterior distribution, and the
664 median absolute deviation (a robust estimate of posterior standard deviation) for each explanatory
665 term included in the final model of giant manta ray visits to station A.

	Mean	MAD Std. Dev.	2.5%	97.5%
Intercept	- 1.3	0.1	-1.9799	0.2080
Day of the Year	0.6	0.3	0.1334	1.2032
Temperature	0.8	0.5	0.0144	2.8502
Minutes After 05:00	1.4	0.9	0.1395	3.5881
Current Strength	1.1	1.3	0.0189	4.6120

666

667

668 **Table 3.** Comparisons between models of cleaning interactions with single term deletions. "ELPD
669 Difference" refers to the computed differences in the model's ELPD values (each model compared
670 to the model described in row 1), and SE difference is the estimated standard error of the
671 difference.

672

	ELPD Difference	SE Difference
Day of the Year + Minutes after High Tide + Minutes after 05:00 + Temperature + Current Strength	0	0
- Minutes After High Tide	- 17.6	2.6
- Day of the Year	-17.7	2.6
- Temperature	-19.1	2.7
- Current Strength	- 19.8	2.3
- Minutes After 05:00	- 20.3	3.2
- Manta Ray Identity Term	- 22.0	2.9

673

674 **Table 4.** The posterior mean, the 0.025- and 0.975-quantiles of the posterior distribution, and the
675 median absolute deviation (a robust estimate of posterior standard deviation) for each explanatory
676 term included in the final interactions model.

677

	Mean	MAD Std. Dev.	2.5%	97.5%
Intercept	-7.812	3.704	-15.40	-0.50
Day of the Year	0.003	0.002	0.001	0.007
Minutes After High Tide	-0.001	0.001	-0.0028	0.0015
Minutes After 05:00	-0.003	0.001	-0.0059	0.0001
Temperature	0.234	0.134	-0.0276	0.5161
Current	-1.904	0.986	-3.9220	0.0126
Manta Ray Identification Term	0.285	0.193	0.2562	0.3328

678

679

680 **Table 5.** Comparisons between models of patch preferences by cleaner species with single term
681 deletions. "ELPD Difference" refers to the computed difference in the model's ELPD values (each
682 model compared to the model described in row 1), and SE difference is the estimated standard
683 error of the difference.

684

	ELPD Difference	SE Difference
Patch * Species + (1|Day)	0	0
Patch + Species + (1|Day)	-6.9	4.4
Patch + (1|Day)	-53.7	13.0
Species + (1|Day)	-455.5	74.5

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689 **Table 6.** The posterior mean, the 0.025- and 0.975-quantiles of the posterior distribution, and the
690 median absolute deviation (a robust estimate of posterior standard deviation) for each explanatory
691 term included in the final patch preferences model. Patch results are expressed in comparison to
692 the "Ventral Head" patch, and results presented for *Thalassoma lunare* are expressed in
693 comparison to *Labroides dimidiatus*.
694

	Mean	MAD Std. Dev.	2.5%	97.5%
Intercept	1.8	0.3	1.2253	2.3584
Patch: Ventral Body	-1.1	0.3	-1.6809	-0.5557
Pectorals	-2.2	0.4	-2.8570	-1.4680
Gills	0.5	0.3	-0.1224	1.0840
Dorsal Lower	-2.3	0.3	-2.8868	-1.6430
Pelvis	2.0	0.3	1.4765	2.5272
Dorsal Head	0.1	0.4	-0.7912	0.7986
Tail	0.0	0.4	-0.9323	0.9139
Thalassoma lunare	-1.1	0.1	-1.3472	0.1894

695

696 **Table 7.** The patch proportions and absolute number of cleaning interactions recorded in each
697 patch for each cleaner fish species.
698

Patch	Patch Proportion	Interactions from *L. dimidiatus*	Interactions from *T. lunare*
Ventral Body	0.186	13	0
Pectorals	0.218	51	22
Gills	0.068	115	89
Ventral Head	0.037	4	7
Dorsal Lower	0.415	12	25
Pelvis	0.012	24	19
Dorsal Head	0.036	5	3
Tail	0.029	2	3
Total	*1.00*	*226*	*168*

699 **Figure Captions**

700

701 **Fig. 1.** The food patches onto which locations of cleaning interactions were mapped during the
702 analysis of the video recordings.

703

704 **Fig. 2.** Manta ray visits to Monad Shoal, and general additive model fits for each of the
705 explanatory variables **(a)** Day of the year **(b)** Time Observed **(c)** Current Strength (m / s) **(d)**
706 Minutes after High Tide **(e)** Minutes After 05:00. Dots represent the presence and absence of giant
707 manta rays with predicted probabilities on the y axis. Lines represent posterior means and shading
708 around the lines indicates 95% credible bands.

709

710 **Fig. 3.** The rate of cleaning interactions compared between **(a)** Minutes After 05:00 **(b)** Manta ray
711 identification term (boxplots summarize the posterior distributions) **(c)** Minutes After High Tide
712 **(d)** Current Strength (m / s) **(e)** Temperature and **(f)** Day of the Year. The solid lines represent the
713 posterior mean predictions with shading denoting the 95% credible bands.

714

715 **Fig. 4.** The effects of patch on the rate of cleaning interactions for *L. dimidiatus* (black), and *T.*
716 *lunare* (grey). Effects are expressed relative to the dorsal head patch (dashed line) after controlling
717 for patch area. Dots are posterior means, vertical bars are 95% credible intervals, and preference
718 is expressed if they do not overlap. The parameter for ventral body, *T. lunare*, has been omitted
719 since it could not be estimated from the data.

Figure 1

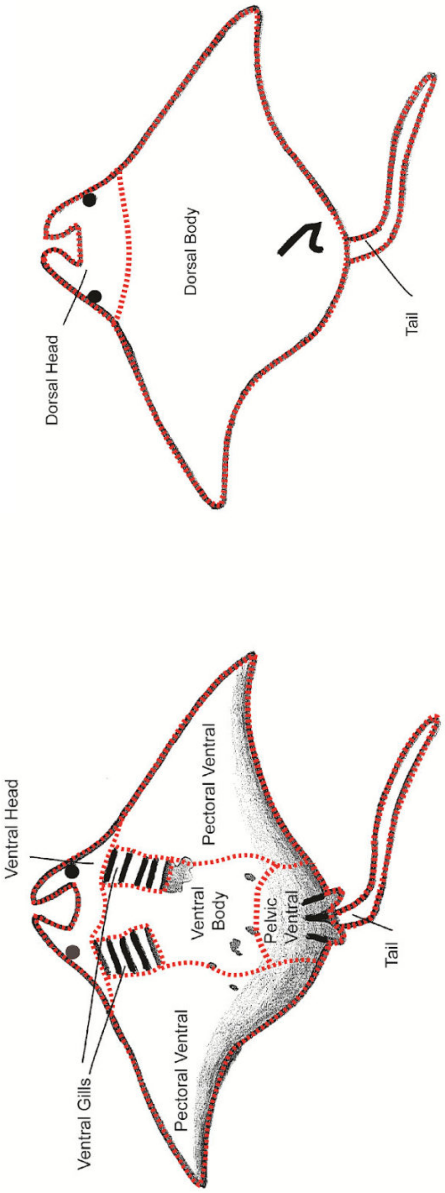
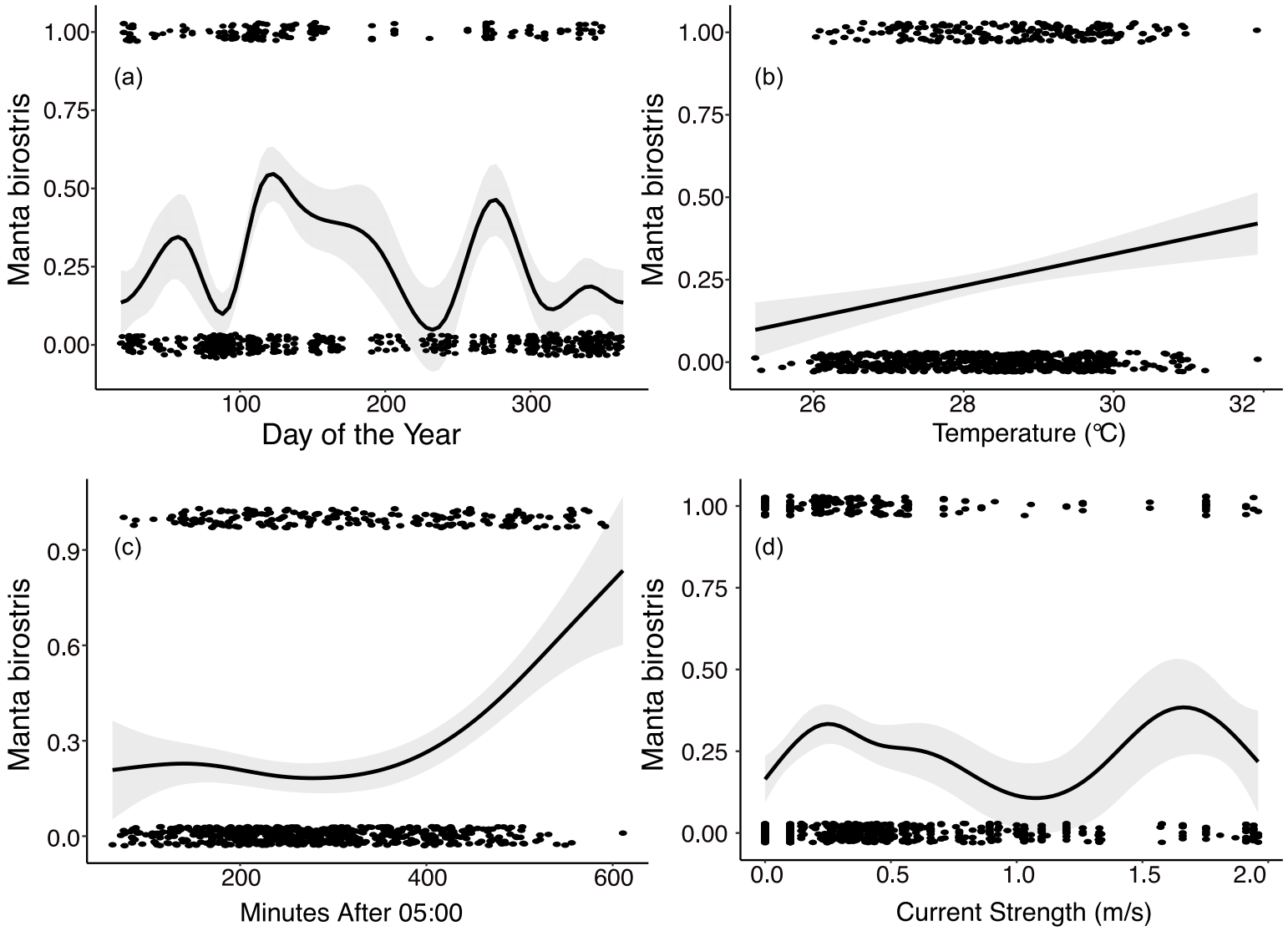

Dorsal Head
Dorsal Body
Tail
Ventral Head
Pectoral Ventral
Ventral Body
Pelvic Ventral
Tail
Ventral Gills
Pectoral Ventral

Figure 2


(a)
Manta birostris
1.00
0.75
0.50
0.25
0.00
100
200
300
Day of the Year
(b)
Manta birostris
1.00
0.75
0.50
0.25
0.00
26
28
30
32
Temperature (℃)
(c)
Manta birostris
0.9
0.6
0.3
0.0
200
400
600
Minutes After 05:00
(d)
Manta birostris
1.00
0.75
0.50
0.25
0.00
0.0
0.5
1.0
1.5
2.0
Current Strength (m/s)

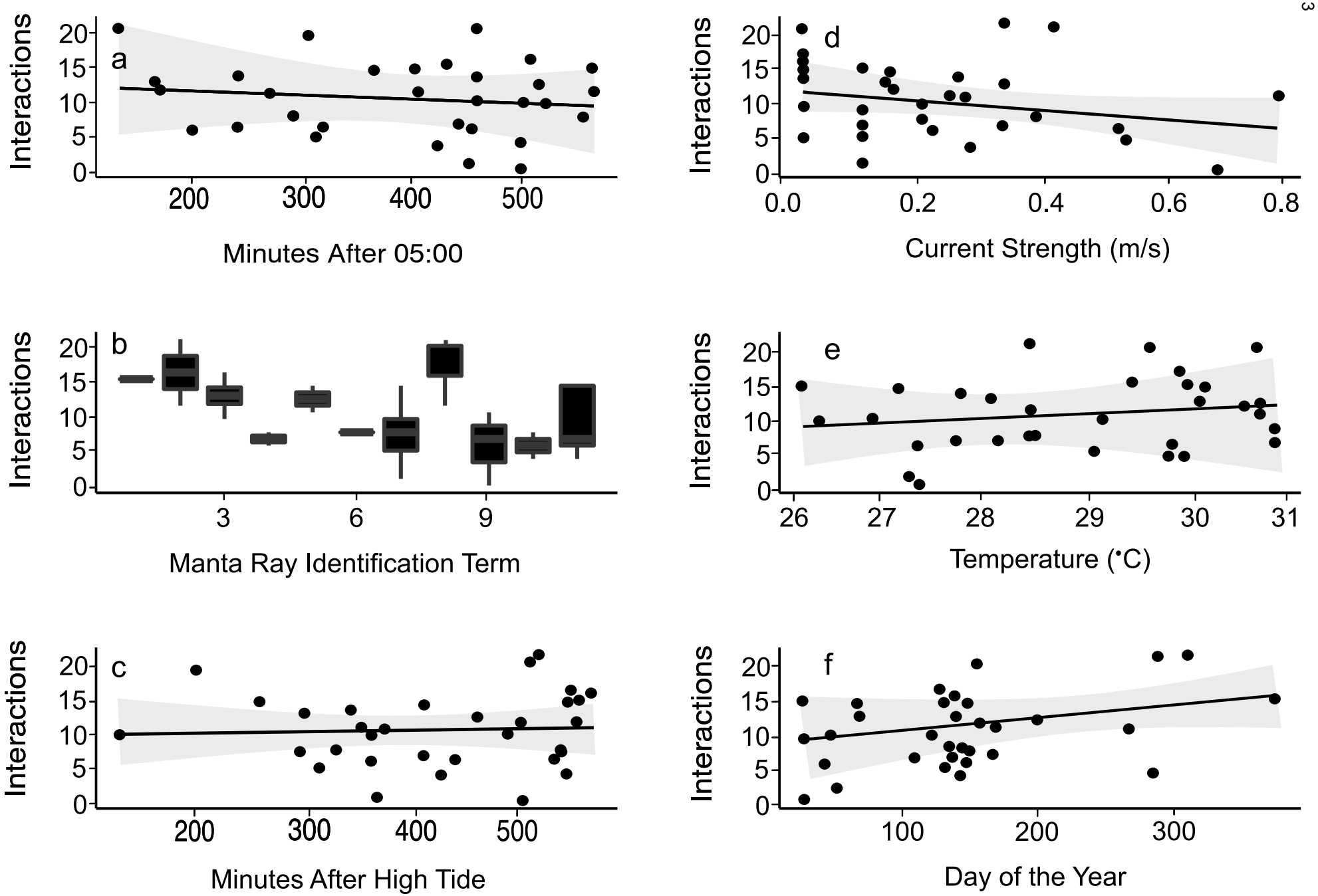

a
Interactions
Minutes After 05:00
b
Manta Ray Identification Term
c
Minutes After High Tide
d
Current Strength (m/s)
e
Temperature (°C)
f
Day of the Year

Figure 4

Species
L. dimidiatus
T. lunare
Effect
20
15
10
5
0
Ventral Head
Ventral Body
Gills
Pelvis
Tail
Dorsal Lower
Pectorals