

Top shelf bottom feeders - Food provisioning in stingrays

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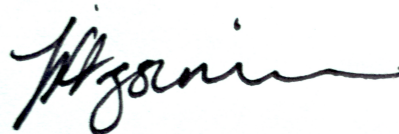
Declaration

I wish to acknowledge the following assistance in the research detailed in this report:

Associate Professor Culum Brown and Nathan A. Knott for their assistance in experimental design, statistical analysis and editing, and overall guidance throughout this project;
Johann Mourier for his assistance with statistical analysis and modelling of the data;
Craig Mercier for his assistance with field training in the tagging method; and
The numerous volunteers for their assistance in field data collection.

All other research described in this report is my own original work.

The work presented here has not been submitted for a higher degree to any other university or institution.

A handwritten signature in black ink, appearing to read 'Joni Pini-Fitzsimmons', with a long horizontal flourish extending to the right.

Joni Pini-Fitzsimmons

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ABSTRACT

Recreational anglers often discard fish waste back into waterways, yet the effects of incidental provisioning as a result of this activity have not yet been assessed, and are not considered in management. At the Woollamia boat ramp in Jervis Bay, Australia, anglers have provisioned short-tail stingrays since 1985.

In Chapter 1, we compared stingray visitation with provisioning activity, which indicated their movements are strongly linked to provisioning. Observations also suggest the area may have reproductive significance to this species.

Short-tail stingrays may be capable of complex social behaviours, yet no assessment of their sociality exists. Aggregation at the provisioning site provided an opportunity to study their social behaviour. In Chapter 2, we assessed dyadic agonistic interactions and observed a dominance hierarchy and social network that was reflective of a despotic society, indicating this species is capable of highly complex social behaviour.

These stingrays may be at risk of experiencing further negative impacts from provisioning, such as dependency, resulting in reduced fitness. The results of these studies highlight that management of recreational fisheries, with respect to appropriately handling waste and its potential impacts on wildlife, needs to be revised. Our data provide a baseline of effects on which monitoring and management programs can be built.

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Note to reviewers: This thesis is submitted as a thesis by publication and chapters are formatted for *Animal Behaviour*, with the exception that text is 1.5 spaced, margins adjusted to conform with thesis submission guidelines of Macquarie University, supplementary materials for both chapters are listed together in the appendix and figures and tables are numbered sequentially throughout both chapters. Additionally, the introduction, methods and discussion sections for both chapters are written in far greater detail than required for submission to *Animal Behaviour* as per submission requirements for Macquarie University.

Chapter 1

The effect of food provisioning on site use in the short-tail stingray, *Bathytoshia brevicaudata*

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41 **ABSTRACT**

42 Food provisioning can have significant effects on marine wildlife. It is common practice for
43 recreational anglers to discard fish waste back into waterways, yet the effects of incidental
44 provisioning as a result of processing marine resources have not yet been assessed, and are likely
45 not being considered in the management of recreational fishing along Australia's coastline. At the
46 Woollamia boat ramp in Jervis Bay, Australia, local anglers have been incidentally provisioning
47 short-tail stingrays through fish cleaning activities for >30 years. This provided an opportunity to
48 investigate the influence of provisioning on a small scale. We used behavioural observations to
49 assess site use patterns against provisioning intensity to determine if this level of provisioning has
50 the potential to cause changes to the movements and behaviours of this large marine mesopredator.
51 Fifteen (adults, $N = 7$; sub adults, $N = 8$) female short-tail stingrays were found to use the site,
52 including at least 5 gravid individuals. Their presence was significantly correlated to the intensity of
53 provisioning events ($P < 0.001$) and significantly more stingrays visited post-provisioning than pre-
54 provisioning ($P < 0.001$) during simulated provisioning trials at other sites. Additionally, stingrays
55 exhibited anticipatory behaviour as evidenced by increased visitation in the afternoon, irrespective
56 of whether the cleaning table was in use. These data indicate a strong influence of provisioning on
57 the stingrays' movements and use of the site, and has management implications for recreational
58 fishing and fish cleaning along Australia's coastline, including a suggested revision of accepted
59 practices for discarding fish waste. Based on the observed population structure, we also suggest the
60 area may have reproductive significance for this species. We provide a baseline of the effects of
61 incidental provisioning as a result of processing marine resources, on which monitoring and
62 management programs can be built.

63

64 Keywords: Batoidea; incidental provisioning; *Bathytoshia brevicaudata*; shark and ray tourism;
65 recreational fishing

66

67

68 **Highlights**

- 69 • Population consisted of 15 female short-tail stingrays
- 70 • The stingrays were strongly influenced by provisioning activity
- 71 • Currumbene Creek may have reproductive significance for this species
- 72 • We suggest revised management regarding the responsible discarding of fish waste
- 73 • This study has implications for global shark and ray tourism management

74

75

75 INTRODUCTION

76 While common worldwide, the topic of feeding wildlife is polarising (Orams, 2002). Backyard
 77 bird feeding is considered ecologically benign (Howard & Jones, 2004), for example, and the Royal
 78 Society for the Protection of Birds in the United Kingdom actively encourages bird feeding (RSPB,
 79 2009), despite research suggesting that feeding wild birds can impact almost every aspect of their
 80 ecology (Robb et al., 2008). Food provisioning (herein provisioning) has been used as a
 81 management tool to successfully aid the recovery of threatened species as part of broader species
 82 conservation strategies (Orams, 2002; Newsome & Rodger, 2008; Martínez-Abraín & Oro, 2013).
 83 Benefits have been identified, including reduced energy expenditure for foraging, which can be
 84 invested into rest, growth and/or reproduction (Orams, 2002; Semeniuk & Rothley, 2008; Semeniuk
 85 et al., 2009; Donaldson et al., 2010). Other benefits may exist from grouping, such as increased
 86 chance of mating and lowered individual predation risk (Semeniuk & Rothley, 2008). There are
 87 also costs, however. Some animals switch to investing significant energy into ‘begging’ for food
 88 (Orams, 2002) or defending the provisioned food source (Monaghan & Metcalfe, 1985). Further,
 89 grouping behaviours can result in increased levels of aggression and disease transmission. In
 90 addition, many perceived benefits may only be short-term, and animals who readily adjust to
 91 utilising provisioned resources may unknowingly incur greater long-term costs, in a phenomenon
 92 termed ‘an ecological trap’ (Schlaepfer et al., 2002). Importantly, there is a growing body of
 93 evidence illustrating the negative, long-term impacts provisioning can have on wildlife and their
 94 environments. Some of these impacts are summarised in Table 1 (see also Oro et al. (2013) &
 95 Orams (2002)).

96
 97 **Table 1.**
 98 Overview of studied impacts from food provisioning activity.

Impact		References and examples
Human-animal interactions	Dependency and human-tolerance; Nuisance animals	Corcoran et al. (2013); Burns and Howard (2003)
Behavioural changes	Altered natural behaviours, activity patterns, energy budgets	Brena et al. (2015); Fitzpatrick et al. (2011); Green and Giese (2004); Orams (2002)
	Changes in abundance and distribution; Altered trophic relationships	Corcoran et al. (2013); Green and Giese (2004); Orams (2002); Boutin (1990)
	Increased conspecific aggression	Clua et al. (2010); Newsome et al. (2004); Orams (2002)
	Altered mating systems	Corcoran et al. (2013); Foroughirad and Mann (2013); Green and Giese (2004); Krause and Ruxton (2002)
Overall health	Overfeeding, malnourishment	Newsome et al. (2004); Lewis and Newsome (2003); Orams (2002)
	Higher risk of disease and parasitisation from unnatural grouping	Semeniuk and Rothley (2008); Lewis and Newsome (2003); Orams (2002)
Environmental	Environment fouling	Turner and Ruhl (2007); Newsome et al. (2004); Lewis and Newsome (2003)

99

100 Provisioning in the aquatic realm is becoming more popular (Brena et al., 2015), but by
101 comparison to provisioning of terrestrial animals, the body of associated research is minimal
102 (Corcoran et al., 2013). Sharks (Subdivision: Selachii) and rays (Subdivision: Batoidea) (Subclass:
103 Elasmobranchii) in particular have increasing appeal for tourism (Cisneros-Montemayor et al.,
104 2013). It is estimated that global shark and ray tourism is worth upwards of AU\$400 million each
105 year, supports over 10,000 jobs and is expected to increase 2.5 fold over the next two decades
106 (Cisneros-Montemayor et al., 2013). These economic benefits have led to the protection of some
107 shark and ray species and their habitats (e.g. stingrays in Hamelin Bay, Western Australia;
108 Department of Fisheries (2012); Department of Fisheries (2015)) (see also Topelko and Dearden
109 (2005)). Most importantly from a conservation perspective, it is becoming apparent that sharks and
110 rays can be worth more to local communities alive than dead (Topelko & Dearden, 2005; Gallagher
111 & Hammerschlag, 2011; Cisneros-Montemayor et al., 2013). The elusiveness of sharks has resulted
112 in much of the shark and ray tourism sector utilising provisioning to facilitate encounters. This
113 elusive nature also imposes logistical constraints on studying them. There is a considerable lack of
114 baseline data on their biology and ecology to inform research, and the use of classical approaches to
115 study them, such as comparisons with control sites, is often unfeasible (Brena et al., 2015). It has,
116 therefore, been suggested that provisioning activities can provide a platform to not only study the
117 impacts caused by such an activity, but also to fill gaps in our knowledge of the biology and
118 ecology of target species (Brena et al., 2015).

119 Sharks and rays play an important role in marine ecosystems as upper level predators, strongly
120 influencing prey assemblages and the environments in which they live (Wetherbee & Cortés, 2004;
121 Navia et al., 2007); however, many elasmobranchs are particularly vulnerable to threatening
122 processes because of their K-selected life history traits (Gallagher & Hammerschlag, 2011).
123 Research indicates a quarter of all extant elasmobranchs are threatened with extinction (Dulvy et
124 al., 2014). In particular, large coastal species of rays are at the highest risk due to greater exposure
125 to the combined threatening processes of habitat degradation and fishing activity experienced in
126 their coastal habitats (Dulvy et al., 2014). Despite this, conservation of elasmobranchs has been
127 largely overlooked.

128 Brena et al. (2015) comprehensively reviewed the current literature (16 papers) investigating the
129 impacts of provisioning on sharks and rays. Only 6 of the papers considered ray provisioning, and
130 only 3 provisioned populations have been assessed (see Newsome et al. (2004); Corcoran et al.
131 (2013); Gaspar et al. (2008)) despite being a common practice globally. The level of impact
132 experienced by rays appears to relate to the intensity of provisioning. For example, in Stingray City,
133 Cayman Islands, southern stingrays (*Hypanus americanus*, former: *Dasyatis americana*) are fed by
134 over 1 million tourists annually (Corcoran et al., 2013), and these stingrays now exhibit

135 dependency, high site fidelity, reduced home ranges, reversed diel patterns, reduced overall health
136 and increased aggression (Semeniuk et al., 2007; Semeniuk & Rothley, 2008; Semeniuk et al.,
137 2009; Corcoran et al., 2013). By contrast, with the shift from incidental to targeted provisioning of
138 short-tail (*Bathytoshia brevicaudata*, former *Dasyatis* sp.) and brown (*B. lata*, former: *D. thetidis*)
139 stingrays at Hamelin Bay, Western Australia, Newsome et al. (2004) identified the stingrays were
140 not yet experiencing the severe impacts highlighted for Stingray City, but they were at high risk in
141 the absence of appropriate management (Newsome et al., 2004). In both cases, provisioning began
142 incidentally from fishermen cleaning their catches. In Australia an increased number of fish
143 cleaning facilities are being built to support the increasing popularity of recreational fishing (see
144 NSW DPI (2016)). These facilities are often built at the water's edge and/or have discard pipes that
145 run into adjacent waters (C. Mercier, NSW Department of Primary Industries, personal
146 communication, 11 April 2017), and it is also accepted practice to discard recreational fish waste
147 back into waterways. The NSW Department of Primary Industries only stipulates that fish waste is
148 disposed of "responsibly" (NSW DPI, 2015). Surprisingly, the effects of incidental provisioning as
149 a result of processing marine resources has not yet been assessed, and in turn the potential effects to
150 marine life along Australia's coastline are likely not being considered in the installation of such
151 facilities and management of recreational fishing.

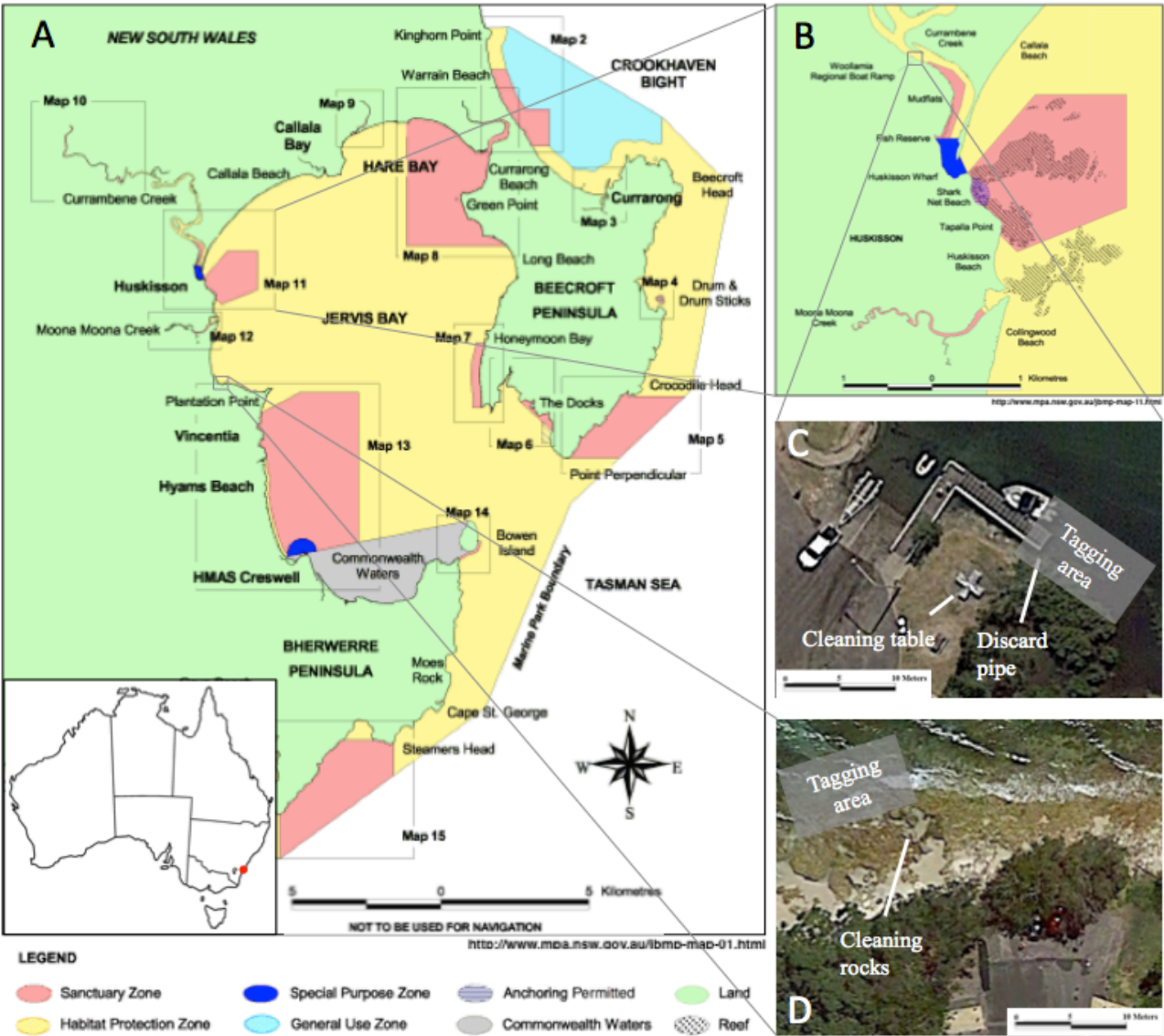
152 In Jervis Bay, Australia, short-tail stingrays are incidentally provisioned fish scraps disposed of
153 via a discard pipe from fish cleaning facilities at the Woollamia boat ramp (WBR) in Currambene
154 Creek. Anecdotal evidence suggests the stingrays have foraged scraps here since the installation of
155 the fish cleaning facilities in 1985 (Michael Strachan, Shoalhaven City Council, personal
156 communication, 12 September 2016). As yet, it is unclear how many short-tail stingrays use the site
157 and how reliant they are on the provisioned resource. This site provided a novel opportunity to
158 obtain baseline data on the effects of incidental provisioning on the behaviour of stingrays as a
159 result of processing marine resources. The outcomes can directly inform monitoring and
160 management programs. Here we address the impact of provisioning on group structure and site
161 occupancy patterns, along with the influences of provisioning intensity, boating activity and tidal
162 current on site use by the provisioned stingrays. We hypothesised that, if the stingrays were affected
163 by provisioning activity (i) there would be a resident population of stingrays with high site
164 attachment; (ii) their presence at the WBR would be driven by food provisioned from fish cleaning
165 activity, boating activity (by learned association) and by tidal currents (potential olfactory cues);
166 and (iii) they would quickly recruit to 'new' provisioning sites, reinforcing the influence of
167 provisioned food on individual activity patterns and movements, and demonstrating their ability to
168 readily alter their behaviours to utilise human provisioning.

169 **METHODS**

170 *Study Species*

171 The short-tail stingray is one of the largest species of stingray with a maximum size of 210cm
172 disc width (DW) and 350kg (Last et al., 2016). They are a common neritic species found in the
173 coastal waters off South Africa, Australia, New Zealand (formerly identified as *Dasyatis* sp.), as
174 well as Japan and eastern Russia (formerly identified as *D. matsubara*) (Last et al., 2016).
175 Although considered ‘Least Concern’ on the IUCN Red List of Threatened Species (Duffy et al.,
176 2016), little is known about the biology and ecology of the species.

177 *Study Sites*



178 **Figure 1.** Study location. (A) Zoning map of the Jervis Bay Marine Park (from www.mpa.gov.au/jbmp-map-01.html),
179 inset: geographic location; (B) Zoning map of lower Currumbene Creek, Jervis Bay (from www.mpa.gov.au/jbmp-map-11.html); (C) Aerial photograph (Google Earth) of the Woollamia boat ramp; (D) Aerial photograph (Google Earth) of
180 the Vincentia boat ramp.
181
182
183

184 Short-tail stingrays were visually tagged at the WBR (35° 1' 32" S, 150° 39' 59" E) and
185 Vincentia boat ramp (VBR) (35° 4' 9" S, 150° 40' 45" E) in the Jervis Bay Marine Park (JBMP),
186 NSW, Australia (Figure 1) during August 2016. Subsequent observations of stingray site use were
187 undertaken at the WBR and simulated provisioning sites in the Currambene Creek (Figure 1; Figure
188 4). The WBR falls within a Habitat Protection Zone in Currambene Creek, situated to the northeast
189 of Jervis Bay (Figure 1A). At the WBR, there is a 4-station cleaning table from which a discard
190 pipe runs from the centre of the table into the waters of the estuary (Figure 1C). A wharf runs
191 parallel to the shore between the boat ramp and the discard pipe, which was used as the observation
192 platform for this study (Figure 1C).

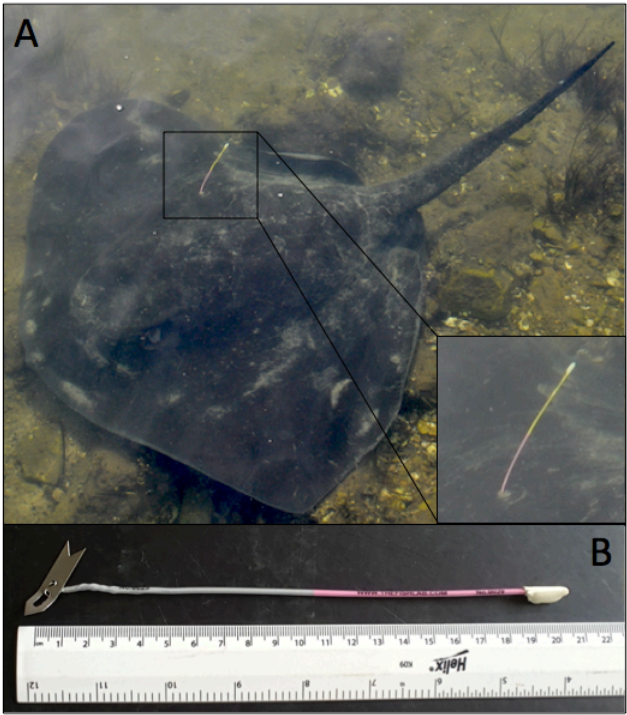
193 Anecdotal accounts suggested anglers regularly clean fish on rocks adjacent to the VBR (Figure
194 1D) and discard the scraps into the water where short-tail stingrays are seen feeding on the scraps
195 and patrolling the area (N. Knott, personal communication, July 2016). In order to identify if short-
196 tail stingrays travel between provisioning sites, we also tagged short-tail stingrays at the VBR,
197 which is situated ~5km SSE from the WBR (Figure 1A).

198 *Visual Tagging*

199 Short-tail stingrays were tagged between the 1st and 10th August 2016 and then opportunistically
200 until 31 August 2016 between observation periods. The stingrays were attracted to the WBR using a
201 chum mixture of locally sourced fish frames and offal in shallow water (max ~1m depth) where
202 they would usually forage provisioned scraps. The amount and species composition of the chum
203 was similar to that discarded during fish cleaning (provisioning) events. The time of first arrival to
204 the tagging area was noted and photographs were taken of the entire dorsal surface. Photographs
205 were used for secondary identification. Following standard size measurements for stingrays (see
206 Yearsley and Last (2016)), disc width (DW) was measured (pectoral fin tip to fin tip) using a 2m
207 length of dowel with 1cm marked gradations, with measurements recorded to the nearest 5cm by an
208 observer looking from the wharf above. Without restraining the stingrays, measurements to the
209 nearest centimetre were difficult to obtain. The sex of each individual was determined by the
210 presence (male) or absence (female) of claspers under the base of the tail.

211 Short-tail stingrays were tagged visually using stainless steel dart tags (SSD; Hallprint PTY.
212 LTD., Hindmarsh Valley, South Australia) with 200mm colour-coded vinyl streamers (Figure 2B).
213 SSD heads are sharpened to allow smooth anchoring in muscle tissue and are made from 316S
214 marine grade stainless steel, giving them higher resistance to corrosion in salt water (Figure 2)
215 (Hall, 2015). Tag streamers consisted of unique combinations of 2 colours (Figure 2B). At the distal
216 end, Passive Integrated Transponder (PIT) tags were attached using waterproof epoxy adhesive
217 (Shelleys, NSW, Australia) (Figure 2B) to address concerns over biofouling hindering individual

218 identification. The modified visual SSD tags were inserted into the dorsal musculature at a 45°
219 angle towards the head, where the pectoral fin joins the body of the stingray (Figure 2A) using a 3m
220 hand-held tagging pole with SSD applicator tip following procedure provided by the tag
221 manufacturer (Hall, 2015). The time each individual was tagged and side in which the tag was
222 inserted were recorded, along with the time to return to the area to continue feeding as a measure of
223 welfare impact. Each tagged individual was given a name that corresponded to the colour
224 combination of the tag used for identification purposes.
225



226
227 **Figure 2.** Short-tail stingray tagged in this study. (A) Anatomical position of visual tags and (B) example of tags used.
228

229 *Provisioning Site Use*

230 *Site attachment*

231 Given the > 30-year history of short-tail stingray provisioning at the WBR it was important to
232 obtain site fidelity and residency measures to monitor changes over time. If provisioning drives
233 short-tail stingrays' space use, we would expect high site attachment reflected by high site fidelity
234 and high residency at WBR. *Site fidelity* was estimated as the proportion of days individuals were
235 observed over the observation period from the 1st to the 23rd August 2016 (following standard
236 practice). A *residency period* was defined as the number of days between the first and last day an
237 individual was seen over the same period, provided the gaps between consecutive days sighted did
238 not exceed 1 day (following Bruce and Bradford (2013)). A 1-day period was chosen to account for
239 missed observations as it is expected resident individuals would use the provisioning site daily and

240 may have visited between observation periods or observation days. The *maximum residency* was
241 calculated as the longest residency period each individual was observed.

242 *Influence of cleaning events, boating activity and tidal currents*

243 To test whether stingray presence at the WBR was driven by the level of food provisioning and
244 boating activity, observations of provisioning site visitation by stingrays, provisioning events and
245 boating activity were undertaken during two 3-hour sessions (0900 – 1200hrs, 1400 – 1700hrs EST)
246 each day between the 11th – 16th and 18th – 23rd August 2016 at the WBR. Observation sessions
247 were set following Gaspar (unpublished data cited in Gaspar et al. (2008)) as time and personnel
248 constraints did not allow full day observations. A visit by a short-tail stingray was classed as any
249 time an individual came within a 10-meter radius from the mouth of the discard pipe (stingray
250 visitation area; Figure 3). If an individual left the visitation area and subsequently re-entered this
251 was classed as a new visit. The time, direction entered and individual identification were noted for
252 each visit. These data were then used to develop a presence/absence dataset for each observation
253 session to develop residency and site fidelity indices and to compare with provisioning events and
254 boating activity. A *provisioning event* was classed as any event where fish, cephalopods,
255 crustaceans and the like were cleaned, rinsed and/or disposed of at the cleaning table. The start and
256 end time of each provisioning event, and the number and type of scraps discarded were noted.
257 These data provided a proxy for the intensity of the provisioning to compare with visitation patterns
258 of the stingrays. The start time began when the tap at the table was turned on or fish cleaning began.
259 The end of the event was when the fisher finished washing down the table and/or turned the tap off.
260



261
262 **Figure 3.** Observation zones at the Woollamia boat ramp. Blue shaded area indicates the observation boundary for
263 boating activity, purple shaded area indicates the observation boundary for stingray visitation, ● indicates the position
264 of the mouth of the discard pipe and ⊙ indicates the observation point.
265

266 The observation boundary for boating activity extended to 50 meters either side of the
267 observation point (wharf) and was inclusive of the entire width of the estuary (Figure 3). The time
268 at which each vessel entered the observation zone and the vessel type were noted. The number of
269 vessels provided a proxy for the intensity of boating activity at the provisioning site and was used to
270 determine whether stingrays had learned an association with boating activity and provisioning
271 activity.

272 To test the influence of tide direction, and in turn, scent trails as olfactory cues, hourly tide
273 height data measured at Port Kembla (BOM, 2017) were adjusted to Australian Eastern Standard
274 Time (AEST; from UTC) and then for Huskisson, Jervis Bay local tide time (Port Kembla AEST
275 +13 minutes; Australian Hydrographic Service (2016)). The predominant tidal direction for each
276 observation session was then determined. These data were then assessed against the short-tail
277 stingray presence/absence data described above.

278 *Simulated Provisioning*

279 From the above observations, we expected stingray use of the WBR and surrounding
280 Currambene Creek area to be strongly correlated with provisioning. To further investigate the link
281 between provisioning and stingray movements, simulated provisioning experiments were run at two
282 novel locations either side of the provisioning site (Upstream non-provisioned site and Downstream
283 non-provisioned site) where the stingrays were not currently being provisioned, nor observed
284 (Figure 4). We expected that provisioned stingrays would visit these ‘new’ provisioning sites post-
285 provisioning, indicating that their movements and use of the surrounding Currambene Creek were
286 strongly driven by provisioned food. Site choice was based on similar environmental settings to the
287 provisioning site (Figure 4C) and ease of access. The upstream site was dominated by oyster-
288 covered boulders and descended much more steeply into deeper water (Figure 4B). The
289 downstream site was dominated by muddy sands and had a similar depth profile to the provisioning
290 site (Figure 4D).

291 Over 6 days (11th – 16th August 2016) baseline observations of short-tail stingray visitation to the
292 two previously non-provisioned sites were recorded following the provisioning site methodology
293 above to confirm the stingrays were not normally using these sites. Over a subsequent 6-day period
294 (18th – 23rd August 2016) assorted locally sourced fish frames, were placed in the water at these
295 sites (attached to ropes) to simulate a typical provisioning event at the provisioning site.
296 Observations of stingray visitation were repeated during this period to determine if the presence of a
297 provisioned food elicited increased short-tail stingray visitation to these new sites.

298

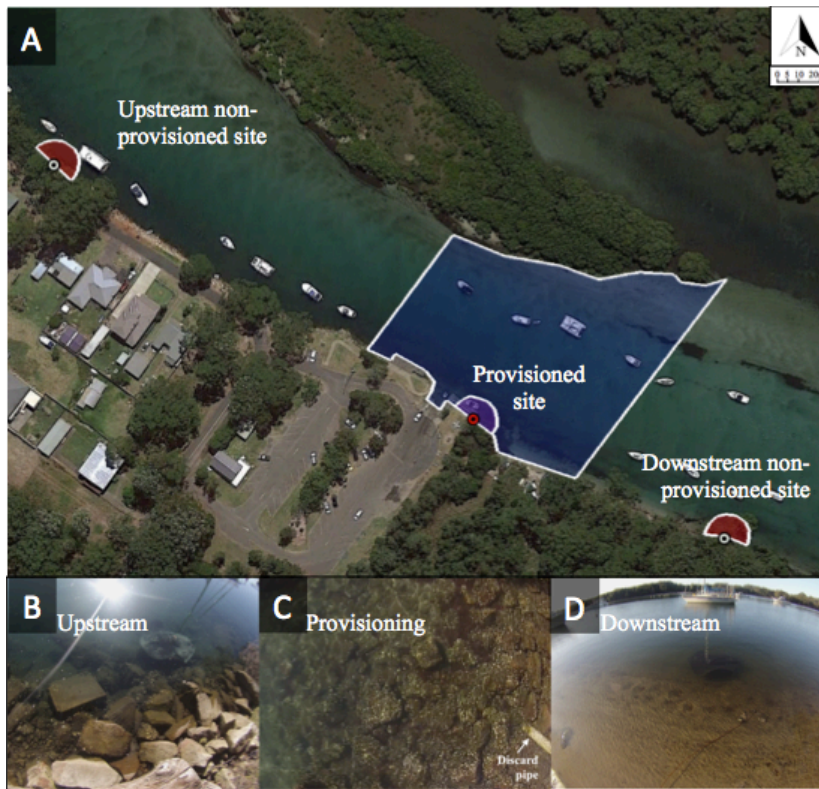


Figure 4. Provisioning (Woollamia) and simulated provisioning sites. (A) Location of sites relative to the provisioning site where ● indicates the observation points and the red shaded area indicates observation area of stingray visitation; (B) – (D) Images comparing site topography.

Data Analysis

Data was recorded and organised using Microsoft® Excel® 2008. All statistical analyses were conducted using R (V.3.3.1) (R Core Team, 2015) with the R Studio interface (V.0.99.903) (RStudio Team, 2015). All data was tested for normality, and in cases where normality was not satisfied the data was transformed in the appropriate way.

Influence of cleaning events, boating activity and tidal currents

Using the *lme4* package (Bates et al., 2015) in R Studio (RStudio Team, 2015), a Generalised Linear Mixed Effects Model (GLMM; *glmer*) was used to determine the influence of fish cleaning and boating activity on the presence of individual short-tail stingrays (*presence*). Presence/absence data were used in place of visitation data to eliminate pseudoreplication from the model. The biomass provisioned during cleaning events could not be determined due to a number of anglers unwilling to disclose their catches to the researchers. The number of cleaning events and the cumulative length of cleaning events per observation session were highly correlated (Pearson product-moment correlation: $N = 480$, $r = 0.67$, $P < 0.001$), and therefore the cumulative length of cleaning events (in minutes) (*clean_length*) was used as a proxy for the level of provisioning occurring at the site. The following model was used:

$$glmer(presence \sim scale(clean_length) * scale(n_boats) + (1 | ID))$$

321 where the dependent variable (*presence*) was binomial (1 = individual was present, 0 = absent). The
322 random effect ($I \mid ID$) is the unique name of each individual tagged stingray. The fixed effects
323 (*clean_length* and *n_boats*) were scaled to resolve scaling errors and the number of iterations was
324 set to 100,000 using the BOBYQA Optimisation (Powell, 2009) to resolve optimisation errors.

325 Using the *lme4* package (Bates et al., 2015) in R Studio (RStudio Team, 2015), a GLMM was
326 used to determine the influence of tide direction (*tide_direction*), observation session (*session*) and
327 the interaction between the two on the presence or absence (*presence*) of individual short-tail
328 stingrays. As above, the presence/absence dataset was used in place of visitation data to eliminate
329 pseudoreplication from the model. The following model was used:

330
$$glmer(presence \sim tide_direction * session + (I \mid ID))$$

331 where the dependent variable (*presence*) was binomial (1 = individual was present, 0 = absent). The
332 random effect ($I \mid ID$) is the unique name of each individual tagged stingray. The fixed effect
333 *tide_direction*, was an integer where 1 = outgoing, 2 = low, 3 = incoming and 4 = high. The fixed
334 effect, *session*, was an integer where 1 = AM and 2 = PM. The BOBYQA Optimisation (Powell,
335 2009) was used resolve optimisation errors.

336 *Anticipation*

337 Anticipatory behaviour is considered an indicator for dependency in previous studies on
338 provisioned stingrays (Newsome et al., 2004; Gaspar et al., 2008; Corcoran et al., 2013). We
339 assessed whether this behaviour was exhibited at the WBR. First, a One-Way ANOVA, using the
340 *aov* function in the *stats* package (R Core Team, 2016) in R Studio (RStudio Team, 2015), was used
341 to compare the number of individual rays present (*n_rays*) and the cumulative length of cleaning
342 events (in minutes) (*clean_length*) within each observation session (AM or PM; *Session*) to
343 determine if there was a relationship with time of day. *Session* was an integer for which AM = 1
344 and PM = 2, and the following model was used:

345
$$aov(Session \sim n_rays * clean_length)$$

346 We found cleaning events were longer and significantly more stingrays used the site in the
347 afternoon (see *Results - Anticipation*); therefore, a Two-Way ANOVA was used to determine if the
348 stingrays used the site during this time regardless of cleaning table use. Stingray visitation rates
349 (number of visits per hour) were calculated for when the cleaning table was in use or not (yes or no;
350 *cleaning*), within each observation session (AM or PM; *Session*) for each observation day.
351 Visitation rates were then log transformed for normality (*LogRate*), and analysed using the
352 following model:

353
$$anova(LogRate \sim Session * Cleaning)$$

354 *Simulated provisioning*

355 A One-Way ANOVA was used to compare stingray visitation before and during simulated
356 provisioning observations (*Provision*), between the two 3-hour observation sessions each day (AM
357 or PM; *Session*) and between the two previously non-provisioned locations (upstream or
358 downstream; *Location*). Visitation data were binned into half hour segments and then negative
359 square root transformed for normality (*Visits_negsqrt*). The following model was used:

360
$$aov(Visits_negsqrt \sim Location * Session * Provision)$$

361 A *TukeyHSD* ('Honest Significant Difference' Method) Post Hoc analysis was used to determine
362 where significant interactions occurred within the data.

363 *Ethical Note*

364 This study was carried out under approval from the Macquarie University Animal Ethics
365 Committee (ARA – 2014/015-7) and NSW DPI Fisheries Scientific Collection Permit P08/0010-
366 4.4. The stingrays showed varied initial responses to tagging, however, all rapidly returned to the
367 provisioning site. Evidence also suggested the tags were lost after less than 4 months at liberty with
368 no tag wounds remaining ($N = 3$) (see Figure A1 in the appendix). Tag selection and project design
369 were carefully considered with regard to the welfare of the stingrays. To the best of our knowledge,
370 there were no negative impacts on the welfare of the animals used in this study.

371 **RESULTS**

372 *Population Structure*

373 A total of 17 short-tail stingrays were tagged during the 5 weeks of this study (Table 2). Fourteen
374 were tagged at the WBR and 3 at the VBR. Of the tagged individuals, 15 were observed using the
375 provisioning site at the WBR during the study period (all except Montie and Raychael). All
376 individuals observed at the WBR during the study period were tagged. All tagged individuals were
377 female ($N = 17$), ranging in disc width from 135 to 165 cm (mean = 149cm, $N = 11$). DW
378 measurements were only available for 11 individuals due to difficulty faced in measuring the
379 unrestrained stingrays. Five individuals observed using the provisioning site were visibly gravid.
380 Following size-class estimates described by Le Port et al. (2012), 2 obviously gravid individuals
381 (Vinnie and Billy Ray) were originally considered sub-adults (DW < 150cm), though for further
382 analysis were considered adults. In addition, unmeasured individuals were smaller than observed
383 adults, and were considered sub-adults. In sum, 7 were considered adults (>150cm DW or gravid)
384 and 8 were sub-adults (70 – 150cm DW).

385

385

386

387

Table 2.
Summary table of individuals tagged during this study.

Date and time tagged (AEST)	Site tagged	Tag colour		PIT tag number*	Nickname	Sex	Disc width (cm)
		Proximal	Distal				
01/08/16 15:51	Woollamia	Pink	Blue	-989	Thickness	F	135 ^S
01/08/16 16:08	Woollamia	Green	Grey	-834	Stumps	F	135 ^S
02/08/16 16:55	Woollamia	Green	Red	-848	Small Fry	F	Unknown ^{LS}
03/08/16 14:15	Vincentia	Green	White	-983	Vinnie	F ^G	140 ^A
06/08/16 15:41	Woollamia	Grey	Red	-976	Billy Ray	F ^G	145 ^A
07/08/16 10:36	Woollamia	Green	Green	-987	Raylene	F ^G	155 ^A
07/08/16 13:28	Woollamia	Pink	Grey	-977	Jocka	F ^G	155 ^A
08/08/16 12:44	Woollamia	White	Red	-990	Miley Cyray	F	155 ^A
08/08/16 15:51	Woollamia	Pink	Green	-984	Dasy	F	135 ^S
09/08/16 09:51	Woollamia	Pink	Pink	-971	Shorty	F ^G	155 ^A
09/08/16 10:14	Woollamia	Grey	Grey	-846	Momma	F	165 ^A
10/08/16 11:04	<i>Vincentia</i>	<i>White</i>	<i>Blue</i>	-972	<i>Raychael</i>	<i>F</i>	<i>Unknown</i>
10/08/16 16:47	<i>Vincentia</i>	<i>White</i>	<i>Yellow</i>	-986	<i>Montie</i>	<i>F</i>	<i>165^A</i>
18/08/16 17:10	Woollamia	Pink	Red	-975	Charlie	F	Unknown ^{LS}
28/08/16 16:44	Woollamia	Pink	Yellow	-982	Desaray	F	Unknown ^{LS}
29/08/16 15:05	Woollamia	Pink	White	-835	Shuga	F	Unknown ^{LS}
30/08/16 10:28	Woollamia	White	Pink	-975	Ellie	F	Unknown ^{LS}

* all PIT tags begin with 900032002394-; ^Ssub-adult individuals; ^Aadult individuals; ^{LS}likely sub-adults; ^Ggravid; individuals in *italics* were not observed during subsequent observations.

388

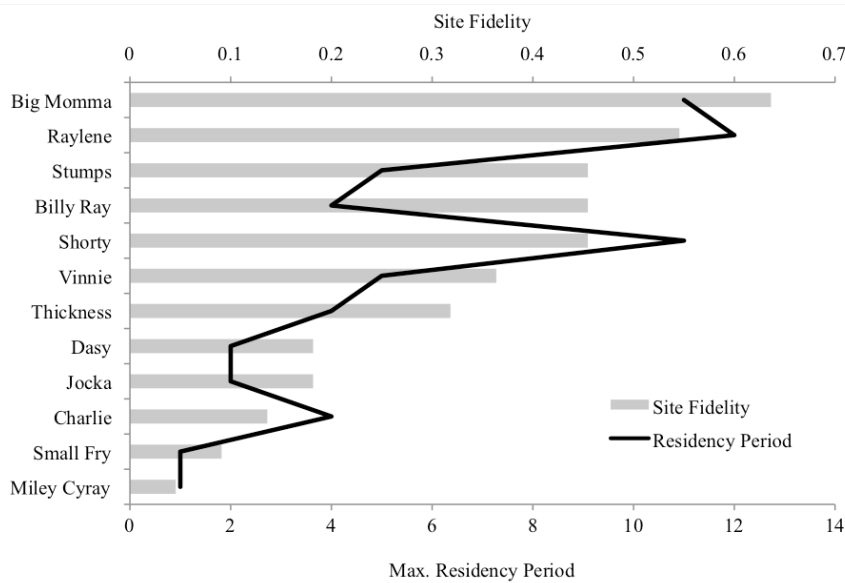
389

390

391 *Provisioning Site Use*

392 *Site fidelity and residency*

393 Site fidelity and maximum residency periods varied greatly among individuals using the
394 provisioning site (Figure 5). Mean site fidelity was 0.322 (SE \pm 0.056; min = 0.045; max = 0.636).
395 The mean maximum residency period was 5.167 days (SE \pm 1.147, min = 1; max = 12).
396

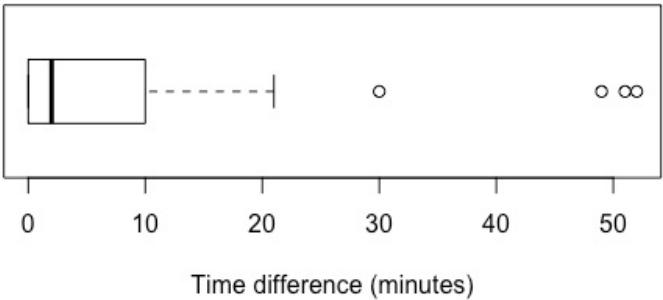


397

398 **Figure 5.** Site fidelity (proportion of days seen) and maximum residency period (number of days) for each individual at
399 the provisioning site.

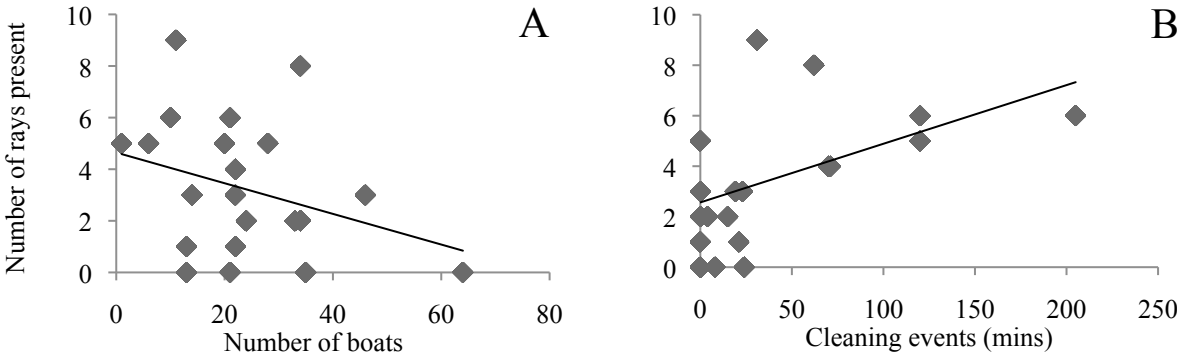
400 *Influence of cleaning events, boating activity and tidal currents*

401 On average, short-tail stingrays arrived at the provisioning site within 2 minutes of the beginning
402 of a cleaning event ($IQR = 0 - 10$ minutes; Figure 6).



403
404 **Figure 6.** Time difference (minutes) between the start time of a cleaning event and the first visit by a stingray at the
405 Woollamia boat ramp.
406

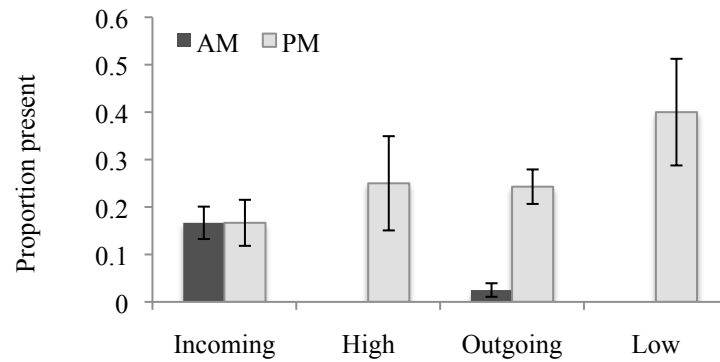
407 Individual stingray presence was significantly correlated with the cumulative length of cleaning
408 events (within each observation period) (GLMM: $\beta \pm SE = 0.51 \pm 0.14$, $N = 480$, $P < 0.001$; Figure
409 7B). Stingray presence was also significantly negatively correlated with the total number of boats
410 (GLMM: $\beta \pm SE = -0.33 \pm 0.16$, $N = 480$, $P = 0.031$; Figure 7A); however, the cumulative length of
411 cleaning events and the number of boats were significantly negatively correlated (Pearson product-
412 moment correlation: $r = 0.15$, $N = 480$, $P < 0.001$). The model output is provided in the appendix
413 (Table A1).
414



415
416 **Figure 7.** Number of stingrays present in comparison with (A) the number of boats and (B) the cumulative length of
417 cleaning events (in minutes).
418

419 Individual stingray presence was significantly correlated with tide direction (GLMM: $\beta \pm SE =$
420 2.47 ± 0.68 , $N = 480$, $P = 0.0003$), observation session (GLMM: $\beta \pm SE = 4.32 \pm 0.97$, $N = 480$, P
421 < 0.0001), and the interaction between the two (GLMM: $\beta \pm SE = -1.30 \pm 0.37$, $N = 480$, $P = 0.0004$).
422 There were significantly more individuals present in the afternoons across all tidal phases, though
423 the observed significance is most likely driven by the ‘low’ tidal phase (Figure 8). The model
424 output is provided in the appendix (Table A2).

425
426



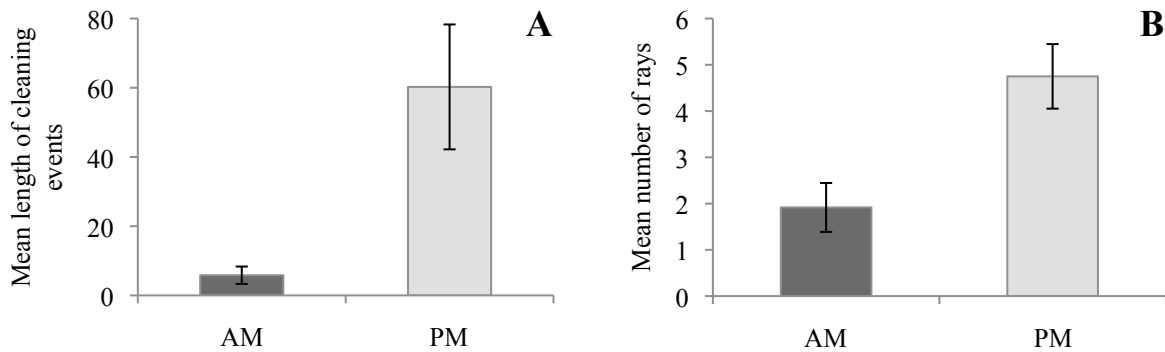
427
428
429

Figure 8. Mean proportions of present individuals (\pm SE) per observation session and tidal phase.

430 *Anticipation*

431 The cumulative length of cleaning events tended to be longer during afternoon observation
432 sessions (One-Way ANOVA: $F_{1,60} = 3.401$, $P = 0.08$; Figure 9A). Significantly more individual
433 stingrays were present in the afternoon observation throughout the study period (One-Way
434 ANOVA: $F_{1,60} = 11.796$, $P = 0.0027$; Figure 9B). The model output is provided in the appendix
435 (Table A3).

436
437



438
439
440
441

Figure 9. Differences in (A) mean cumulative length of cleaning events (in minutes) (\pm SE) and (B) the mean number of stingrays present (\pm SE) between observation sessions (AM / PM).

442

443 Observation period had a significant effect on stingray visitation rates (Two-Way ANOVA: $F_{1,44}$
444 $= 8.117$, $P = 0.0067$), with rates being higher in the afternoon (Figure 10). Whether or not the
445 cleaning table was in use had no significant effect (Two-Way ANOVA: $F_{1,44} = 0.34$, $P = 0.563$;
446 Figure 10). The model output is provided in the appendix (Table A4).

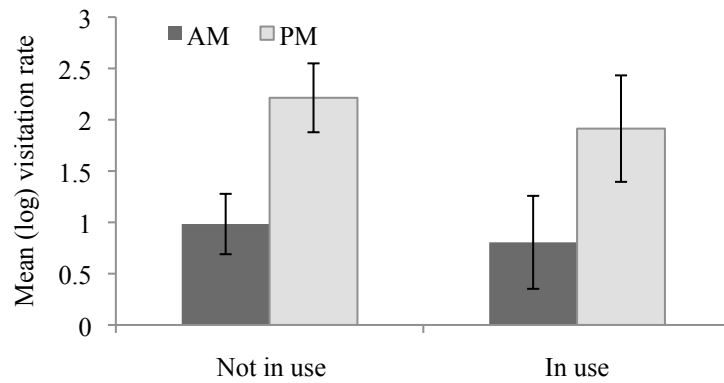


Figure 10. Average (log) stingray visitation rates (\pm SE) when the cleaning table at the Woollamia boat ramp was in use and not in use during each observation session (AM / PM).

Simulated Provisioning

There was a significant effect of provisioning on stingray visitation (One-Way ANOVA: $F_{1,280} = 14.784$, $P < 0.001$), with more visits post- rather than pre-provisioning (Figure 11). There was a marginal but non-significant effect of sampling session (AM or PM) (One-Way ANOVA: $F_{1,280} = 3.122$, $P = 0.078$) and a marginal but non-significant effect of location (One-Way ANOVA: $F_{1,280} = 3.499$, $P = 0.063$). There was a significant interaction between session and provisioning (or not) (One-Way ANOVA: $F_{1,280} = 4.089$, $P < 0.05$; Figure 11), with the effect being more pronounced in the morning (TukeyHSD Post Hoc: AM*Provisioned–AM*Non-provisioned, $P < 0.001$; PM*Provisioned–AM*Non-provisioned, $P < 0.001$). There were no further significant interactions. The ANOVA output and TukeyHSD Post Hoc analysis results are provided in Table A5 and Table A6, respectively.

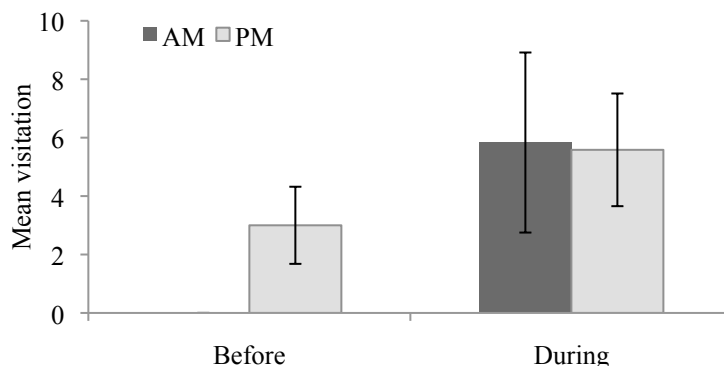


Figure 11. Mean daily stingray visitation (\pm SE) before and during simulated provisioning during each observation session (AM / PM).

DISCUSSION

Short-tail stingray movements were strongly influenced by food provisioning at the Woollamia boat ramp (WBR). These results were further supported by simulated provisioning experiments where stingrays rapidly recruited to newly provisioned locations. Site attachment to the WBR was

470 relatively moderate; however, we suggest it may be high within the estuary generally. Collectively
471 the data suggest the stingrays spend most of their time in the lower reaches of the estuary and visit
472 the provisioning site in the afternoons when food is usually available, but they visit irrespective of
473 whether the cleaning table is in use or not, which is indicative of anticipatory behaviour. Tidal
474 currents likely play an important role in the distribution of scent trails used as an olfactory cue.
475 Significantly more stingrays were observed in the afternoon, which may be related to increased fish
476 cleaning activity throughout the day. The population of provisioned short-tail stingrays consisted
477 entirely of adult ($N = 7$) and sub adult ($N = 8$) females. Contrary to previous studies, the relationship
478 between boating activity and stingray site use was weak because of the negative relationship
479 between boating activity and the appearance of provisioned food.

480 *Influence of Provisioning, Boating Activity and Tidal Currents*

481 Short-tail stingray use of the WBR was strongly influenced by provisioning, as shown by a
482 significant correlation between the length of cleaning events and the number of stingrays present
483 (Figure 7B). This is further supported by the simulated provisioning experiments, where
484 significantly more short-tail stingrays were observed when provisioned food was made available
485 (Figure 11). This does not mean the stingrays would not be using the estuary in the absence of
486 provisioning (discussed further below), but rather the stingrays would likely not use the immediate
487 boat ramp area probably due to the high risks associated with interactions with people, boats and
488 fishing gear. The observed negative relationship between stingray visitation and boating activity
489 (Figure 7A) supports this. In addition, grouping at the provisioning site results in individuals
490 entering into potentially costly agnostic interactions (see Chapter 2). The benefits gained by
491 accessing provisioned food therefore must outweigh these potential costs. This may be detrimental
492 to the stingrays' health in the long term, however, as benefits may only be short-term, resulting in
493 an ecological trap. This has been described for provisioned southern stingrays in Stingray City
494 (Semeniuk & Rothley, 2008).

495 Non-natural food items often exhibit differences in macronutrients and essential fatty acids,
496 which are important for immune function and disease resistance, stress management and
497 reproduction (Semeniuk et al., 2007; Semeniuk & Rothley, 2008; Semeniuk et al., 2009). For
498 example, southern stingrays in Stingray City have been shown to experience significant health
499 impacts from being fed an unnatural, imported species of squid (Semeniuk et al., 2007; Semeniuk &
500 Rothley, 2008; Semeniuk et al., 2009). Short-tail stingrays are believed to naturally forage on
501 juvenile fish, squid, invertebrates and macroinfauna (Le Port et al., 2008). The fish discarded at the
502 WBR are often large, pelagic species (Pini-Fitzsimmons, personal observation); however, all fish
503 cleaned here are locally caught. Therefore, the difference between the nutrient and essential fatty

504 acid profiles of provisioned versus natural prey are not expected to be substantial. It is worth noting,
505 however, much of the discarded scraps are frames with minimal little flesh and offal, so the level of
506 nutrients obtained likely differs from their natural diet. It remains unclear what proportion of the
507 short-tail stingrays' diet comes from provisioning at the WBR, therefore we suggest a
508 comprehensive assessment of the natural short-tail stingray diet as well as comparative isotopic
509 analysis between non-provisioned and provisioned short-tail stingrays to fully understand the
510 importance of the provisioned food and the potential health impacts from this unnatural food
511 source.

512 The relationship between boating activity and stingray presence was unclear. Whilst significantly
513 fewer stingrays were observed with increased boating activity (Figure 7A), the number of boats was
514 strongly negatively related to the level of provisioning activity and provisioning activity was
515 strongly correlated to stingray presence (Figure 7B). It is therefore difficult to separate the effect of
516 boating activity from provisioning activity and comment on its influence on stingray presence.
517 However, it is possible to state that the strong associations between stingray presence and boating
518 activity described by Newsome et al. (2004), Gaspar et al. (2008) and Corcoran et al. (2013) for
519 short-tail and brown stingrays, pink whiprays (*Pateobatis fai*, former: *Himantura* sp.), and southern
520 stingrays, respectively, were not observed at WBR. The associations described in these studies are
521 likely related to the history of the provisioning activity and how it is undertaken today. For these
522 populations provisioning began offshore from boats that were specifically entering these sites to
523 either clean their catches (Newsome et al., 2004; Corcoran et al., 2013) or directly provision the
524 rays (Gaspar et al., 2008). By comparison, boats that enter the WBR area usually dock at the wharf
525 before being retrieved via the boat ramp, after which anglers begin cleaning their catches at the
526 cleaning table. The time between the boat entering the site and cleaning catches is highly
527 unpredictable, impeding on the rays' ability to learn an association.

528 Stingray presence was significantly correlated to tide direction, with outgoing and low tides
529 resulting in increased stingray presence (Figure 8). Short-tail stingrays have been observed resting
530 on shallow mudflats just downstream from the WBR (Currambene Creek mud flats; Figure 1B,
531 Figure A2) during the day (R. Simpson, Simos Fishing Charters, personal communication, August
532 2016). The observed relationship with tides may indicate that olfactory cues are important to short-
533 tail stingray recruitment to the provisioning site. Olfaction is a key sense used by elasmobranchs for
534 locating prey (Hodgson & Mathewson, 1971; Collin, 2012), and olfactory stimuli have been used in
535 Mo'orea in place of food provisioning to facilitate encounters between people and pink whiprays
536 with good success (Gaspar et al., 2008). Olfaction is effective over hundreds of meters for
537 elasmobranchs and detection is largely dependent on water movement and concentration (Collin,
538 2012). The WBR is approximately 2km upstream from the mouth of Currambene Creek (Figure

539 A2), suggesting the stingrays need to be within the estuary to pick up on the olfactory cue. In
540 further support of this, we observed that on average the first visit of a short-tail stingray occurred
541 after just 2 minutes and the vast majority arrived within 10 minutes of the beginning of a cleaning
542 event (Figure 6). This suggests that short-tail stingrays must be reasonably close by (i.e. within the
543 estuary) to detect olfactory cues, potentially resting on the mudflats (~500m downstream from the
544 WBR) between provisioning events. The fact that significantly more stingrays were observed at the
545 downstream site during simulated provisioning trials further supports this. Acoustic telemetry
546 should be employed to shed further light on this suggestion.

547 *Anticipation*

548 Anticipatory behaviour has been described as an indicator for dependency and has been observed
549 for provisioned pink whiprays (Gaspar et al., 2008), southern stingrays (Corcoran et al., 2013) and
550 short-tail and brown stingrays (Newsome et al., 2004). Southern stingrays in Stingray City are
551 considered to have lost their natural foraging ability, resulting in complete dependence on
552 provisioned food (Corcoran et al., 2013). This can have significant trophic implications with
553 reduced predation pressures on natural prey communities (Brena et al., 2015). At the WBR, short-
554 tail stingrays appear to show anticipatory behaviour in the afternoon. The cumulative length of
555 cleaning events is considerably higher in the afternoon than the morning, and significantly more
556 short-tail stingrays were observed in the afternoon (Figure 9). Moreover, stingray visitation in the
557 afternoon was high regardless of whether the cleaning table was in use or not (Figure 10), indicating
558 the stingrays may have developed an association between afternoons and increased provisioning.
559 This is further supported by the simulated provisioning data, where stingrays were observed in the
560 afternoon but not the morning during the non-provisioning stage (Figure 11), suggesting the
561 individuals were in the general vicinity. It could be argued that the stingrays visit the WBR as part
562 of their natural foraging regime; however, nothing is known about foraging periodicity for short-tail
563 stingrays. We suggest acoustic telemetry should be used to determine movement patterns within the
564 estuary and greater bay area. Continued monitoring of the intensity of provisioning at the WBR
565 along with group composition and residency patterns is also important to identify changes over time
566 and implement mitigation measures if necessary.

567 *Residency*

568 Short-tail stingray habitat use and site attachment has not been comprehensively assessed. In the
569 present study, 6 individuals exhibited above average site fidelity, and of these 3 exhibited above
570 average maximum residency periods (Figure 5). As mentioned above however, individuals
571 responded relatively quickly to provisioning events and as such their site fidelity and residency
572 within the estuary may be high, which may not be reflected by their use of the WBR area.

Increases in shark and ray site fidelity and residency over time at provisioning sites is common (Brena et al., 2015), and can provide the first indication that provisioning activities may be influencing the natural movements of the target species. As we have shown here, increases in the intensity of provisioning can lead to increases in group size. This in turn has been shown to lead to increases in site attachment due to increased competition for access to the provisioned resource (Bruce & Bradford, 2013). Increased group size can also result in social amplification with the presence of conspecifics acting as positive feedback for other individuals (social facilitation, see Brown and Laland (2003)), even when the provisioned food source is limited (Brena et al., 2015). Corcoran et al. (2013) questioned whether observed increases in the number of immature southern stingrays using Stingray City was linked to social learning from older individuals. Social learning is an important form of information gathering in elasmobranchs (Guttridge et al., 2009), and in light of this, the level of provisioning at the WBR should be closely monitored with regard to changes in group size and composition. Continued monitoring is integral to highlight changes to behaviour and implement mitigation measures early. It remains unclear, however, whether the stingrays have learned to associate the estuary with provisioning activity, or whether they are using the estuary for another purpose and the provisioned food is an additional benefit (discussed further below). As previously mentioned, acoustic telemetry could be used to monitor their movement patterns to investigate their broader site use.

Population Structure

The population of short-tail stingrays being provisioned at the WBR is estimated to be at least 15 female individuals – 7 adults (5 gravid) and 8 sub-adults (Table 2) – which is comparable to that of short-tail and brown stingrays provisioned at Hamelin Bay as described by Newsome et al. (2004). The scale at which provisioning occurs at the WBR is relatively small, and therefore it is likely that only a small population of stingrays can be supported. Individuals observed using the WBR were adult and sub-adult females, with many in breeding condition. Newsome et al. (2004) and Corcoran et al. (2013) described provisioned stingray populations consisting of over 80% (mostly mature) females in Hamelin Bay and Stingray City, respectively. However, Gaspar et al. (2008) observed an equal sex ratio for provisioned pink whiprays in Mo'orea; the cause of these observed differences remains unclear. The observed sex ratio may be explained by the increased female energy requirements associated with breeding (Wearmouth & Sims, 2008). Utilisation of the provisioning site at the WBR by gravid females may aid in meeting the nutritional demands of their pups during gestation whilst reducing the energetic costs associated with foraging. Females are also larger than males, so they could be competitively excluding males from the site, which has been suggested for provisioned rays in Stingray City (Corcoran et al., 2013) and Hamelin Bay (Newsome et al., 2004).

607 This would also explain the lack of juveniles. Spatial sexual segregation, related to preferred
608 temperature, foraging and reproductive differences, is common in elasmobranchs (Wearmouth &
609 Sims, 2008) and may provide another possible explanation for the absence of males at the WBR. A
610 lack of behavioural and habitat preference data for short-tail stingrays makes interpretation difficult;
611 therefore, it is important to assess natural movements and habitat use of both male and female short-
612 tail stingrays of all life stages through acoustic telemetry.

613 We suggest Currumbene Creek may serve as a gestation, pupping and/or nursery ground for
614 short-tail stingrays. Nursery grounds for sharks and rays are typically highly productive, protected
615 inshore environments, such as mangroves and tidal creek systems (Heupel et al., 2007), and
616 Currumbene Creek fits this definition (Figure A2). Pregnant females may use the warmer waters of
617 the estuary to aid in gestation, which is common in elasmobranchs and has been suggested to
618 markedly reduce gestation periods (Ramsden et al., 2017) and increase the size of offspring in
619 sharks and rays, thereby enhancing their chances of survival (Schlaff et al., 2014). In some
620 locations, short-tail stingrays migrate to deeper waters in winter (Le Port et al., 2008), yet anecdotal
621 accounts suggest short-tail stingrays are observed in the estuary year-round (R. Simpson, Simos
622 Afloat Fishing Charters, personal communication). Immature brown stingrays in Kaneohe Bay,
623 Oahu, Hawaii (Dale et al., 2011) remain in nursery grounds until they reach sexual maturity. We
624 suggest the role of this environment in the reproductive cycle of this species would be a fertile topic
625 for future research.

626 *Management Implications*

627 We have provided the first assessment of incidental provisioning from a fish cleaning facility on
628 Australia's coast, and we have shown that this activity greatly influences the movements of a large
629 mesopredator. As discussed above, this population of short-tail stingrays may also be at high risk of
630 experiencing further biological and ecological impacts in the absence of continued monitoring and
631 appropriate management. Risks include dependency on the provisioned resource, health impacts
632 from the provisioning of inappropriate foods and alterations to trophic interactions. Management
633 should involve the monitoring of physical injury from interactions with humans and watercraft
634 (Corcoran et al., 2013), and healing rates and parasite loads as a measure of immunological health
635 (Semeniuk et al., 2009). Future research should include the acoustic tracking of individuals to
636 monitor their natural foraging behaviour to assess dependency (Corcoran et al., 2013), and
637 assessment of the ecological significance of short-tail stingrays in Jervis Bay to investigate potential
638 impacts on trophic relationships (O'Shea et al., 2012).

639 An increasing number of fish cleaning facilities are being built around Australia to support
640 recreational fishing (see NSW DPI (2016)). It is commonplace for these facilities to include a

641 discard pipe draining into the water, as is the case at the Woollamia boat ramp, and it is accepted
642 practice for anglers to discard fish waste into waterways (C. Mercier, NSW Department of Primary
643 Industries, personal communication, 11 April 2017). In Tasmania, it is stipulated that fish waste
644 must be discarded offshore where the fish was caught or fish should be taken home whole and
645 waste discarded in household rubbish (Wild Fisheries Management Branch, 2015). In NSW, it is
646 only vaguely stipulated that fish waste is disposed of “responsibly” (NSW DPI, 2015). No such
647 regulations are described for any other Australian state or territory. A potential solution is the
648 removal of discard pipes, with biological fish waste discard bins made available instead to ensure
649 fishing discards do not enter waterways. This is undertaken by some local councils already, from
650 which waste is discarded at local waste facilities (C. Mercier, NSW Department of Primary
651 Industries, personal communication, 11 April 2017). Fish waste has a broad range of applications
652 including animal feed, compost and fertiliser, bio-fuel, cosmetics and food packaging
653 (Arvanitoyannis & Kassaveti, 2008). Fish discards can also aid in the assessment of fish stocks. For
654 example, in Western Australia, anglers can donate frames from species of interest to the
655 Department of Fisheries to be used in monitoring of important fish stocks (Department of Fisheries,
656 2016).

657 *Summary*

658 Stingrays are provisioned worldwide, although only limited studies into the ecological,
659 physiological and behavioural impacts exist. There is also a significant lack in baseline data on the
660 natural biology, ecology and behaviour of many of these species. Many marine tourism enterprises
661 have developed from incidental provisioning, although the activity typically does not receive
662 scientific attention until provisioning has already reached a large, commercial scale and impacts are
663 considerable. The discarding of biological fish waste from recreational fishing is commonplace
664 along Australia’s coast, and as yet the effects have not been comprehensively addressed. We have
665 provided a case study for a small population of short-tail stingrays, and shown that despite not
666 exhibiting the boat association observed for stingrays at Hamelin Bay or pink whiprays in Mo’orea
667 (Gaspar et al., 2008), nor the site attachment, dependency or health impacts (Semeniuk & Rothley,
668 2008) observed for southern stingrays in Stingray City, the population is clearly influenced by this
669 small scale provisioning. Use of the site is clearly linked to provisioning activity, there are already
670 signs of anticipatory behaviour and we warn that this population is at risk of developing
671 dependency. Long-term monitoring of this population of short-tail stingrays is important to identify
672 whether they are experiencing detrimental effects from provisioning. Further, current accepted
673 practices for the discarding fish waste produced from recreational fishing activities around Australia

674 need to be revised, as these practices are likely affecting a significant number of species at other
675 fish cleaning sites.

676 Importantly, we suggest that Currumbene Creek may have reproductive significance to short-tail
677 stingrays in Jervis Bay, and since almost nothing is known about this species' reproduction it is
678 integral that this is a future direction of research. While this species is currently listed as least
679 concern, it is at heightened risk of threat from human activity on coastlines within its range (Dulvy
680 et al., 2014), and it is therefore even more imperative to continue research into the population
681 studied here with expansion to include individuals within the greater region. This study has
682 highlighted the significant knowledge gaps regarding the biology and ecology of this species and
683 these knowledge gaps impede the interpretation of findings. The baseline data provided by this
684 study provide an important foundation on which to base long-term monitoring of this population,
685 which will allow implementation into the management of shark and ray provisioning activities
686 worldwide. Future research should address dietary preferences, habitat use, sexual segregation, and
687 reproduction. Acoustic telemetry would augment the present study and prove invaluable in
688 addressing these aspects, allowing greater comparison with previous studies.

689 **ACKNOWLEDGEMENTS**

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879 1

Chapter 2

Social organisation of the short-tail stingray (*Bathytoshia brevicaudata*) over provisioned food

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40 ABSTRACT

41 Sharks and rays are often considered solitary; however, research suggests that many of these
42 species are capable of developing and maintaining complex behaviours based on their high brain
43 complexity and brain-to-body mass ratios. Short-tail stingrays have among the highest brain
44 complexity and brain-to-body mass ratio within the elasmobranchs and this species is believed to
45 form large breeding aggregations, yet no assessment of their sociality exists to date. In Jervis Bay,
46 NSW, Australia, short-tail stingrays have been provisioned fish scraps by local anglers at the
47 Woollamia boat ramp since 1985. We took advantage of their attraction to this site to examine their
48 social behaviour. Specifically, we looked for evidence that these individuals form a dominance
49 hierarchy and/or social network based on their agonistic interactions over the provisioned resource.
50 Thirteen female short-tail stingrays were observed interacting over the 7-day study period. We
51 observed a stable dominance hierarchy that was relatively linear ($h' = 0.4$) but quite shallow
52 (steepness = 0.14) and dominated by a single individual. Social network analysis revealed a non-
53 random social network centred around the dominant individual. The observed social structure was
54 reflective of a despotic society. Contrary to previous research, size did not predict dominance or
55 network centrality. The factors determining dominance and centrality of lower ranks were difficult
56 to discern, which is also typical of despotic societies. This study provides the first comprehensive
57 heterarchical assessment of short-tail stingray sociality, and indicates this species is capable of
58 complex social behaviour. Given the area may serve as a gestation, pupping and or nursery ground
59 for species and higher dominance and centrality relate to greater access to the provisioned resource,
60 the observed social structure has obvious fitness implications in this species.

61
62 Keywords: *Bathytoshia brevicaudata*; social network analysis; social organisation; dominance;
63 heterarchy

64

65

66

67 **Highlights**

- 68 • First heterarchical assessment for the sociality of short-tail stingrays
- 69 • Short-tail stingrays can develop complex social structure
- 70 • Short-tail stingrays exhibited a despotic society with a single alpha
- 71 • Individual size was not a determining factor of dominance or centrality

72

72 INTRODUCTION

73 Animal sociality is highly diverse. Some species only come into contact with conspecifics very
74 briefly (e.g. for mating in sea turtles, Schofield et al. (2006)), some spend their lives in large, tight-
75 knit and cooperative groups (eusocial species such as ants and termites, Crespi and Yanega (1995)),
76 and others fall somewhere between. The nature of social relationships is highly dynamic across time
77 and space, and can be altered by means of individual experience, position and importance within the
78 group, as well as group composition and the environment within which they live (Sih et al., 2009).
79 The complexity of how these factors differ and interact has made the quantitative assessment of
80 sociality difficult. Previously, social relationships have been mainly assessed through examination
81 of hierarchy structure, however, recent improvements in social network theory have substantially
82 broadened our understanding of animal societies (Krause et al., 2009; Sih et al., 2009). Most
83 recently the use of hierarchy and network assessment in conjunction, in what is termed ‘heterarchy’
84 (Cumming, 2016), has allowed us to gain important new insights into animal behaviour, including
85 mate choice and mating tactics, competition, cooperation, tolerance, affiliation, social learning and
86 the flow of information (Sih et al., 2009).

87 Interactions between individuals are the basis on which a social environment is built. Interaction
88 types and their contexts are highly varied, including cooperation in alloparental care, migration or
89 foraging, interactions related to breeding such as acquiring a mate and mating itself, and those in
90 competitive contexts (agonism) that are related to asserting dominance or gaining access to limited
91 resources, and observed social relationships may only be specific to these contexts. Agonistic
92 interactions in response to limited resources, such as mates, shelter and/or food, are of particular
93 interest. As these resources are typically key to survival, interactions associated with access are
94 seen across the entire spectrum of sociality. The primary method to quantify individual success in
95 such contexts is to rank them based on the proportion of their successes (dominant individual or
96 won interactions), failures (subordinate individual or lost interactions) and drawn (neutral)
97 interactions to generate a dominance hierarchy.

98 For highly social species, dominance structures are typically defined along a spectrum from
99 ‘egalitarian’ to ‘despotic’. These terms are used to describe the degree to which dyadic agonistic
100 interactions are asymmetrical (a clear dominant and subordinate) (Vehrencamp, 1983). Within
101 egalitarian societies dominant individuals are more tolerant of other individuals, subordinates
102 exhibit more retaliation, and post-conflict reconciliation is more common (Flack & de Waal, 2004)
103 than in despotic societies. The dominance structures within these societies typically have weak
104 linearity and a shallow dominance gradient (de Vries et al., 2006). By contrast, despotic societies
105 are characterised by higher levels of aggression and minimal counter-aggression (asymmetrical

106 interactions), and are ruled by a single dominant individual (alpha). In general, despotic societies
107 can take two forms: (i) high levels of aggression between each individual and their immediate
108 subordinate, which is characterised by strong linearity and high dominance gradient (de Vries et al.,
109 2006); or (ii) high aggression between the alpha and all subordinates, with subordinates exhibiting
110 relatively even dominance rank (Beaugrand et al., 1984). The latter is characterised by weak
111 linearity and low dominance gradients, making it difficult to distinguish from an egalitarian
112 sociality. It is here that social network analysis can help clarify the two through egocentric
113 measures such as eigenvector centrality (individuals' influence over the entire network) and
114 strength (number of interactions with other individuals), where high values for the most dominant
115 individual and low values for all others would be reflective of a despotic society.

116 Complex social behaviour has typically been attributed to 'higher' vertebrates (de Waal &
117 Tyack, 2003), though it is becoming clear that a much broader range of species are capable of
118 developing and maintaining highly complex social interactions. High forebrain complexity and
119 brain-to-body-mass ratios have been linked to species' ability develop and maintain complex social
120 behaviours (otherwise known as the Machiavellian Intelligence or the social brain hypothesis;
121 Dunbar and Shultz (2007)). In the past, sharks and rays have been considered solitary and relatively
122 primitive. However, many elasmobranchs actually exhibit brain size and complexity that rivals
123 highly social bird and mammal species (Yopak et al., 2010; Klimley & Oerding, 2013), with
124 stingrays among the highest (Lisney et al., 2008; Klimley & Oerding, 2013). We might predict,
125 therefore, that rays would be capable of complex social behaviours. Further, it is becoming evident
126 that grouping in many species of elasmobranchs is relatively common (e.g. Bass et al. (2016)), as
127 are complex social behaviours (Sims et al., 2000; Newsome et al., 2004; Sperone et al., 2010; Furst,
128 2011; Maljković & Côté, 2011; Clua et al., 2013). Consistent social interactions, for example,
129 facilitate social learning (Guttridge et al., 2013), which can influence social cohesion and
130 robustness to perturbations such as fishing pressure (Mourier et al., 2017). Within the
131 elasmobranchs, species that group typically exhibit both social congregation (i.e. for reproduction,
132 e.g. Port Jackson sharks (*Heterodontus portusjacksonii*), Bass et al. (2016)) and non-social
133 aggregation (i.e. attraction to limited resources; e.g. white (*Carcharodon carcharias*) and tiger
134 sharks (*Galeocardo cuvier*), Clua et al. (2013)). In some cases, non-social grouping may also be a
135 condition under which social grouping later develops (e.g. Basking sharks (*Cetorhinus maximus*),
136 Sims et al. (2000)). Formal assessment of elasmobranch social behaviours, however, is generally
137 lacking.

138 Many sharks and rays are inherently elusive, with low local population densities (Clua et al.,
139 2010), which imposes logistical constraints on researching them, resulting in a considerable lack of
140 baseline data on the biology and ecology of many of these species. A quarter of all extant

141 elasmobranch species are threatened with extinction, primarily due to anthropogenic impacts
142 (Dulvy et al., 2014), with recovery hindered by their K-selected life history traits (Gallagher &
143 Hammerschlag, 2011). Sharks and rays play an important role in marine ecosystems as upper-level
144 predators, exerting top-down control on prey assemblages and the environments in which they live
145 (Wetherbee & Cortés, 2004; Navia et al., 2007). Their elusiveness also precludes the use of
146 classical study approaches, which rely on observation (Brena et al., 2015). Temporary aggregations
147 formed by these species over limited resources (e.g. food), seen especially in large, solitary shark
148 species, have provided unique opportunities to gain insights into their inter- and intra-specific
149 interactions (Dudley et al., 2000; Dicken, 2008; Clua et al., 2013). The provisioning of sharks and
150 rays by humans, which is common in elasmobranch ‘eco-tourism’, has also provided avenues to
151 study sociality in these species (Newsome et al., 2004; Sperone et al., 2010; Maljković & Côté,
152 2011; Clua et al., 2013). Such contexts have been particularly useful in the study of sociality in
153 rays. For example, Furst (2011) showed that provisioned pink whiprays (*Pateobatis fai*, former:
154 *Himantura* sp.) in Mo’orea, French Polynesia exhibited a strong dominance hierarchy that was
155 based on size, sex and colour. Newsome et al. (2004) described a similar social structure for
156 provisioned stingrays at Hamelin Bay, Western Australia, with large female short-tail stingrays
157 (*Bathytoshia brevicaudata*, former: *Dasyatis* sp.) dominating over smaller male and female short-
158 tail stingrays, brown stingrays (*B. lata*, former: *D. thetidis*) and even smaller southern eagle rays
159 (*Myliobatis tenuicaudatus*, former: *M. australis*).

160 The short-tail stingray is one of the largest species of stingray and is a common benthopelagic
161 ray found in the neritic zone off the coasts of South Africa, southern Australia, New Zealand, and
162 Japan and eastern Russia (formerly *D. matsubarai*) (Last et al., 2016). Despite being listed as ‘Least
163 Concern’ on the IUCN Red List of Threatened Species (Duffy et al., 2016), almost nothing is
164 known about its biology and ecology. Based on the risk assessment for elasmobranchs provided by
165 Dulvy et al. (2014), this species’ coastal habitat exposes it to increased risk of anthropogenic
166 threats. Adults aggregate annually in large numbers at the Poor Knight Island Marine Reserve
167 (PKIMR), in New Zealand, presumably for breeding purposes (Le Port et al., 2012). Juveniles and
168 sub adults have also been observed here in high numbers and it has been suggested that the PKIMR
169 may also serve as a nursery ground (Le Port et al., 2012). This species possesses among the highest
170 forebrain complexity and brain-to-body mass ratio for elasmobranch described to date (Lisney et
171 al., 2008), suggesting an ability to develop and maintain complex social behaviours. Pink whiprays
172 have a similar brain-to-body mass ratio (Lisney et al., 2008), and exhibit complex social
173 organisation over provisioned food (Furst, 2011). The social behaviour of short-tail stingrays has
174 not yet been comprehensively assessed.

175 In Jervis Bay, on the southern coast of New South Wales, Australia, a small population of short-
176 tail stingrays are incidentally provisioned fish scraps discarded by local anglers cleaning their
177 catches at the Woollamia boat ramp. For the present study we took advantage of their attraction to
178 this site to conduct the first comprehensive heterarchical assessment (Cumming, 2016) of the
179 sociality of short-tail stingrays. We provide the first ethogram of agonistic behaviours described for
180 this species, which was used to examine the dominance hierarchy and social network in this species,
181 from which we assessed the factors influencing individuals' dominance and network position. Such
182 an assessment has only been conducted for one other species of provisioned batoid (pink whipray,
183 Furst (2011)). Further, our comprehensive assessment alongside the influence of individuals'
184 attributes allowed us to form a more complete picture of social structure within this population. The
185 heterarchical approach used in this study allowed us to test the hypothesis that this population of
186 short-tail stingrays exhibit a despotic social structure as characterised by (i) a highly linear and
187 steep dominance hierarchy, and (ii) a non-random social network, with the most dominant
188 individuals being central. This approach also allowed us to adequately address the alternate
189 hypothesis that the observed population was merely exhibiting non-social spatial proximity over a
190 food resource, as would be characterised by a (i) horizontal dominance relationship and (ii) random
191 social network. Further, dominance in elasmobranchs is typically considered size-dependent (Allee
192 & Dickinson, 1954; Myrberg & Gruber, 1974; Newsome et al., 2004; Clua et al., 2010; Maljković
193 & Côté, 2011); therefore, we also hypothesised that larger individuals would be more dominant and
194 more central to the network. We discuss the biological and ecological implications of our findings,
195 as well as provide future research directions.

196 **METHODS**

197 *Study Site*

198 The Woollamia boat ramp (WBR) (35° 1' 32" S, 150° 39' 59" E) is located in the lower
199 Currambene Creek (Figure 12B) in the northeast of Jervis Bay, Australia (Figure 12A). Jervis Bay
200 is the largest component of the Jervis Bay Marine Park (Figure 12A) and is situated on the south
201 coast of New South Wales (Figure 12A Inset). Anecdotal evidence suggests short-tail stingrays
202 have been incidentally provisioned fish scraps by anglers since the installation of cleaning facilities
203 at the WBR in 1985 (R. Simpson, Simos Afloat Fishing Charters, personal communication, August
204 2016). Fish scraps are discarded into the shallow water just adjacent to the main wharf via a discard
205 pipe that runs from the centre of the cleaning table (Figure 12C).

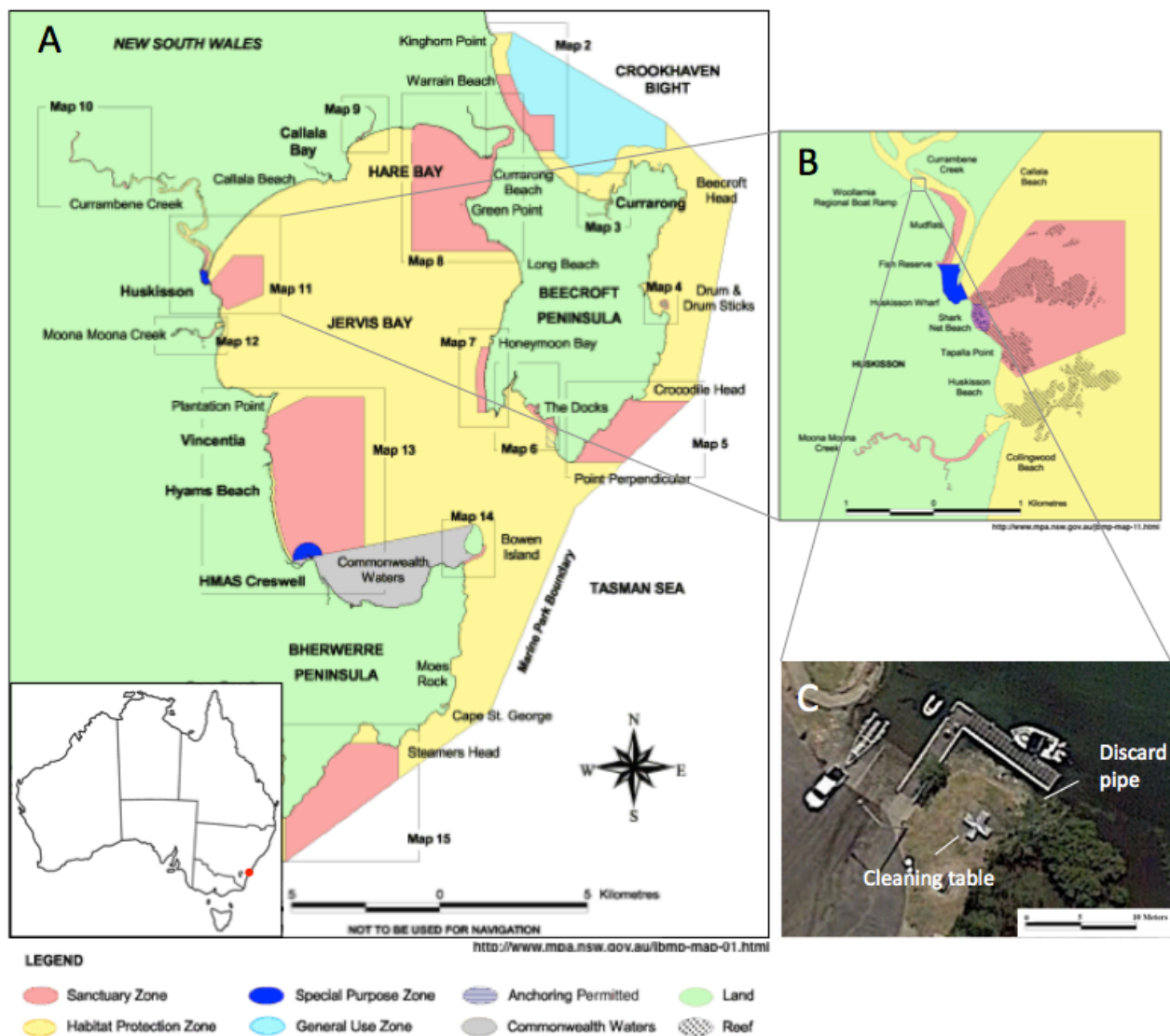


Figure 12. Study location. (A) Zoning map of the Jervis Bay Marine Park (from www.mpa.gov.au/jbmap-map-01.html), inset: geographic location; (B) Zoning map of lower Currumbene Creek, Jervis Bay (from www.mpa.gov.au/jbmap-map-11.html); (C) Aerial photograph (Google Earth) of the Woollamia boat ramp indicating location of the cleaning facilities.

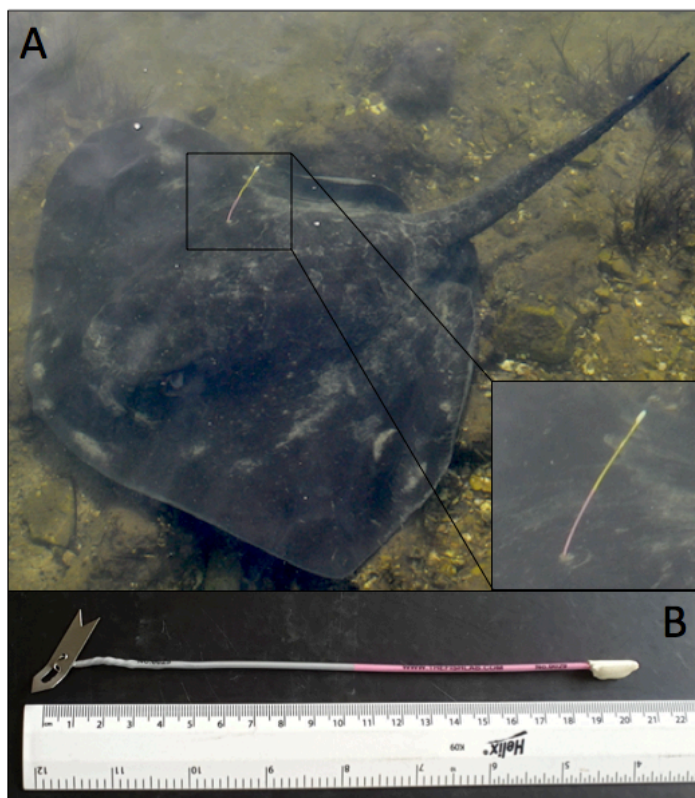
Visual Tagging

Short-tail stingrays were tagged between the 1st and 31st August 2016 with visual tags (Figure 13) to allow rapid identification of individuals engaging in social interactions in the field. Stingrays were attracted to the WBR for tagging by use of bait prior to the observation period (25th August – 2nd September 2016). Subsequently, stingrays were tagged opportunistically between observation sessions. The stingrays were baited into the immediate vicinity of the discard pipe (~10m radius) using a mixture of locally sourced fish frames and offal. For each new stingray, the time of first arrival was documented and photographs of the entire dorsal surface were taken for secondary identification. Sex was determined by the presence or absence of male claspers under the base of the tail. The disc width (DW) for each new stingray was measured from pectoral fin tip to fin tip

222 (following Yearsley and Last (2016)) to the nearest 5cm using a marked 2m length of dowel. High
223 accuracy measurements were unobtainable because the stingrays were unrestrained.

224 The visual tags employed were 316S marine grade stainless steel dart (SSD) heads (Hallprint
225 PTY. LTD, Hindmarsh Valley, South Australia) with 200mm long 2-colour coded vinyl streamers,
226 and Passive Integrated Transponder (PIT) tags affixed to the distal end (Figure 13B). The PIT tags
227 were affixed using waterproof epoxy adhesive (Shelleys, NSW, Australia) to allow secondary
228 identification in the case of biofouling. Following procedure provided by the tag manufacturer
229 (Hall, 2015), the tags were inserted into the musculature where the pectoral fin meets the body of
230 the stingray at a 45° angle toward the head (Figure 13A) using a 3m hand-held tagging pole with an
231 SSD applicator tip. The colour of tag, the time tagged and the side it was inserted were recorded.
232 Each individual was given a short name to allow rapid data recording in the field during social
233 interactions.

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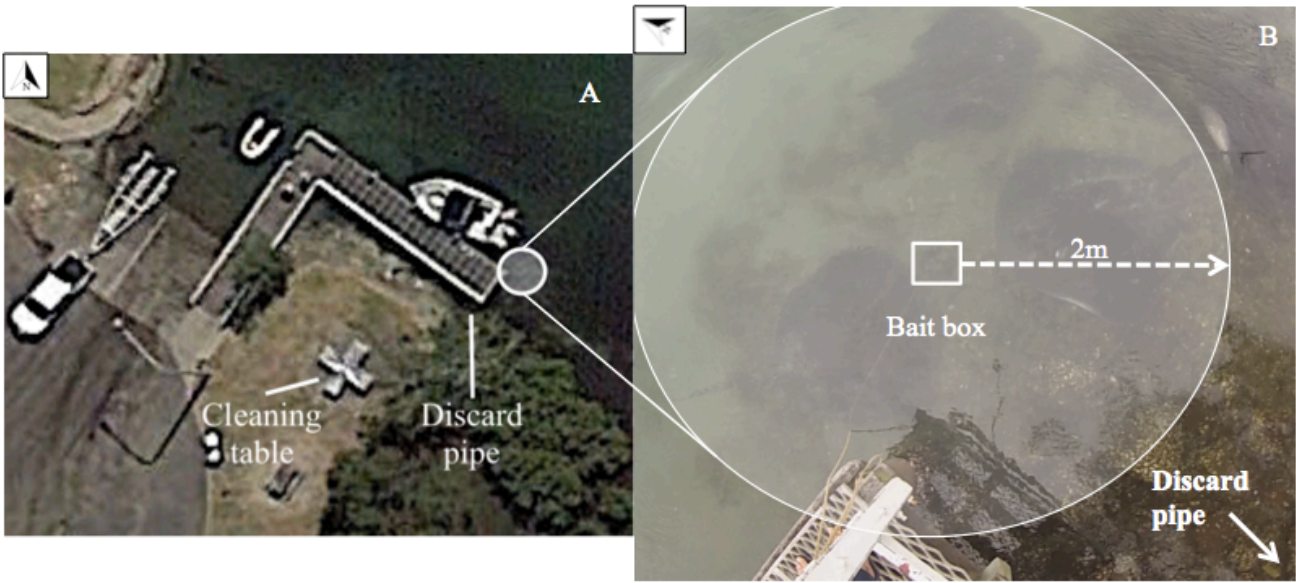
236 **Figure 13.** Short-tail stingray tagged in this study. (A) Anatomical position of visual tags and (B) example of tags used.

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238 *Social Interactions*

239 Dominance measures and social network construction were based on dyadic agonistic
240 interactions during simulated provisioning events at the WBR observed between 25th August and
241 2nd September 2016. To maximise sampling across tidal cycles, the *interaction zone* was located
242 approximately 3m from the creek bank, close to the mouth of the discard pipe (Figure 14A), where

243 the water depth never dropped below 1 metre. To simulate the provisioning event, a bait box
244 measuring 18x18x18cm and made from UV stabilised heavy duty recycled plastic gutter mesh
245 (Whites Super Gutter Guard, NSW, Australia) and plastic cable ties, was filled with locally sourced
246 fish frames, to allow olfactory cues to disperse but the stingrays could not access the bait. This is a
247 common protocol in social studies for free living shark species (e.g. Findlay et al. (2016), Sperone
248 et al. (2010) & Laroche et al. (2007)). The bait box, which was weighed down using a 1kg weight
249 and tied to the wharf via rope, was placed into the centre of the interaction zone, which was defined
250 as a 2m radius around the bait box (Figure 14B).
251



252
253 **Figure 14.** (A) Location of the social interaction zone relative to the cleaning facilities; (B) Schematic for the social
254 interaction zone around the bait box.
255

256 An ethogram of dyadic interactions was compiled over 1.5 observation days, which was then
257 compared with the ethograms available for ray (Furst, 2011) and shark species (Myrberg & Gruber,
258 1974; Sperone et al., 2010; Clua et al., 2013) to ensure the observed behaviours were suitable and
259 objective. A visual representation of the developed ethogram is given in Figure 15. Detailed
260 descriptions for the interaction types are given in the appendix (Table A7).

261 Dyadic interaction data were collected during half hour observation sessions run at random
262 intervals over 7 days. Half hour sessions were chosen arbitrarily to allow observers and scribes to
263 address any issues faced during the fast-paced observation sessions. Every interaction between a
264 dyad was recorded and classified following the ethogram (Figure 15). The time of each interaction
265 and the individuals involved were recorded. Every observation session was filmed using a GoPro
266 Hero4 attached to an arm that was fixed to the wharf, positioned so the bait box was in the centre of
267 the field of view, to create an archive and for instances when interactions could not be clearly
268 defined in the field.

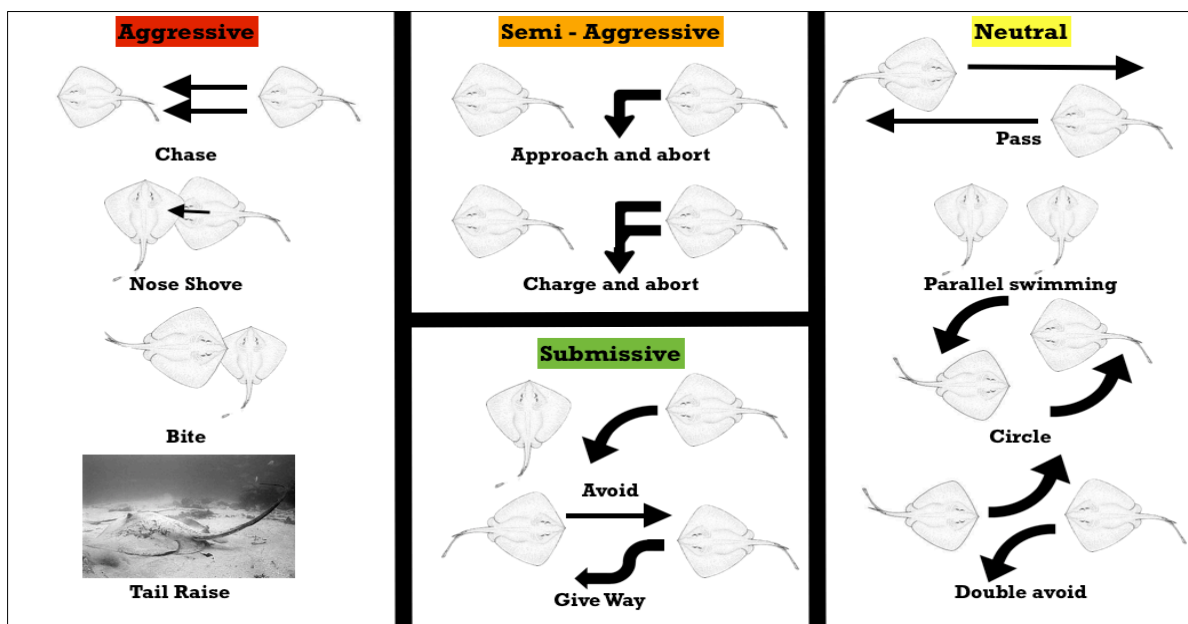


Figure 15. Visual ethogram of agonistic dyadic interactions exhibited over simulated provisioning.

Data Analysis

Data was recorded and organised using Microsoft® Excel® 2008. All statistical analyses were conducted using R (V.3.3.1) (R Core Team, 2015) with the R Studio interface (V.0.99.903) (RStudio Team, 2015).

Dominance measures

The dominance relationships between individuals were quantified using *David's Scores* (DS) (David, 1987) and *Elo Ratings* (ER) (Elo, 1978). DS is a dominance ranking system that takes into account the overall success of individuals across all observed dyadic interactions (Bayly et al., 2006), with individuals who dominate most interactions receiving higher scores than those who typically lose (Gammell et al., 2003). For statistical analyses, normalised DS (normDS) were generated from DS. ER accounts for the sequence of interactions, showing temporal influence on individual dominance (Neumann et al., 2011). DS have been used extensively in social mammals, especially primates (de Vries et al., 2006; Koren et al., 2008; Jaeggi et al., 2010; Schülke et al., 2010; Balasubramaniam et al., 2013; Yeater et al., 2013), whereas the utility of ER in ethology has only recently been realised (Neumann et al., 2011).

An interaction matrix of all interactions was generated from observed dyadic interactions. From this, an asymmetrical interaction matrix for all dyadic interactions was generated, where the dominant individual for each interaction was given a value of 1 and the subordinate was given a value of 0. For neutral, or drawn, interactions both individuals were given a value of 0.5, following (Neumann & Kulik, 2014b). DS and normDS matrices were generated using the *Dij* method

(matrices of dyadic dominance indices corrected for chance) as described by de Vries (1998), from which dominance rankings (DS and normDS scores) for each individual were generated. Linearity of the dominance hierarchy (normDS) was calculated using the *modified Landau's h'* described by de Vries (1995), by use of the *devries* formula in the *compete* package (Curley, 2016) in R Studio (RStudio Team, 2015). The observed linearity was then tested against 10,000 permutations to test its significance (de Vries et al., 2006). The steepness (slope or 'dominance gradient', see de Vries et al. (2006)) of the dominance hierarchy (normDS) was assessed using the *Steepness* package (Leiva & de Vries, 2014) in R Studio (RStudio Team, 2015) based on the *Dij* matrices generated above. The observed steepness was then assessed against 10,000 permutations to test its significance (de Vries et al., 2006).

A time-stamped dataset of all dyadic interactions, with both dominant-submissive (winner-loser, asymmetrical) and neutral (drawn, symmetrical) interactions, was used to generate ER using the *EloRating* package (Neumann & Kulik, 2014a) in R Studio (RStudio Team, 2015), following Neumann and Kulik (2014b). As ER are temporally mediated, a significant correlation with DS (overall dominance) would suggest the temporal dynamics of won and lost interactions has little influence on the overall dominance, indicating a stable hierarchy. Final ER and normDS for each individual were extracted and their correlation tested using a Pearson product-moment correlation. As the two were significantly correlated (see *Results - Dominance*), we used normDS for further analyses of dominance.

Social network analysis

A directed social network was constructed from the time-stamped dyadic interaction dataset described above, with the omission of drawn interactions, using the *igraph* package (Csardi, 2015) in R Studio (RStudio Team, 2015). This network was used to calculate four egocentric network metrics (following Farine and Whitehead (2015)): (i) out-degree, as a measure of influence over other individuals; (ii) in-degree, as a measure of how influenced the individual was by other individuals; (iii) strength, as a measure of the individuals association rates; and (iv) eigenvector centrality, as a measure of each individuals influence over the entire network. To test the hypothesis that the observed social network was not random, the strength (weighted degree) of the observed social network was tested against the weighted degrees of 10,000 network permutations produced using the group-by-individual methodology described by Farine (2013).

Factors influencing dominance and network centrality

As dominance hierarchies are typically considered size-dependent in sharks (Allee & Dickinson, 1954; Myrberg & Gruber, 1974; Clua et al., 2010; Maljković & Côté, 2011), as has been speculated for rays (Newsome et al., 2004), we expected the observed dominance hierarchy to be determined

327 by stingray size. In addition, we expected more central individuals in the observed social network to
328 be more dominant, and therefore for eigenvector centrality to be determined by size. Pearson
329 product-moment correlations were used to compare normDS and DW, eigenvector centrality and
330 DW, and normDS and eigenvector centrality.

331 *Ethical Note*

332 Short-tail stingrays showed varied initial responses to tagging, however all rapidly returned to
333 the provisioning site. Evidence also suggested the tags were lost after less than 4 months at liberty
334 with no tag wounds remaining ($N = 3$) (see Figure A1 in the appendix). Tag selection and project
335 design were carefully considered with regard to animal welfare, and to the best of our knowledge,
336 there were no negative impacts on the welfare of the animals used in this study. This study was
337 carried out under approval from the Macquarie University Animal Ethics Committee, under
338 ARA2014/015-7, and NSW DPI Fisheries Scientific Collection Permit P08/0010-4.4.

339 **RESULTS**

340 Fifteen short-tail stingrays were tagged at the WBR, though only 13 were observed during social
341 interaction observations (Table 3). All 15 individuals were female, with a mean DW of 149cm ($N =$
342 9, Range = 135 – 165cm). DW measurements were only available for 9 individuals due to logistical
343 difficulty faced in measuring the unrestrained stingrays. Five individuals showed advanced stages
344 of pregnancy (obvious bulging on either side toward posterior of dorsal surface); however, as this
345 was determined by sight only it is unclear whether other individuals were also in earlier stages of
346 pregnancy also. Following size-class estimates described by Le Port et al. (2012), 2 of the obviously
347 gravid individuals (Vinnie and Billy Ray) were originally considered sub-adults ($DW < 150\text{cm}$);
348 though for further analysis were considered adults. In addition, the 4 individuals without DW
349 measurements appeared ‘smaller’ than the observed adults (determined by sight in the field).
350 Therefore, we considered 7 to be adults ($>150\text{cm}$ DW or gravid) and 8 to be sub-adults (70 –
351 150cm DW).

352 Across the 7-day observation period, 56 hours of observations were recorded, averaging 3.5
353 hours per day (7 half hour sessions). A total of 688 dyadic interactions were documented, with 65%
354 of interactions exhibiting clear dominant and subordinate individuals (aggressive, semi-aggressive
355 and submissive interactions; asymmetrical), and the remainder being neutral or drawn
356 (symmetrical) interactions.

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Table 3.
Summary table of individuals tagged during this study.

Date and time tagged (AEST)	Tag colour		PIT tag number*	Nickname	Sex	Disc width (cm)
	Proximal	Distal				
01/08/16 15:51	Pink	Blue	-989	Thickness	F	135 ^S
01/08/16 16:08	Green	Grey	-834	Stumps	F	135 ^S
02/08/16 16:55	<i>Green</i>	<i>Red</i>	-848	<i>Small Fry</i>	<i>F</i>	<i>Unknown^{LS}</i>
03/08/16 14:15	Green	White	-983	Vinnie	F ^G	140 ^A
06/08/16 15:41	Grey	Red	-976	Billy Ray	F ^G	145 ^A
07/08/16 10:36	Green	Green	-987	Raylene	F ^G	155 ^A
07/08/16 13:28	Pink	Grey	-977	Jocka	F ^G	155 ^A
08/08/16 12:44	<i>White</i>	<i>Red</i>	-990	<i>Miley Cyray</i>	<i>F</i>	<i>155^A</i>
08/08/16 15:51	Pink	Green	-984	Dasy	F	135 ^S
09/08/16 09:51	Pink	Pink	-971	Shorty	F ^G	155 ^A
09/08/16 10:14	Grey	Grey	-846	Big Momma	F	165 ^A
18/08/16 17:10	Pink	Red	-975	Charlie	F	Unknown ^{LS}
28/08/16 16:44	Pink	Yellow	-982	Desaray	F	Unknown ^{LS}
29/08/16 15:05	Pink	White	-835	Shuga	F	Unknown ^{LS}
30/08/16 10:28	White	Pink	-975	Ellie	F	Unknown ^{LS}

* all PIT tags begin with 900032002394-; ^Ssub-adult individuals; ^Aadult individuals; ^{LS}likely sub-adults; ^Ggravid. Individuals in *italics* were not observed during social interactions.

Dominance

DS differed for all individuals (Figure 16), indicating the presence of a dominance hierarchy. The linearity (h') of the observed dominance hierarchy was 0.401, and was significantly different from random as judged against 10,000 permutations (right-tailed $P = 0.049$). Despite its significance, the observed linearity is not considered strong ($h' < 0.9$; Lehner (1996)), Martin and Bateson (1993). The observed dominance hierarchy was not very steep (steepness = 0.140) and was not significantly different from random ($P = 0.483$). The difference in normDS between the highest (Raylene, see Table 4) and second highest ranking (Thickness, see Table 4) individuals was 0.849, while the average difference between all other neighbouring subordinates was only 0.132 ($IQR = 0.047 - 0.190$).

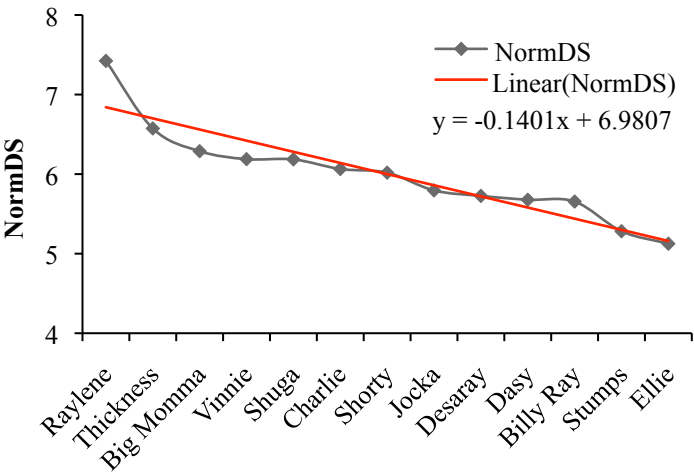


Figure 16. Individual normalised David's Scores (normDS) indicating the dominance gradient (red line).

ER fluctuated over time for most individuals ($N = 12$; Figure 17), with 4 showing declines in dominance (slope < -15), 4 showing increases in dominance (slope > 15) and 4 showing relatively stable dominance (slope < 10). It should be noted that data for 'Charlie' is not provided due to insufficient interaction data to calculate ER over time. NormDS and final ER were significantly correlated (Pearson product-moment correlation: $N = 13$, $r = 0.68$, $P = 0.01$), indicating the observed dominance hierarchy was stable over time. NormDS was not significantly correlated with DW (Pearson product-moment correlation: $N = 9$, $r = 0.30$, $P = 0.43$), suggesting the observed dominance hierarchy was not based on size.

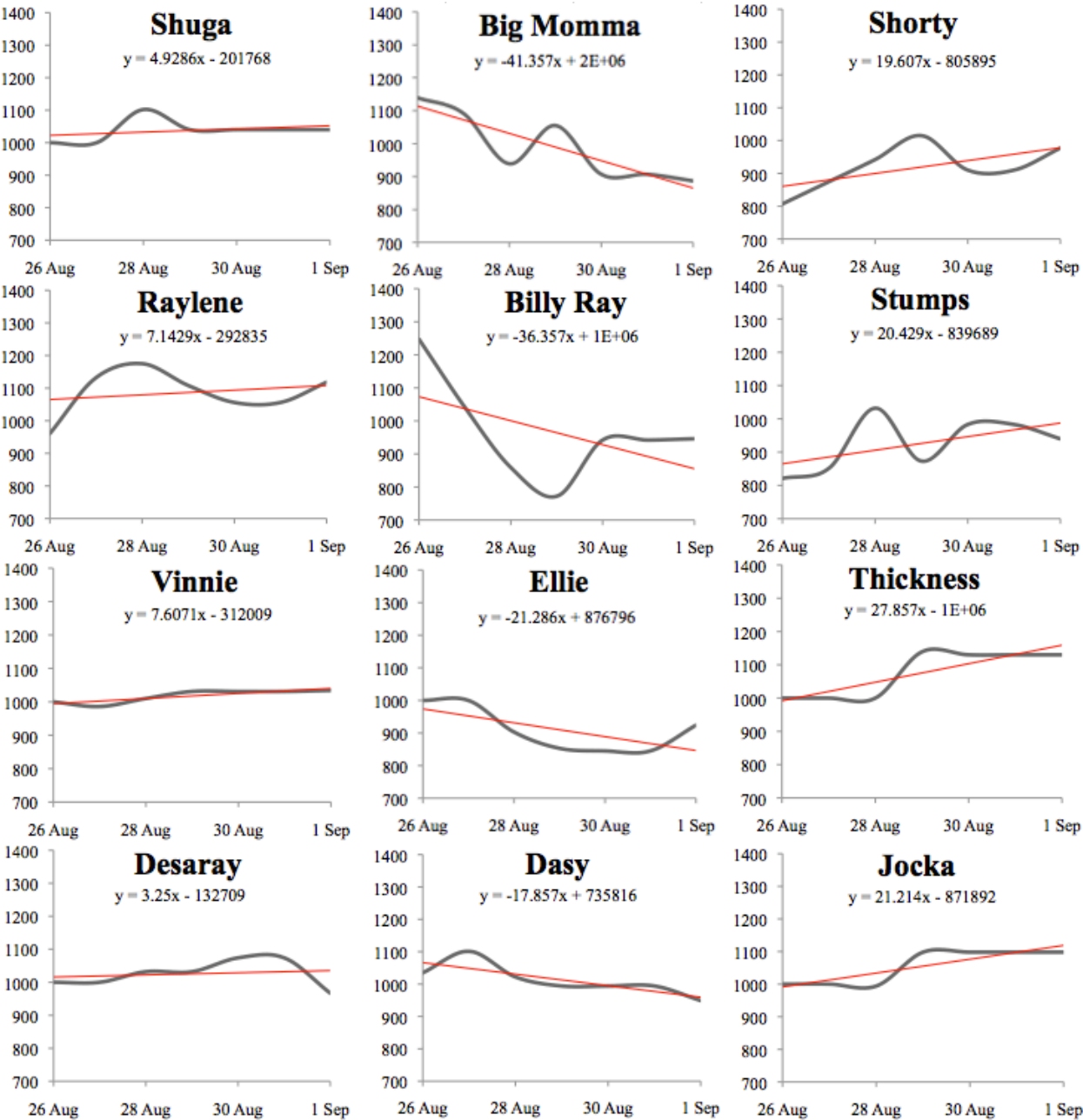
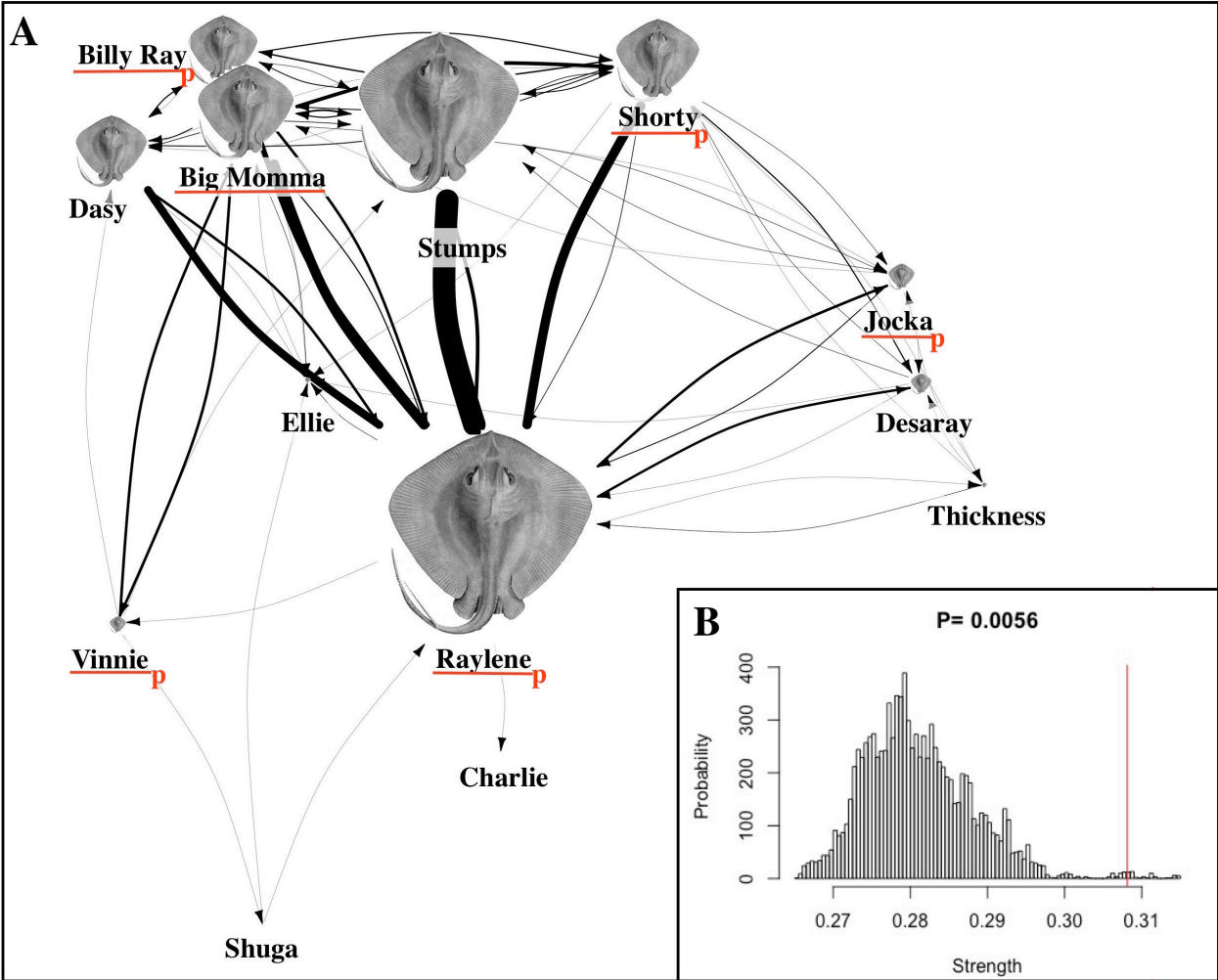


Figure 17. Individual Elo Ratings over time, with the exception of Charlie. Trend lines are given in red, with the line equation given under individual ID.

391 A visual representation of the observed social network is provided in Figure 18A with a
392 summary of the egocentric metrics calculated in Table 4. The strength (weighted degree) of the
393 observed social network was significantly higher ($P = 0.006$) than expected by chance (Figure
394 18B), indicating that the observed social network was not random. Eigenvector centrality was not
395 significantly correlated to normDS (Pearson product-moment correlation: $N = 13$, $r = 0.23$, $P =$
396 0.44), indicating that the most central individuals in the network were not the most dominant.
397 Further, eigenvector centrality was not correlated to DW (Pearson product-moment correlation: $N =$
398 9 , $r = 0.280$, $P = 0.47$), indicating that larger individuals were not necessarily most central to the
399 network. The most central individual, Raylene, did however exhibit the highest egocentric metrics
400 and dominance (Table 4).

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402 **Figure 18.** The observed social network. (A) Weighted and directed social network, where arrows show direction of
403 interaction, line thickness indicates total number of interactions between individuals in the given direction (degree),
404 node sizes show eigenvector centrality, adults are underlined in red and gravid individuals are denoted by 'p'; (B)
405 Histogram of the weighted degrees (strength) of 10,000 network permutations compared to that of the observed social
406 network (red-line).
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Table 4.Summary of egocentric metrics calculated for the social network provided in **Figure 18**.

ID	Out-degree	In-degree	Strength	Eigenvector Centrality	NormDS
Raylene	11	9	20	1	7.423
Thickness	4	2	6	0.027	6.574
Big Momma	8	7	15	0.469	6.288
Vinnie	4	2	6	0.082	6.188
Shuga	2	1	3	0.007	6.185
Charlie	0	1	1	0.007	6.064
Shorty	9	7	16	0.408	6.018
Jocka	4	5	9	0.13	5.795
Desaray	4	4	8	0.103	5.726
Dasy	5	6	11	0.35	5.678
Billy Ray	6	5	11	0.341	5.655
Stumps	6	8	14	0.787	5.282
Ellie	1	7	8	0.03	5.125

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DISCUSSION

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We observed a dominance hierarchy in a wild population of short-tail stingrays that was relatively linear but quite shallow, with a single alpha individual (Raylene). Analysis revealed a non-random social network with Raylene as the central individual. Collectively these results support the hypothesis that the population of short-tail stingrays incidentally provisioned at the WBR exhibit a social structure indicative of a despotic society and are not merely co-occurring over food. It is important to note that the observed dominance hierarchy and social network may only be specific to this context, where individuals are competing over a limited food resource. Contrary to observations for provisioned (Allee & Dickinson, 1954; Myrberg & Gruber, 1974) and free-living (Allee & Dickinson, 1954; Myrberg & Gruber, 1974) shark populations, body size was not a determining factor for dominance or network centrality. Further assessment of the factors influencing dominance and social organisation in this species is required to fully understand the observed dynamics.

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In the present study, asymmetrical interactions accounted for the majority of observed agonistic dyadic interactions. In addition, while dominance did not explain eigenvector centrality (and vice versa) a single individual (Raylene) was observed to have the highest strength, dominance rank and eigenvector centrality (Table 4). These data indicate the dominance structure observed (Figure 16) is reflective of a despotic social structure with Raylene as the alpha. Some may argue that the shallow dominance hierarchy observed here is indicative of an egalitarian society (van Schaik (1989) cited in de Vries et al. (2006)); however, a despotic social system can be characterised by the most and second most dominant individuals having a difference in normDS that is greater than that between all other neighbouring subordinates (Beaugrand et al., 1984). Here, the difference between

434 the normDS of Raylene and the next subordinate (Thickness) was 6.5-fold higher than the average
435 difference between all other neighbouring subordinates (see Figure 16; values given in Table 4).
436 Despotic systems are also characterised by low counter aggression from subordinates to dominants
437 (Thierry, 2007). It is clear from the edges in the social network (Figure 18), that Raylene received
438 minimal counter aggression. Therefore, we can be confident that the social hierarchy observed here
439 is reflective of a society at the despotic end of the spectrum.

440 Despoticism is typically described for highly social, group living species such as wolves (*Canis*
441 *lupus lupus*) (Cordoni & Palagi, 2008), spotted hyenas (*Crocuta crocuta*) (Wahaj et al., 2001) and a
442 number of non-human primates (see Palagi and Norscia (2015)), that live in groups at all times and
443 benefit from reduced predation risk, increased foraging efficiency, and often alloparental care.
444 Individuals continually reinforce and reconcile relationships to maintain social unity (Palagi &
445 Norscia, 2015). It is unknown whether grouping of short-tail stingrays observed at the WBR
446 extends outside of the observed context (competing over food), therefore acoustic tagging would
447 provide important new insights into this species social behaviour. Nevertheless, observation of such
448 a highly social system having developed over the repeated provisioning of a limited food resource
449 within short-tail stingrays, therefore, is rather extraordinary and reinforces the suggestion that this
450 species is capable of forming and maintaining complex social behaviours.

451 An individuals' success in agonistic interactions carries with it direct and indirect fitness
452 implications. Successful individuals usually have greater access to better quality resources, such as
453 mates, shelter and food, when compared to less successful individuals (Dugatkin, 2009). The
454 restriction of access to limited resources by dominant individuals resulting in the reduced
455 reproductive success of subordinates is well documented (Lomnicki, 1988; Koenig, 2002),
456 particularly among highly social primates (Fedigan, 1983; Ellis, 1995). In the present study,
457 observations were made for a population of short-tail stingrays that are competing over provisioned
458 food, which serves as a limited resource, and supporting observations suggest these individuals may
459 be developing dependence on this resource (see Chapter 1). More dominant and central individuals
460 gained access to the bait box more often, which likely reflects access to provisioned food during
461 normal provisioning events (fish scraps discarded by fishermen). Further, it has been suggested that
462 Currumbene Creek, within which the Woollamia boat ramp is situated, may serve as a gestation,
463 pupping and/or nursery ground for short-tail stingrays (see Chapter 1) and during our observations
464 we observed 5 heavily gravid individuals entering agonistic interactions with the most dominant
465 (Raylene) exhibiting the most advanced stages of pregnancy. We suggest that dominance increases
466 her net gain from the provisioned resource, which in turn aids her in meeting the nutritional
467 demands of her pups during gestation and reduces the energetic costs associated with foraging
468 naturally. These observations may have implications for reproduction and management in this

469 species. If individuals become dependent on the provisioned resource, the net gain for less
470 successful individuals may not be sufficient to meet the nutritional needs of their pups and only few
471 breeding individuals will likely be supported. Short-tail stingrays, being a large, coastal species, are
472 at high risk of threatening processes. Further, almost nothing is known about their reproduction. We
473 suggest the use of ultrasound to determine the health/stage of pups of provisioned short-tail
474 stingrays at the Woollamia boat ramp to identify whether dominance rank is related to breeding
475 success. We also recommend further research into whether Currambene Creek has reproductive
476 significance for this species.

477 Dominance rank and society structure is related to how much stress an individual incurs. This is
478 important as stress can have hormonal, cardiovascular, immunological and reproductive
479 implications (Sapolsky, 2005). In despotic social systems, individuals must maintain their
480 dominance ranks to continue to gain the associated benefits, and depending on the mechanism by
481 which this is done, individuals of different ranks experience differing levels of stress. Individuals
482 can maintain their dominance rank in two ways: (i) by frequently asserting their dominance over
483 others and/or (ii) through intimidation (Sapolsky, 2005). Both mechanisms appeared to occur in the
484 population of short-tailed stingrays observed in this study. For example, the majority of interactions
485 involving Raylene were asymmetrical with her being the aggressor. In addition, Raylene often put
486 considerable effort into chasing individuals out of the interaction zone. This behaviour has been
487 shown to cause high levels of stress for the aggressor, presumably due to the associated physical
488 demands of such behaviour (Creel, 1996; Cavigelli, 1999; Sapolsky, 2005). Other fitness costs can
489 also be incurred. For example, when normally solitary brown hares (*Lepus europaeus*) were forced
490 to interact due to clumped and limited food resources, individuals developed dominance hierarchies
491 and subsequently dominant individuals spent more time defending the provisioned resource than
492 feeding (Monaghan & Metcalfe, 1985). With regard to intimidation, subordinate short-tail stingrays
493 often exhibited submissive behaviours towards Raylene, such as avoidance or giving way, which
494 could be interpreted as intimidation. Intimidation is often described in despotic primate societies
495 (Manogue et al., 1975; Sapolsky, 1990; Bercovitch & Clarke, 1995), and typically results in
496 increased stress for subordinates, presumably due to the frequency of the psychological stress
497 experienced (Sapolsky, 2005). Avoidance behaviour is likely beneficial to subordinates, however,
498 by reducing the costs associated with entering into aggressive interactions with dominants. Blood
499 samples of provisioned short-tail stingrays at the WBR should be assessed for harmful levels of
500 psychosocial and physiological stress indicators, to determine whether provisioning is causing
501 further biological implications for these individuals.

502 Submissive behaviours may also indicate that short-tail stingrays are capable of individual
503 recognition, which can help formalise relationships in group living (Tibbetts & Dale, 2007).

504 Individual recognition is common in social species (Tibbetts & Dale, 2007) and it has been
505 suggested that sharks are capable of social recognition (Myrberg (1991); see also Guttridge et al.
506 (2009) for review), though further research is needed on this topic.

507 Dominance hierarchies in provisioned shark aggregations are thought to be size-dependent
508 (Newsome et al., 2004; Clua et al., 2010; Maljković & Côté, 2011), which is supported by previous
509 studies on free-living shark social behaviour (Allee & Dickinson, 1954; Myrberg & Gruber, 1974).
510 Additionally, Newsome et al. (2004) commented that larger female short-tail stingrays would chase
511 smaller individuals away from provisioned food in Hamelin bay, Western Australia. Based solely
512 on our observations, we would have suggested the same; however, the influence of individual size
513 on dominance and centrality within the network was not significant. Further, Raylene was not the
514 biggest female within the group, with regard to disc width. However, disc width may not be the
515 most suitable measure of size in this species, rather weight may be more suited. Alternatively, there
516 might be an effect of personality in short-tail stingray dominance and centrality (Byrnes & Brown,
517 2016).

518 Contrary to the social structure described by Furst (2011) for pink whiprays, sex and colour
519 could not be determining factors for dominance as only females were observed and there were not]
520 discernible differences in colour. Genetics may also provide a possible explanation of network
521 position and dominance. In his review, Drews (1993) highlights that dominance can be inherited. In
522 other words, individuals can inherit traits, such as aggressiveness, that are directly related to their
523 ability to 'win' in aggressive interactions and gain higher dominance rank (Holekamp & Smale,
524 1991). This has been shown in birds, dogs, insects and teleost fish (see Drews (1993) for review).
525 Further, it has been suggested that genetic relatedness may influence individuals' network position
526 in sharks (Mourier et al., 2012). Some shark and ray species are known to migrate to nursery
527 grounds and exhibit natal philanthropy (Wearmouth & Sims, 2008), and Currambene Creek has
528 been suggested as a potential pupping/nursery ground for this species (Chapter 1). This coupled
529 with all observed individuals being female, of apparently different ages (based on size class
530 differences, Le Port et al. (2012)), could indicate that the individuals using the site may be related.
531 Genetic analysis may provide exciting insights into the influence of genetic relatedness on
532 individual dominance rank and network position, as well as potentially fill some knowledge gaps
533 about reproduction in this species.

534 In their review of social capacity in elasmobranchs, Jacoby et al. (2011) highlight that there is a
535 need for fine-scale analysis of shark and ray groups in the form of social network analysis in order
536 to better inform shark and ray conservation. We provide a comprehensive social network analysis of
537 a provisioned population of stingrays, which has indicated that short-tail stingrays are not only
538 capable of exhibiting social behaviours, but also capable of maintaining a highly complex despotic

539 social structure. We have identified that there are significant risks to this species biology and
540 ecology due to its high social ability, and it is therefore integral to monitor this population with
541 regard to changes in group structure and social organisation. We suggest continued monitoring of
542 this population and the level of provisioning that occurs at the WBR, as well as genetic assessment
543 to determine the relatedness of the individuals and provide insights into whether Currambene Creek
544 acts as a nursery ground for this species.

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SUMMARY

Short-tail stingrays are considered ‘Least Concern’ on the IUCN Red List of Threatened Species, due to their common occurrence and a stable population trend (Duffy et al., 2016), yet almost nothing is known about their biology and ecology. Further, large coastal species of ray are considered at increased risk of threatening processes due to increased exposure to human activity (Dulvy et al., 2014). The population provisioned over the past 30+ years at the Woollamia boat ramp in Jervis Bay, Australia provided a unique opportunity to address some of the knowledge gaps that surround this species.

Within the studies presented in this thesis, we provide three main findings that have implications for the management of the target population of short-tail stingrays and of recreational fishing activities. Firstly, we demonstrated that small-scale incidental provisioning significantly influenced site use by short-tail stingrays. When compared to previous studies on ray provisioning (e.g. Corcoran et al. (2013), Gaspar et al. (2008), Newsome et al. (2004)) it is clear that this population is at high risk of experiencing negative impacts in the absence of appropriate management. There are already clear signs of anticipatory behaviour in this population, which indicates a level of dependency. Secondly, we suggest that Currumbene Creek, within which the Woollamia boat ramp is situated, may serve as a gestation, pupping and/or nursery ground for this species. The population size for short-tail stingrays within the greater Jervis Bay area is unknown, and almost nothing is known about reproduction in this species (Duffy et al., 2016). Therefore, if this provisioned population of females is experiencing negative effects from provisioning activity, this could have implications for the overall reproductive success of the population within Jervis Bay. Thirdly, we demonstrated that this species is capable of developing and maintaining highly complex social behaviour that is typically exhibited by highly social, group living species, such as primates.

Food provisioning has been shown to cause significant effects in marine ecosystems (Brena et al., 2015), yet the discarding of fish waste by recreational anglers back into waterways from cleaning facilities is still a common and accepted practice. To our knowledge, the effects of this activity have not yet been assessed, and it is therefore unlikely that the impacts are being considered in the management of recreational fishing along Australia’s coastline. Discussions with local fishermen at the Woollamia boat ramp highlighted that many consider the ‘free feed’ obtained by the stingrays as inconsequential. Yet, when this activity is likely occurring at fish cleaning facilities at almost every boat ramp around Australia on a daily basis, the sheer biomass of provisioned food is probably quite considerable. If provisioning activity from a small, coastal town boat ramp, such as Woollamia, is enough to alter the natural movements of a large marine mesopredator, such as short-tail stingrays, then the impacts along Australia’s coastline are likely significant. Continued monitoring of the level of provisioning occurring at Woollamia, as well as the size and composition

of the provisioned population of short-tail stingrays is needed to ensure impacts can be mitigated early. In addition, a broad-scale monitoring and quantitative assessment of provisioning intensity at cleaning facilities around the coast of Australia should be implemented to determine the level of effects, identify the affected species and develop integrated management approaches.

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APPENDIX

Figures

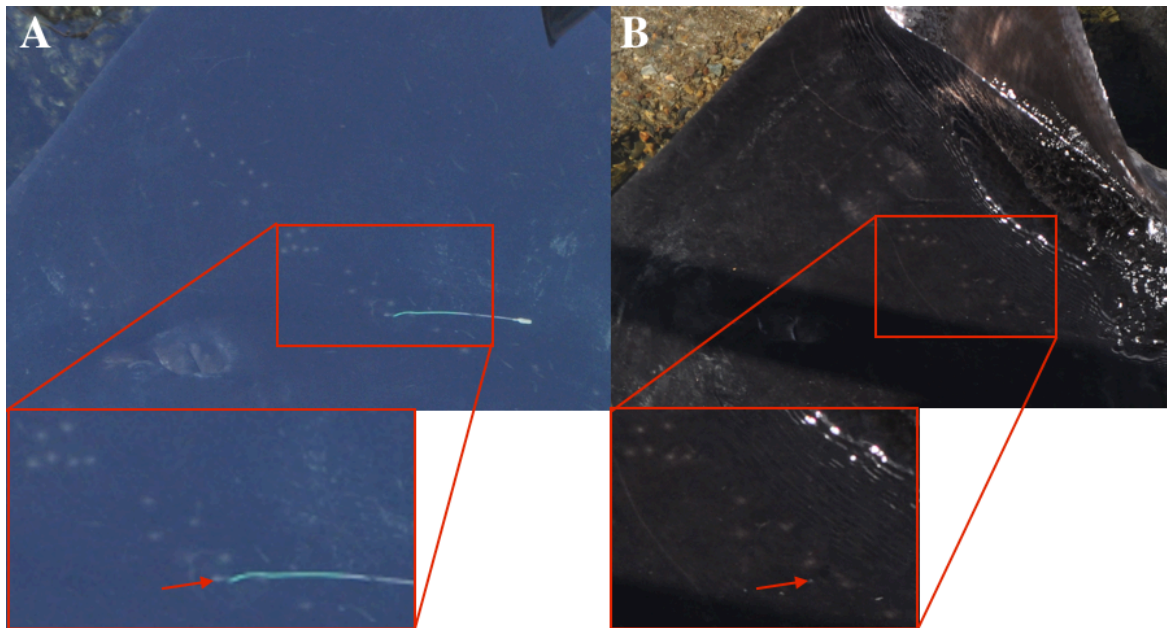


Figure A1. Photographs indicating tag loss and healing for a short-tail stingray tagged in the present study (Stumps). Image A was taken 16 August 2016 and image B was taken 14 January 2017. Arrows indicate point of tag entry. Note distinct cluster of white dots used to identify this individual in top left of the inset images.

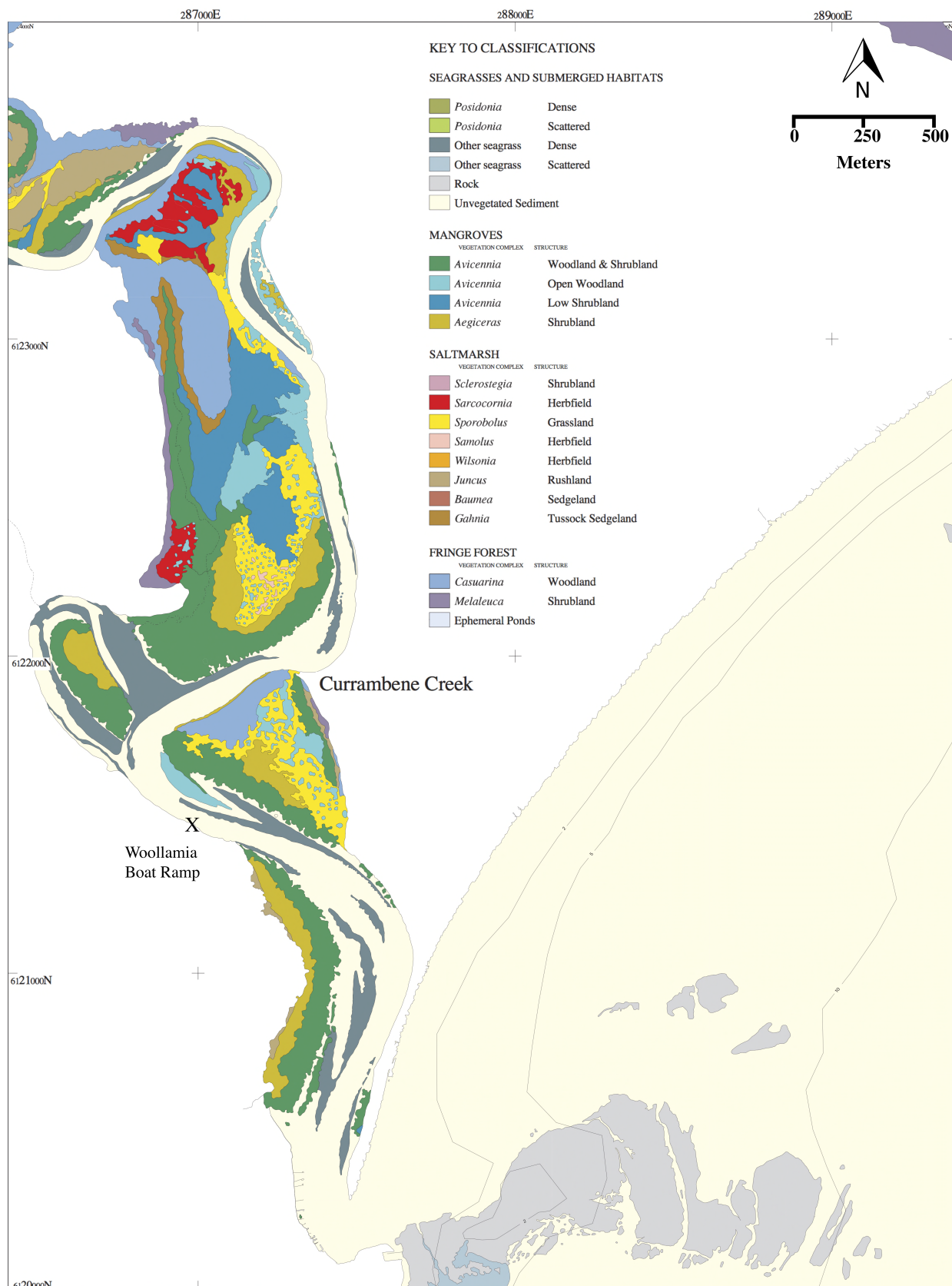


Figure A2. Map detailing habitat types within Currambene Creek. Adapted from Map 6 of the Jervis Bay Habitat Distribution Maps 1985-1991 series by The Marine Environment Research Program (CSIRO Division of Fisheries). Base Data/Data provided by CSIRO and reproduced with the permission of CSIRO.

Tables

Table A1.

Generalised Mixed Effects model output for $presence \sim scale(clean_length) * scale(n_boats) + (1 | ID)$, where $presence$ is binomial (present = 1, absent = 0), $clean_length$ is the cumulative length of cleaning events per observation session (in minutes), n_boats is the total number of boats during the observation session and $(1 | ID)$ is the random effect of individual ID.

	B	SE	z	P value
Intercept	-2.235	0.386	-5.798	<0.0001***
~ $scale(clean_length)$	0.507	0.141	3.605	0.0003***
~ $scale(n_boat)$	-0.337	0.156	-2.159	0.031*
~ $scale(clean_length) * scale(n_boat)$	0.288	0.2023	1.424	0.155

Significance codes: <0.001***; <0.01**; <0.05*

Table A2.

Generalised Mixed Effects Model for $presence \sim tide_direction * session + (1 | ID)$, where $presence$ is binomial (present = 1, absent = 0), $tide_direction$ is an integer denoting the predominant tide direction during the observation session (1 = outgoing, 2 = low, 3 = incoming, 4 = high), $session$ is an integer denoting the observation session (1 = AM, 2 = PM) and $(1 | ID)$ is the random effect of individual ID.

	B	SE	z	P value
Intercept	-10.068	1.902	-5.293	<0.0001 ***
~ $tide_direction$	2.469	0.676	3.651	0.0003 ***
~ $session$	4.316	0.974	4.432	<0.0001 ***
~ $tide_direction * session$	-1.296	0.367	-3.533	0.0004 ***

Significance codes: <0.001***; <0.01**; <0.05*

Table A3.

One-Way Analysis of variance output for $Session \sim n_rays * clean_length$, where $Session$ is an integer representing the observation session (AM = 1, PM = 2), n_rays is the number of individuals present in the observation session and $clean_length$ is the cumulative length of cleaning events per observation session (in minutes).

One-Way ANOVA: $Session \sim n_rays * clean_length$

	DF	Sum Sq	Mean Sq	F value	P value
~ n_rays	1	1.935	1.9353	11.769	0.0027**
~ $clean_length$	1	0.559	0.5593	3.401	0.08
~ $n_rays * clean_length$	1	0.217	0.2166	1.317	0.2647
Residuals	20	3.289	0.1644		

Significance codes: <0.001***; <0.01**; <0.05*

Table A4.

Two-Way Analysis of variance output for $LogRate \sim Session * Cleaning$, where $LogRate$ is the rate of stingray visitation (per hour, log transformed) for whether or not the cleaning table was in use ($Cleaning$; yes / no) during each observation session ($Session$, AM / PM).

Two-Way ANOVA: $LogRate \sim Session * Cleaning$

	DF	Sum Sq	Mean Sq	F value	P value
~ $Session$	1	16.404	16.404	8.1172	0.0067**
~ $Cleaning$	1	0.688	0.6877	0.3403	0.563
~ $Session * Cleaning$	1	0.044	0.0445	0.022	0.883
Residuals	44	88.919	2.0209		

Significance codes: <0.001***; <0.01**; <0.05*

Table A5.

One-Way Analysis of variance output for *Visits_negsqrt* ~ *Location* * *Session* * *Provision*, where *Visits_negsqrt* is the total number of visits per observation session (square root transformed for normality), *Location* is the site (upstream / downstream), *Session* is the observation session (AM / PM) and *Provision* is whether it was during the non-provisioned or provisioned observations.

One-Way ANOVA: <i>Visits_negsqrt</i> ~ <i>Location</i> * <i>Session</i> * <i>Provision</i>					
	DF	Sum Sq	Mean Sq	F value	P value
~ <i>Location</i>	1	0.253	0.2533	3.499	0.062
~ <i>Session</i>	1	0.226	0.226	3.122	0.078
~ <i>Provisioned</i>	1	1.07	1.0704	14.784	<0.001***
~ <i>Location</i> * <i>Session</i>	1	0.236	0.2365	3.266	0.071
~ <i>Location</i> * <i>Provisioned</i>	1	0.033	0.0335	0.462	0.497
~ <i>Session</i> * <i>Provisioned</i>	1	0.296	0.296	4.089	0.0441*
~ <i>Location</i> * <i>Session</i> * <i>Provisioned</i>	1	0.028	0.0275	0.38	0.538
Residuals	280	20.273	0.0724		

Significance codes: <0.001***, <0.01**, <0.05*, marginal .

Table A6.

TukeyHSD Post Hoc Analysis output for the *location* (Upstream / Downstream) and *session* (AM / PM) interaction and the *session* and *provisioning* (Yes / No) interaction for the One-Way ANOVA in **Table A5**.

TukeyHSD Post Hoc: <i>Location</i>*<i>Session</i>				
	Difference	Lower 95% CI	Upper 95% CI	Adj. P value
<i>Downstream</i> * <i>AM</i> – <i>Upstream</i> * <i>AM</i>	0.002	-0.114	0.118	0.999
<i>Upstream</i> * <i>PM</i> – <i>Upstream</i> * <i>AM</i>	-0.001	-0.117	0.115	0.999
<i>Downstream</i> * <i>PM</i> – <i>Upstream</i> * <i>AM</i>	0.115	-0.001	0.231	0.052
<i>Upstream</i> * <i>PM</i> – <i>Downstream</i> * <i>AM</i>	-0.003	-0.119	0.113	0.999
<i>Downstream</i> * <i>PM</i> – <i>Downstream</i> * <i>AM</i>	0.113	-0.003	0.229	0.058
<i>Downstream</i> * <i>PM</i> – <i>Upstream</i> * <i>PM</i>	0.117	0.001	0.233	0.048
TukeyHSD Post Hoc: <i>Session</i>*<i>Provisioned</i>				
<i>PM</i> * <i>No</i> – <i>AM</i> * <i>No</i>	0.120	0.004	0.236	0.039*
<i>AM</i> * <i>Yes</i> – <i>AM</i> * <i>No</i>	0.186	0.070	0.302	<0.001***
<i>PM</i> * <i>Yes</i> – <i>AM</i> * <i>No</i>	0.178	0.062	0.294	<0.001***
<i>AM</i> * <i>Yes</i> – <i>PM</i> * <i>No</i>	0.066	-0.050	0.182	0.457
<i>PM</i> * <i>Yes</i> – <i>PM</i> * <i>No</i>	0.058	-0.058	0.174	0.571
<i>PM</i> * <i>Yes</i> – <i>AM</i> * <i>Yes</i>	-0.008	-0.124	0.108	0.998

Significance codes: <0.001***, <0.01**, <0.05*, marginal .

Table A7.

Ethogram of short-tail stingray agonistic social interactions over simulated provisioning. *Dom* refers to the dominant individual and *Sub* refers to the subordinate individuals in asymmetrical interactions

Class	Behaviour	Dom	Sub	Description
Aggressive	Chase	A	B	Individual A actively chases individual B at a distance of less than 1.5 body lengths.
	Nose shove	A	B	Individual A shoves individual B with its snout on any part of the body of individual A.
	Bite	A	B	Individual A bites part of the dorsal surface of individual B. Bite often leaves 'kiss'- or "()"-shaped mark left by the dental plates.
	Tail raise	A	B	Individual A raises its tail in a defensive posture when facing individual B.
	Tail swipe	A	B	Individual A swipes its tail horizontally through the water while facing individual B.
Semi-aggressive	Charge & abort	B	A	Individual A swims at speed towards individual B and turns away before reaching individual B.
	Approach & abort	B	A	Individual approaches individual B as a slower speed than above and turns away before reaching individual B.
Neutral	Swim over	NA	NA	Individual A swims over the top of individual B.
	Follow	NA	NA	Individual A follows individual B at a slower speed than chase and at a distance between B and 4 body lengths.
	Pass	NA	NA	Individual A and individual B swim towards each other and pass without contact.
	Parallel swim	NA	NA	Individual A and individual B swim parallel, moving in the same direction as each other without touching.
	Circle	NA	NA	Individual A and individual B follow each other in a circular motion.
	Double avoid	NA	NA	Individual A and individual B approach each other head-on but both turn away before making contact.
Submissive	Avoid	B	A	Individual A avoids an interaction with individual B by turning away when it sees the individual B.
	Give way	B	A	Individual A moves out of the way of individual B allowing individual B to not divert from its swimming path.