

1 **Multiyear social stability and social information in marine**  
2 **predators with diel fission-fusion dynamics**

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22

23 **ABSTRACT**

24 Animals across vertebrate taxa form social communities and often exist as fission-fusion  
25 societies. Central place foragers (CPF) may form social groups, from which they will  
26 predictably disperse to forage, either individually or in smaller groups, before returning to  
27 fuse with the larger group. However, the function and stability of social associations in  
28 predatory fish acting as CPFs is unknown, as individuals do not need to return to a shelter,  
29 yet show fidelity to core areas. Using dynamic social networks generated from acoustic  
30 tracking data, we document spatially structured sociality in CPF grey reef sharks at a Pacific  
31 Ocean atoll. We show that sharks form stable, social groups over multi-year periods, with  
32 some dyadic associations consistent for up to four years. Groups primarily formed during the  
33 day, increasing in group size before sharks dispersed from the reef to forage at night. Our  
34 simulations suggest that multiple individuals sharing a central place and using social  
35 information while foraging (i.e. local enhancement), will outperform non-CPF social  
36 foragers. We show multiyear social stability in sharks and suggest that social foraging with  
37 information transfer could provide a generalisable mechanism for the emergence of sociality  
38 with group central place foraging.

39 **INTRODUCTION**

40 Gregarious animals face a constant trade-off regarding the costs and benefits associated  
41 with group living (Krause and Ruxton 2002). This trade-off can be heavily influenced by  
42 reproductive strategy, competition, the distribution and quality of food or predators in space  
43 and by processes that facilitate collective decision-making (Clark and Mangel 1984, Janson  
44 and Goldsmith 1995, Smola et al. 2015, Gil et al. 2017). In most cases, animal groups will  
45 exhibit fission-fusion dynamics, where individuals split from (fission) and re-join (fusion)  
46 other group members (Couzin and Laidre 2009). Fission-fusion dynamics can contribute to or

47 dictate group sizes and patterns of assortativity amongst group members (Couzin and Laidre  
48 2009, Sueur et al. 2011). The extent of fission-fusion dynamics in animal social groups are  
49 likely related to spatial and temporal variability in the environment, as well as the strength of  
50 social associations between individuals and their energetic state (Sueur et al. 2011). One  
51 important aspect of fission-fusion societies is the stability of associations between group  
52 members, which will determine the persistence of social communities (Silk et al. 2014).  
53 Surprisingly, multiyear social stability has only been found in a few avian and mammalian  
54 species with fission-fusion dynamics, including swallows, bats and hyenas (Kerth et al. 2011,  
55 Shizuka et al 2014, Silk et al 2014, Ilany et al. 2015).

56 Central place foragers (CPF) may refuge in groups and will often show fission-fusion  
57 dynamics over short temporal scales, with animals making excursions individually or in  
58 smaller groups to/from the larger group at the central place (Swift et al. 2014). For example,  
59 seals and seabirds reside in groups or colonies on land but head offshore to forage in much  
60 smaller groups (e.g. Wakefield et al. 2013, Hooker et al. 2015, Jones et al. 2020). In most  
61 cases, the central place is the location of a nest, shelter, or haul-out site which explains  
62 loyalty and fidelity to the central place. Sociality in refuging central place foragers is often  
63 thought to be driven by reproduction, but social foraging and information sharing may also be  
64 important (Buckley 1997, Evans et al. 2016, Lang and Farine 2017). Social information  
65 sharing in a foraging context can include local enhancement (where animals in a group are  
66 within sensory range of other foraging individuals and can simultaneously forage and observe  
67 conspecifics, Buckley 1997), recruitment (an individual ‘recruits’ others to a patch, with  
68 foraging success increasing with group size, i.e. the recruitment hypothesis, Buckley 1997),  
69 and public information (where uninformed individuals follow informed individuals to prey  
70 patches, Barta and Giraldeau 2001, Bijelvelde et al. 2010, Harel et al. 2017). The transmission  
71 of social information has been proposed as being responsible for driving the evolution and

72 maintenance of coloniality (information centre hypothesis), or simple aggregations of social  
73 foragers (Barta and Giraldeau 2001, Bijelveld et al. 2010, Riotte-Lambert and Matthiopoulos  
74 2019).

75 Models predict that the use of social information increases foraging success in  
76 gregarious animals, but only if prey patches are ephemerally distributed, unpredictable, and  
77 have short residence times (Buckley 1997, Boyd et al. 2016). These models all assume that  
78 central place foraging is a prerequisite of the social system; which is a reasonable assumption  
79 for animals that must return to a nest or shelter (Buckley 1997). However, some large marine  
80 predators such as sharks are central place foragers but have no obvious need to return to a  
81 central place (Klimley and Nelson 1984, Papastamatiou et al. 2018a). While information  
82 sharing may lead to the development of animal aggregations, the advantage of CPF itself in a  
83 social foraging context has not been explored (Riotte-Lambert and Matthiopoulos 2019). A  
84 central place may allow individuals or subgroups to find each other and ‘fuse’ with the larger  
85 group, which will help maintain social associations over diel or seasonal timescales (Sueur et  
86 al. 2011). Social associations between individuals can then potentially increase foraging  
87 success via social information sharing (Giraldeau and Berchamp 1999).

88 Tropical reef sharks often only use small proportions of available reef habitat and show  
89 multiyear fidelity or residency, returning to the same ‘central place’ over diel, tidal, or  
90 seasonal timescales (Klimley and Nelson 1984, Heupel and Simpfendorfer 2014,  
91 Papastamatiou et al. 2018a, b). Some sharks will form social associations under both  
92 laboratory and field conditions and are likely capable of social learning (Jacoby et al. 2010,  
93 Guttridge et al. 2013, Schilds et al. 2019, Mourier et al. 2012, 2018). Within a CPF context,  
94 they likely display fission-fusion dynamics, forming groups during the day and potentially  
95 dispersing in small groups (or individually) at night to forage (Klimley and Nelson 1984,  
96 Heupel and Simpfendorfer 2005, Papastamatiou et al. 2018a). Mating and reproduction in

97 reef sharks is seasonal, which influences patterns of movement, but residency on the reef can  
98 occur extensively throughout the year (Heupel and Simpfendorfer 2014, Papastamatiou et al.  
99 2018b). The function of sociality and central place foraging in these animals with potential  
100 diel fission-fusion dynamics are unknown. While most reef sharks are more active at night,  
101 they will also hunt during the day within their central place, potentially with multiple other  
102 individuals (Shiple et al. 2017, Papastamatiou et al. 2018a). Hence, the benefits of local  
103 enhancement and social associations may persist day and night (to varying degrees), and we  
104 may expect multi-year social stability between dyadic pairs if social foraging is beneficial.

105        Grey reef sharks (*Carcharhinus amblyrhynchos*) are central place foragers that can  
106 show high residency to coral reefs but are also capable of longer range dispersal (Heupel and  
107 Simpfendorfer 2014, White et al. 2017, Papastamatiou et al. 2018a). They form daytime  
108 aggregations but disperse more widely at night when they are more active, although they will  
109 forage opportunistically during the day (Papastamatiou et al. 2018a). At Palmyra Atoll, in the  
110 Pacific Ocean, 80% of grey reef shark diet is estimated to be pelagic prey, and sharks have  
111 been seen feeding on offshore bait balls during the day (McCauley et al. 2012, Papastamatiou  
112 YP Per. Obs.). Hence, prey patches are likely to be ephemeral and unpredictable in  
113 distribution, and sharks should benefit from social foraging with local enhancement. If central  
114 place foraging represents a mechanism for maintaining social associations in groups with diel  
115 fission-fusion dynamics and increases foraging success via social information sharing, then  
116 we would predict that a) sharks form social communities assorted by patterns of space use, b)  
117 group size should increase throughout the day as individuals (or sub groups) return to the  
118 central place, c) social associations amongst community member should be stable over  
119 multiyear periods, d) groups of individuals using social information to forage (local  
120 enhancement) and sharing a central place, will outperform non-CPF social foragers in  
121 behavioural simulations. We test these predictions with a population of grey reef sharks at

122 Palmyra Atoll, using a combination of acoustic telemetry, biologgers, dynamic social  
123 networks and individual based models.

## 124 METHODS

125 **Study population and location.** Palmyra Atoll (5°54'N 162°05'W) is located at the northern  
126 end of the Line Island chain, in the Central Pacific Ocean, and has been a US Federal  
127 Wildlife refuge since 2001, with only a research station on the island. Consequently, the atoll  
128 has large numbers of upper level predators, including grey reef sharks (*Carcharhinus*  
129 *amblyrhinchos*), with approximately 8000 individuals distributed heterogeneously around the  
130 forereef, with average densities of 21 sharks/km<sup>2</sup> (Bradley et al. 2017).

131 **Quantifying movements and community assignment.** Sharks were caught on hook and line  
132 and had a uniquely coded V16 (69 kHz, Vemco Ltd, Nova Scotia) acoustic transmitter  
133 surgically implanted into their body cavity. Individual animals (n = 41) were detected and  
134 tracked across a network of 65 VR2W acoustic receivers, which were attached to the reef and  
135 retrieved and downloaded annually. Receivers that were overlapping in their detection ranges  
136 (specifically in the SW of the atoll) were reduced in number to avoid detections being  
137 recorded multiple times simultaneously, a prerequisite for the mixture model analysis (see  
138 below). This resulted in the exclusion of 18 receivers but did not reduce the total area under  
139 acoustic surveillance.

140 Movement networks were constructed from the departure and arrival profile of the  
141 acoustic data, with receivers treated as nodes and movements between receivers as edges in a  
142 movement network (Jacoby et al. 2012). Prior to quantifying social behaviour we wanted to  
143 understand how tagged individuals were organised based on their space use. Therefore,  
144 'communities' were derived from the collective movement network across all individuals  
145 using the Fast-Greedy algorithm, implemented in the R package *igraph*, revealing statistically

146 significant clusters of movement (Clauset et al. 2004, Casardi and Nepusz 2006, Finn et al.  
147 2014). Community modularity within the movement network was high ( $Q = 0.589$ ),  
148 suggestive of area restricted movements, and resulted in the formation of five distinct  
149 movement communities. Note that movement communities do not consist of individual  
150 sharks, but rather receivers that showed significantly higher movements within than between  
151 locations. We then calculated a residency index (RI) for each individual across each location  
152 before assigning individual sharks to movement communities based on their most resident  
153 receiver location (i.e. the receiver with the highest RI). RI for each individual per location can  
154 be defined as;

$$RI_i = \frac{D_h}{D_{al}} \times 100$$

155 where  $D_h$  is the number of hours detected at a given location/receiver and  $D_{al}$ , the hours at  
156 liberty in the array as a whole. Thus, a location where an individual spends all of its time at  
157 liberty is assigned a 1 and none of its time at liberty a 0. Finally, as a metric of space use, we  
158 calculated 50% bivariate normal kernel utilization distributions (UDs) for each tagged  
159 individual within each movement community with >100 detections, at a minimum of two  
160 unique receiver locations (n=34), in the package *adehabitatHR* in R.

161 **Dynamic social networks.** We produced dynamic social networks using a ‘gambit of the  
162 group’ approach, where animals co-occurring in time and space are assumed to represent  
163 social associations after controlling for individual spatial preferences (Franks et al. 2010).  
164 Shark social networks were inferred directly from the detection data stream using the  
165 Gaussian mixture modelling approach, *GMMEvents* (Psorakis et al. 2012, Jacoby et al. 2016).  
166 Clusters of detections, produced by visits of multiple individuals to the same place at the  
167 same time, varied temporally to reflect the variation expected in the temporal distribution of  
168 animal aggregations, and were determined using a Variational Bayesian mixture model. From

169 these clusters, associations were assigned to an adjacency matrix. Randomisation of the  
170 individual-by-location bipartite graph, a procedure built in to the GMMEvents model,  
171 excludes non-random associations attributable to purely spatial drivers of aggregation,  
172 leaving only significant associations to populate the adjacency matrix.

173 Networks were constructed in this way for each of the four years of tracking data  
174 separately and tested for weighted assortative mixing ( $r^w_d$ ) by spatial community membership  
175 using the R package ‘*assortnet*’ (Farine 2014). Each annual network was then tested for  
176 significant assortment by spatial community against 10,000 networks in which interactions  
177 were randomised. Constraining the number of individuals per community and the number of  
178 associations measured that particular year, edge weights were randomly assigned and  $r^w_d$   
179 calculated for each permutation. The observed assortativity coefficient was then compared to  
180 the posterior distribution from the null model. We tested for social stability between years  
181 using Mantel tests reflecting the correlation in strength of dyadic relationships year on year  
182 when individuals were present across two consecutive years (1&2, 2&3, 3&4) and finally for  
183 those dyads that remained at liberty for the duration of the study (years 1&4).

184 **Changes in group size.** To determine how the number of tagged sharks visiting the central  
185 place varied temporally, we modelled the change in the number of tagged sharks detected  
186 throughout the day at core receivers. We performed this analysis for the two social  
187 communities with large numbers of tagged sharks (the blue and red communities, figure 1),  
188 and for year two (2012-2013) to reduce computation times (results were consistent for all  
189 years examined). We determined the effect of hour of day on the number of sharks detected  
190 (i.e. group size), using a Poisson generalized linear mixed model (GLMM) with an AR(1)  
191 (first-order auto-regressive) process to account for serial correlation, using the *mgcv* package  
192 (Wood 2011) in R. Model fit was assessed by examining residual diagnostic plots, and



193 Akaike's information criterion (AIC) was used to assess model performance against a null  
194 model (intercept only), with improved model fit indicated by a minimum  $\Delta AIC$  value  $> 3$ .

195 To estimate minimum group sizes, we deployed animal borne camera tags on two  
196 grey reef sharks caught off the SW region of the atoll in July 2013. Sharks had DVL400  
197 video loggers (Little Leonardo, Japan) attached to the dorsal fin which record at 640x480  
198 pixels at 30 frames/second and recording duration of 11 h (Papastamatiou et al. 2018a).  
199 Cameras were embedded in copolymer floats along with VHF (ATS) and SPOT satellite  
200 (Wildlife Computers) transmitters. A time release mechanism caused tags to pop-off 48-72h  
201 later, where they would float to the surface and could be recovered via the VHF and SPOT  
202 transmitters. Cameras were programmed to turn on the day after capture at 7:00-8:30 AM, to  
203 avoid the period of stress associated with capture. For each 30-minute segment we produced  
204 a conservative estimate of the minimum number of sharks in a group ensuring that  
205 individuals could not be counted twice (i.e. sharks in frame or seen sequentially while  
206 swimming in a straight line), including the individual carrying the camera (i.e. minimum  
207 size=1).

208 **Individual based models:** In order to investigate potential determinants and subsequent  
209 benefits to both sociality and central-place foraging in reef sharks, we developed two-  
210 dimensional individual-based models (IBMs) to examine a range of scenarios that may have  
211 influenced the evolution of these behavioural strategies. All models were constructed in the  
212 individual-based multi-agent modelling environment Netlogo 5.5 (Wilensky 1999), and the  
213 basic parameters of these models were previously described (Papastamatiou et al. 2018b).

214 In brief, in all model contexts outlined below, starting conditions comprised 100  
215 simulated individual 'sharks' that moved and foraged within a simple environment consisting  
216 of a fixed number of prey patches (100 or 200 depending on the specific simulation set)

217 randomly distributed across an unbounded torus. Simulated individuals moved at a constant  
218 speed (Papastamatiou et al. 2018a) and initially used a naive random search pattern. On  
219 discovering a prey patch, individuals remained there until the prey moved, at which point the  
220 predator commenced a more restricted search pattern based on a tighter turn angle for a set  
221 number of time-steps (models presented use 300 time-steps but simulations with shorter  
222 periods produce qualitatively similar results e.g. 167 steps Fig S2). Simulated shark lifespans  
223 were constrained by an energy term, with all individuals starting with 800 energy units,  
224 losing one unit per time-step while searching for prey patches, and dying if this reached zero.  
225 Successfully locating a prey patch resulted in an energy gain for the shark (150, 300 or 450  
226 units depending on the specific set of simulations). If individuals gained sufficient energy  
227 (individual energy score  $> 1000$  units) then they could potentially reproduce, with the  
228 probability of reproduction of a single offspring drawn from a log-normal distribution  
229 (reflecting the low reproductive rates of this species). Prey patches (i.e. simulated pelagic or  
230 reef fishes) followed a random walk within model space with step length drawn from a  
231 normal distribution (mean = 0, SD = 2). In addition, to incorporate less predictable prey  
232 movements, at each time step there was a 5% chance of prey patches relocating to another  
233 random position in model space. Finally, following discovery and the commencement of  
234 foraging, prey patches had an increased probability of dispersing, mimicking predator  
235 avoidance and escape behaviour. These movements could be either localized or larger jumps  
236 as described above, and were made more likely through a doubling of the acceptability  
237 threshold for movement from a random draw made at each time-step. Undiscovered prey  
238 patches were only detectable at short distances (0.3 unit radius). However, following  
239 discovery and commencement of feeding by a ‘shark’, such discovered patches became  
240 visible to other individuals at a four-fold greater distance. One hundred simulations were run  
241 for each combination of model parameters (number of prey patches, energetic value of prey  
242 patches), with each simulation run for 4000 time-steps.

243 The initial model included two types of individual: i) 'social' foragers that are able to  
244 both discover prey for themselves (i.e. private information), and to observe successful  
245 feeding in others and aggregate around prey patches, mimicking passive social information  
246 transfer including visual and chemical cues in the water; and ii) 'lone' foragers that are only  
247 able to find prey for themselves and do not recognize or move towards other foraging  
248 individuals. In these models, undiscovered prey patches were only detectable at short  
249 distances (0.3 unit radius). However, following discovery and commencement of feeding by  
250 either a 'lone' or 'social' individual, such discovered patches became visible to other 'social'  
251 individuals at a four-fold greater distance. 'Lone' individuals could also join discovered  
252 patches, but would only locate them through moving to close proximity as described above.  
253 One hundred simulations were run for each combination of food patch density (100 or 200  
254 patches) and energy gain (150, 300 or 450 units per successful forage), with the proportion of  
255 'social' and 'lone' individuals recorded through model time.

256 We used these models to examine whether there is any additional benefit to being a  
257 central place forager, as opposed to moving freely throughout model space, under varying  
258 levels of prey patch predictability. Thus, in these simulations, a varying proportion (20, 50 or  
259 80%) were central-place foragers ('central place'), returning to a fixed spatial location at  
260 every 500<sup>th</sup> timestep, with the rest starting in random positions and moving continuously  
261 through model space throughout each simulation run ('wanderer'). All simulations had three  
262 fixed locations positioned based on draws from a random number generator. These three  
263 fixed locations remained the same for all simulations within a model set (i.e. central places  
264 were fixed but prey patches and 'wanderer' starting locations changed with each simulation).  
265 100 simulations were run for each combination of food patch density and energy gain, with  
266 the maximum length of model time the 'central place' and 'wanderer' individuals survived  
267 recorded for each simulation. Simulations were run at three different levels of prey patch

268 predictability i.e. the spatial stability of prey patches varied from an initial ‘high stability’  
269 level (5% chance at each timestep of prey patches relocating to another random position in  
270 model space) to a ‘medium stability’ (25% chance of a long-range prey patch movement) and  
271 ‘low stability’ (50% chance of movement at each timestep). Such variation in prey patch  
272 stability simulates an increasing dependence on pelagic, as opposed to reef-dwelling, prey  
273 that are less predictable in time and space.

## 274 RESULTS

275 We tracked the movements of 41 individual grey reef sharks (*Carcharhinus*  
276 *amblyrhinchos*) over 13,800 accumulative tracking days (26 Female, 13 Male, 1 unknown,  
277 Total Length:  $142 \pm 18$  cm). Tagged grey reef sharks were assigned to five distinct movement  
278 communities, based on similarity of individual movement networks (network modularity,  $Q =$   
279 0.589). Thus, individuals were organised into groups that predominantly only used small,  
280 sub-sections of the available reef. Community members had 50% utilization distributions  
281 ranging in area from  $<1$  to  $7.53 \text{ km}^2$  (mean  $\pm$  SE,  $1.26 \pm 0.32 \text{ km}^2$ , Fig. 1b). Although  
282 movements of individuals between areas were limited, there was some spatial overlap  
283 between movement communities, suggesting that subsequent social patterns were not simply  
284 artefacts of animals having restricted and non-overlapping home ranges (particularly as  
285 spatial preferences were also controlled for in our inference models; see Methods).

286 **Dynamic social networks** Calculating a weighted assortativity coefficient for each annual  
287 network revealed significant social assortment ( $r_d^w$ : Y1 = 0.204; Y2 = 0.129; Y3 = 0.176; Y4  
288 = 0.130) when tested against a null model of 10,000 random networks (Fig. 1c). Each year,  
289 social associations were positively assorted by spatial community membership with no  
290 evidence for assortment based on sex ( $r_d^w$  (SE): Y1: -0.074 (0.065), Y2: 0.129 (0.015), Y3:  
291 0.177 (0.025), Y4: -0.043 (0.042)). Mantel tests revealed that there was a strong correlation in

292 the dyadic association strength between pairs for years 1&2 (n=29, Mantel  $r=0.74$ , CI=0.13-  
293 0.30,  $p<0.001$ ), 2&3 (n=35, Mantel  $r=0.85$ , CI=0.13-0.29,  $p<0.001$ ), 3&4 (n=31, Mantel  
294  $r=0.78$ , CI=0.13-0.27,  $p<0.001$ ) and finally for the duration of the study for years 1&4 (n=22,  
295 Mantel  $r=0.76$ , CI=0.16-0.35,  $p<0.001$ ).

296 **Changes in group size.** The number of tagged sharks increased throughout the day, for both  
297 communities (blue and red), peaking about 1500 (GLMM  $R^2 = 0.18, 0.10$ ;  $F = 244.9, 111.9$ ,  $p$   
298  $< 0.001$ , community 2, community 4, respectively; Fig. 2a). The number of tagged sharks  
299 detected then decreased, reaching a minimum by 2000-2100 before starting to increase at  
300 0500-0600 (Fig. 2a). Footage from camera tags deployed on two sharks showed that group  
301 size typically varied between 2-16 individuals, with group size increasing throughout the day  
302 and peaking in the afternoon (Fig. 2c, supplementary video). Close following behaviour,  
303 where individuals were approximately less than 1 m from a conspecific, was commonly  
304 observed (Movie 1).

305 **Individual based models.** Our first IBMs showed that individuals using only private  
306 information to locate resources (loners) have much lower fitness than those using social and  
307 private information (Fig. S1). Under all simulated scenarios of starting ratios of prey quality  
308 (energetic reward) and patch density, the proportion of 'loner' individuals rapidly declined  
309 typically to extinction, unless energetic rewards were extremely high (Fig. S1). Our second  
310 series of models (private and social info/some CPFs, others wanderers), showed that,  
311 regardless of prey quality, patch density, or the starting ratio of wanderers to CPFs, in all  
312 modelling scenarios CPFs had much greater survival times (Fig. 3a, b). When simulations  
313 were run with less predictable spatial stability of prey patches, CPFs always had longer  
314 survival times than wandering foragers regardless of patch density or quality (Fig. 3 c-f).  
315 However, the difference in survival time was greatest at higher patch densities and quality  
316 (Fig. 3 c, d).

317 DISCUSSION

318 Grey reef sharks form spatially assorted social communities, with dyadic associations  
319 that can last multiple years. These stable associations persist despite sharks displaying diel  
320 fission-fusion dynamics, with individuals generally fusing within a larger group throughout  
321 the day. These results, combined with our simulations, suggest that CPF facilitates the  
322 maintenance of fission-fusion groups, and improves foraging success via social information  
323 sharing. As such, sharks can display a degree of social complexity traditionally associated  
324 more with mammals and birds. Unlike other social CPFs which refuge in groups (e.g. birds,  
325 bats), we can rule out reproductive explanations for sharks as they do not display any parental  
326 care, which further highlights the potential importance of information sharing in driving the  
327 formation of social groups.

328 Grey reef sharks only use small regions of the available reef habitat and show low rates  
329 of movement to adjacent regions (Papastamatiou et al. 2018b). Reduced movement between  
330 neighbouring regions has been hypothesized in both seabirds and sharks to arise through  
331 density-dependent intraspecific competition in combination with sharing of social  
332 information between group members (Wakefield et al. 2013, Papastamatiou et al. 2018b).  
333 Here, we show that sharks also form social communities with associations assorted by  
334 patterns of space use, with social structure persisting for multiple years. Although some  
335 individuals moved between the communities defined by the movement networks, their  
336 associations with adjacent community members were weak or random. Hence social structure  
337 was not purely due to individuals never encountering those from adjacent communities.  
338 Similar spatial assortativity of social communities has also been seen in blacktip reef sharks  
339 off French Polynesia (Mourier et al. 2012). Our dynamic social network approach also  
340 showed that these dyadic associations are temporally stable, signifying that the same  
341 individuals were associating with one another over multiple years. While our data only spans

342 a maximum of four years, such associations have the potential to last for much longer. Spatial  
343 assortment of social communities is relatively common in animals of higher cognitive  
344 abilities, including birds, bats, dolphins, and seals (e.g. Wolf et al. 2007, Kerth et al. 2011,  
345 Shizuka et al. 2014, St Clair et al. 2015, Titcomb et al. 2015). However, rarely is multiyear  
346 social stability detected in wild animal populations, with some examples from birds and  
347 mammals (Kerth et al. 2011, Shizuka et al. 2014, Ilany et al. 2015). Unlike bats and birds,  
348 shark social communities are not seasonal, but instead occur year-round with long term  
349 residency to central place locations (Papastamatiou et al. 2018a, b).

350 We also show that sharks form fission-fusion societies over diel time frames with  
351 group size increasing throughout the day as individuals return from nighttime forays. Both  
352 telemetry and camera tag data suggests that sharks leave individually or in smaller groups  
353 during nighttime periods, before fusing with larger groups during the day. Similarly, juvenile  
354 blacktip sharks develop larger aggregations during the day than they do at night (Heupel and  
355 Simpfendorfer 2005). However, individual sharks were rarely detected over consecutive days  
356 suggesting that they spend multi-day periods offshore or in other regions, before returning.  
357 The long-term social associations persist despite sharks exhibiting fission-fusion dynamics,  
358 within the confines of community membership, a pattern also documented in bats (Kerth et  
359 al. 2011).

360 The central place itself may facilitate fusion of individuals or smaller groups, enabling  
361 the persistence of long-term social structure, often an issue for fission-fusion groups (Suer et  
362 al. 2011). Here, we provide evidence that social information sharing, likely within a foraging  
363 context, can potentially explain social community formation for CPFs. Models of local  
364 enhancement and/or public information sharing suggest increased foraging success and  
365 benefits of group foraging, but only if prey patches are ephemeral distributed,  
366 unpredictable, and short lived (Clarke and Mangel 1984, Buckley 1997, Barta and Giraldeau

2001, Boyd et al. 2016). Competition will counteract the advantages of larger group sizes, although this effect may be reduced if patch quality is highly variable and if travel times to patches are short (Sernland and Olsson 2003, Smolla et al. 2015). Empirical support for these predictions can be found in bats and seabirds where social foraging is generally only seen in species or individuals foraging on ephemeral prey (Egert-Berg et al. 2018, Jones et al. 2020). Our series of IBMs supplement these studies by suggesting that for sharks using social information (local enhancement), central place foraging, with multiple individuals using the same central place, provides a significant advantage over random wandering within a home range. These advantages persist under scenarios of both more and less predictable prey patches. For predictable prey patches, central place foraging improves foraging outcomes, because the forager can potentially learn the location of patches while using only memory requirements and dead reckoning abilities (Fagan et al. 2013). This advantage would increase in situations with less predictable prey, as CPF enables individuals to begin foraging in closer proximity to each other, boosting local enhancement opportunities and social grouping mechanisms in general. Our models do not incorporate any public information sharing (e.g. following among individuals or orienting in the direction of returning sharks) that may also occur and further benefit the foraging success of CPF individuals (Wakefield et al 2013, Boyd et al. 2016). We also don't include density-dependent effects related to group size, such as increased competition. Models of seabird foraging actually predict that foraging success via local enhancement will increase as colony size increases (Boyd et al. 2016).

As grey reef sharks forage on pelagic baitfish, they will likely benefit from social information sharing, similar to predictions from seabird models (McCauley et al. 2012, Boyd et al. 2016). However, unlike other CPFs, grey reef sharks will, at times, forage during the day on the reef within the central place, where prey (reef fishes) are likely more predictable (Papastamatiou et al. 2018a). Hence, social associations should still exist even during



392 daytime aggregations, and our model would still suggest a potential advantage of CPF  
393 behavior over wandering. Gregariousness will likely vary spatial-temporally, with seabirds  
394 for example, showing highest levels at foraging patches but weaker levels while commuting  
395 (Swift et al. 2014, Jones et al. 2020). We would predict that social associations in grey reef  
396 sharks may be strongest at the central place, and at offshore foraging patches, but weaker  
397 during commutes to patches.

398 We measure associations via a ‘gambit of the group’ approach, and only consider time  
399 periods when sharks are within range of acoustic receivers. The distance between individuals  
400 at receivers could be a few hundred meters, although random associations should be removed  
401 by our analysis due to the long time frame over which they are measured. While we were  
402 only tracking a small proportion of the grey reef shark population, densities per area of the  
403 forereef are relatively low (Bradley et al. 2017) and our camera deployments suggest group  
404 sizes of approximately 20 individuals. Furthermore, sharks at geographic locations were  
405 generally all caught and tagged at the same time and depth, hence we are confident that we  
406 likely caught and tagged individuals within groups (for example sharks carrying camera tags  
407 actually filmed each other over different days). However, future studies should aim to  
408 quantify the distance between individuals, and measure associations continuously over the  
409 diel cycle (e.g. Klimley et al. 2001). Despite these issues, we show that shark communities  
410 display temporally stable, complex social structures comparable to seabirds and potentially  
411 even some mammals. Sharks may provide a model system to study the role of information  
412 sharing in animal gregariousness in general, as breeding related mechanisms are likely of  
413 lower importance (over annual time scales although breeding will be of importance  
414 seasonally, Heupel and Simpfendorfer 2014). Social information transfer could be a key  
415 foraging mechanism and by itself sufficient to drive central place foraging behaviour with  
416 group refuging, in animals that do not require the use of a nest or shelter, including other

417 marine predators (e.g. carangid fishes Meyer et al. 2006). Social information links individual  
418 behaviour to population- and community-level dynamics and can contribute to patterns of  
419 spatial separation between communities as well as changing the frequency and strength of  
420 species interactions (Wakefield et al. 2013, Gil et al. 2018). While the importance of social  
421 information in colonial birds and mammals is now well established, we show that these  
422 concepts likely also apply to some species of shark. Tantalisingly, our analyses suggest a  
423 process that may be much more widespread than originally thought in free-ranging, marine  
424 animals that behave as CPF with no obvious reason for doing so.

425 Author contributions: YPP and DMPJ conceived the study. DMPJ, RF, and DB performed  
426 the analysis. TWB built the individual based models. YPP, DB, AMF, and JEC performed  
427 field work. YPP and DMPJ wrote the paper with input from all authors.

428 Ethics statement: All shark tagging and handling was approved by the University of  
429 California Santa Barbara IACUC committee Protocol no. 856, and U.S. Fish and Wildlife  
430 Service special use permits (Permit numbers #12533–14011, #12533–13011, #12533–12011,  
431 #12533–11007, #12533–10011, #12533–09010, #12533–08011, and #12533–07006).

432

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436 Data availability: Should the manuscript be published, data will be made available in Dryad

437

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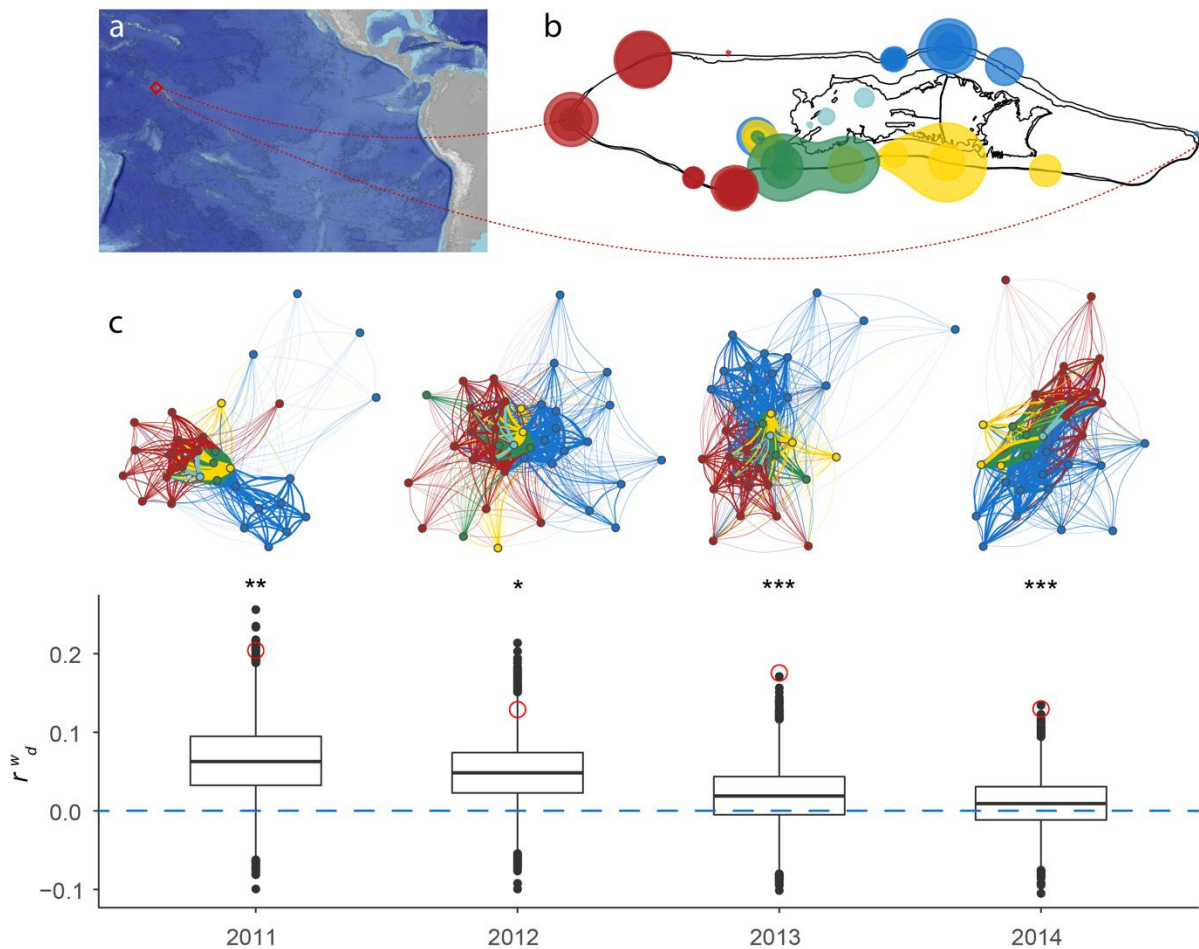
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574 Figures

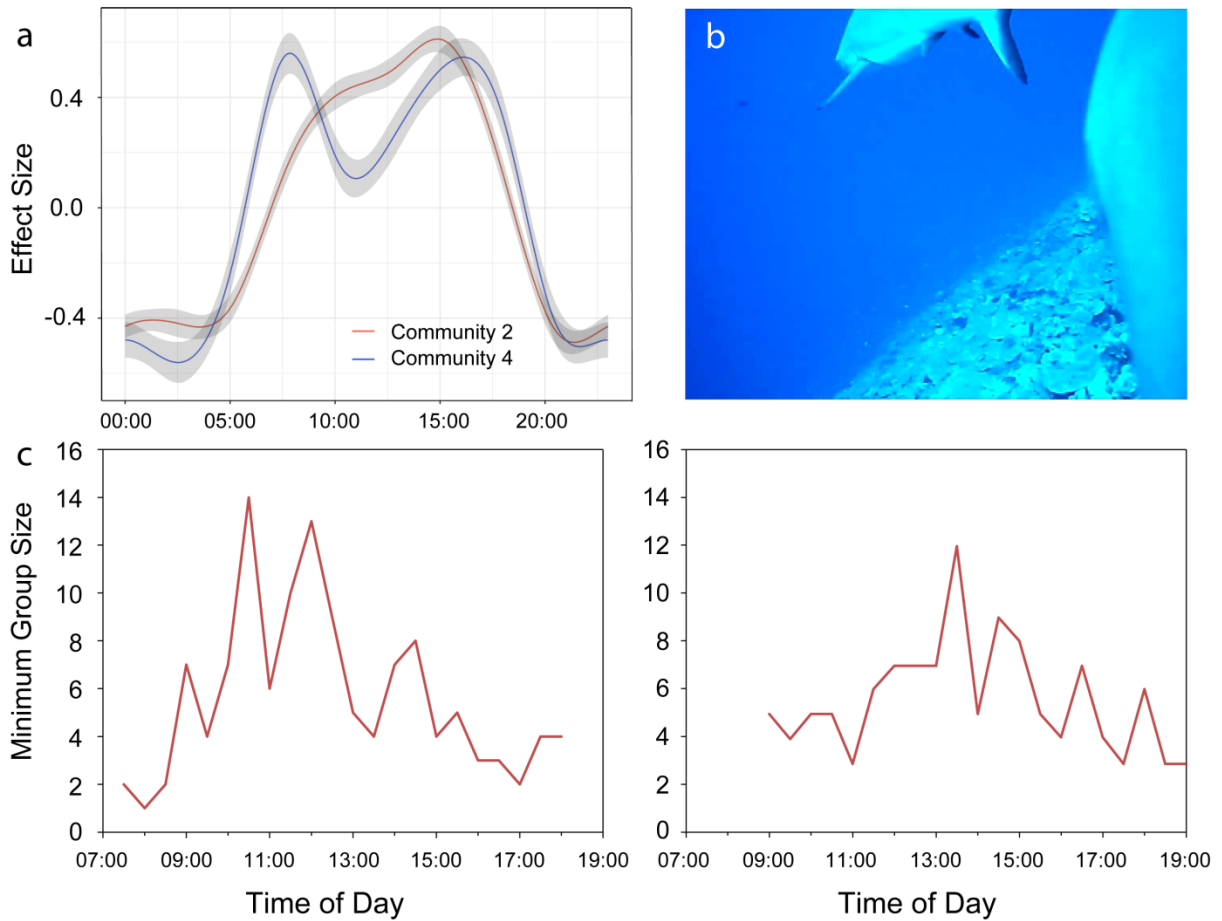


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577 Figure 1. **Spatial and social assortment.** **a**, Palmyra Atoll US National Wildlife Refuge (red  
578 diamond) in the Central Pacific Ocean. **b**, Space use measured as the 50% utilisation distribution  
579 (UD) of sharks assigned to their respective communities which were defined using community  
580 detection of movement networks in addition to residency behaviour (colours reflect communities in  
581 **c**). **c**, Social networks and the distribution of weighted assortativity coefficients ( $r_d^w$ ) for 10,000  
582 random networks (boxes) and observed networks (red circles) across four years of shark telemetry  
583 data. Each node in the network represents an individual shark, with clusters showing closely  
584 associated dyadic pairs. Networks were all significantly, positively assorted by community,  
585 represented as different coloured nodes. No assortment is illustrated by blue dashed line. ( $p < 0.05^*$ ,  $p$   
586  $< 0.01^{**}$  and  $p < 0.001^{***}$ ).

587



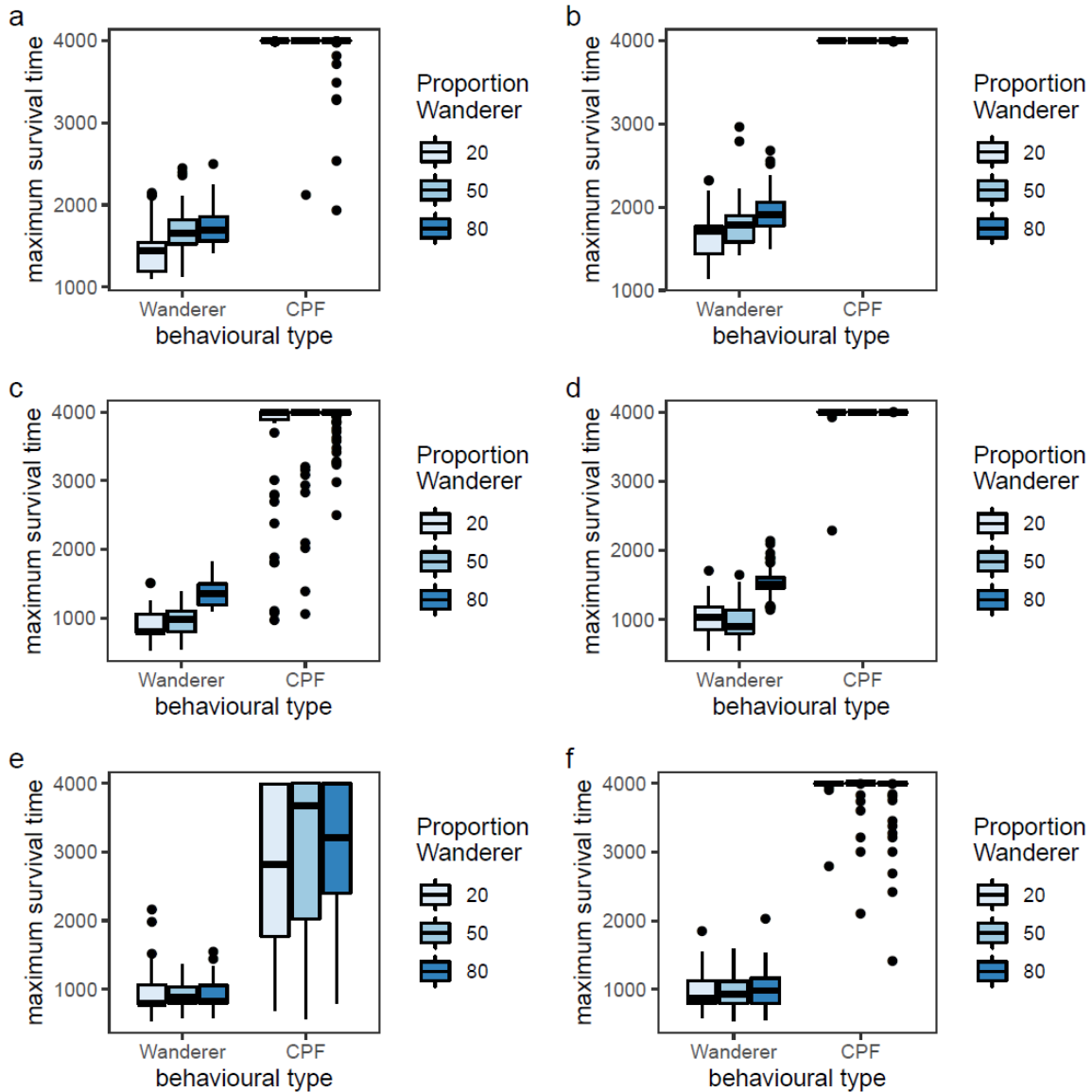
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589 **Figure 2. Diel period predicts changes in group size within the two largest social communities.** a)  
 590 Number of acoustically tagged sharks detected at core receivers increase significantly throughout the  
 591 day for individuals within the two largest communities (red and blue, see Fig. 1). b) Frame capture  
 592 from an animal-borne camera of a grey reef shark engaging in close following behaviour. c) Camera  
 593 tag derived minimum group size changes throughout the day for two female grey reef sharks within  
 594 community 2.

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599 **Figure 3. Strategy and survivorship modelling.** Survival time of simulated sharks behaving either as  
 600 central place foragers (CPF) or wanderers (do not use a central place) under different levels of food  
 601 patch stability (**a, b**: 5% instability, **c, d**: 25% instability, **e, f**: 50% instability). Regardless of prey  
 602 abundance (**a, c, e**: 100 prey patches, **b, d, f**: 200 prey patches), or the starting ratio between the two  
 603 foraging strategies, under all conditions CPF individuals survive for longer durations, and only CPF  
 604 successfully survive for the full duration of model time under more stable conditions. Once prey  
 605 density is sufficiently stable and/or high, there is no variation in likelihood of survival of CPF.