

Research



Cite this article: Papastamatiou YP, Bodey TW, Caselle JE, Bradley D, Freeman R, Friedlander AM, Jacoby DMP. 2020 Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics. *Proc. R. Soc. B* **287**: 20201063. <http://dx.doi.org/10.1098/rspb.2020.1063>

Received: 8 May 2020
Accepted: 22 July 2020

Subject Category:
Behaviour

Subject Areas:
behaviour, ecology

Keywords:
social network, local enhancement,
central place foraging, grey reef sharks

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5087229>.

Multiyear social stability and social information use in reef sharks with diel fission–fusion dynamics

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Animals across vertebrate taxa form social communities and often exist as fission–fusion groups. Central place foragers (CPF) may form groups from which they will predictably disperse to forage, either individually or in smaller groups, before returning to fuse with the larger group. However, the function and stability of social associations in predatory fish acting as CPFs is unknown, as individuals do not need to return to a shelter yet show fidelity to core areas. Using dynamic social networks generated from acoustic tracking data, we document spatially structured sociality in CPF grey reef sharks at a Pacific Ocean atoll. We show that sharks form stable social groups over multiyear periods, with some dyadic associations consistent for up to 4 years. Groups primarily formed during the day, increasing in size throughout the morning before sharks dispersed from the reef at night. Our simulations suggest that multiple individuals sharing a central place and using social information while foraging (i.e. local enhancement) will outperform non-CPF social foragers. We show multiyear social stability in sharks and suggest that social foraging with information transfer could provide a generalizable mechanism for the emergence of sociality with group central place foraging.

1. Introduction

Gregarious animals face a constant trade-off regarding the costs and benefits associated with group living [1]. This trade-off can be heavily influenced by reproductive strategy, competition, the distribution and quality of food or predators in space, and by processes that facilitate collective decision-making [2–4]. In most cases, animal groups will exhibit fission–fusion dynamics, where individuals split from (fission) and re-join (fusion) other group members [5]. Fission–fusion dynamics can contribute to or dictate group sizes and patterns of assortativity among group members [5,6]. The extent of fission–fusion dynamics in animal social groups are likely related to spatial and temporal variability in the environment, as well as the strength of social associations between individuals and their energetic state [6]. One important aspect of fission–fusion societies is the stability of associations between group members, which will determine the persistence of social communities [7]. Surprisingly, multiyear social stability has only been measured in a few avian and

mammalian species with fission–fusion dynamics, including swallows, bats and hyenas [7–10].

Central place foragers (CPF) may refuge in groups and will often show fission–fusion dynamics over short temporal scales, with animals making excursions individually or in smaller groups to/from the larger group at the central place [7]. For example, seals and seabirds reside in groups or colonies on land but head offshore to forage in much smaller groups (e.g. [11–13]). In most cases, the central place is the location of a nest, shelter or haul-out site which explains loyalty and fidelity to the central place. Sociality in refuging CPF is often thought to be driven by reproduction, but social foraging and information sharing may also be important [14–16]. Social information sharing in a foraging context can include local enhancement (where animals can detect other individuals foraging and can simultaneously forage and observe conspecifics, [14]), recruitment (an individual ‘recruits’ others to a patch, with foraging success increasing with group size, i.e. the recruitment hypothesis, [14]) and public information (where uninformed individuals follow informed individuals to prey patches, [17,18]). The transmission of social information has been proposed as being responsible for driving the evolution and maintenance of coloniality (information centre hypothesis), or simple aggregations of social foragers [17,19].

Models predict that the use of social information increases foraging success in gregarious animals, but only if prey patches are ephemeral, distributed, unpredictable, and have short residence times [14,20]. These models all assume that central place foraging is a prerequisite of the social system, which is a reasonable assumption for animals that must return to a nest or shelter [14]. However, some large marine predators such as sharks are CPF but have no obvious need to return to a central place [21,22]. While information sharing may lead to the development of animal aggregations, the advantage of CPF itself in a social foraging context has not been explored [19]. A central place may allow individuals or subgroups to find each other and ‘fuse’ with the larger group, which will help maintain social associations over diel or seasonal timescales [6]. Social associations between individuals can then potentially increase foraging success via social information sharing [23].

Tropical reef sharks may only use small proportions of available reef habitat and show multiyear fidelity or residency, returning to the same ‘central place’ over diel, tidal or seasonal timescales [21,22,24,25]. Some sharks will form social associations under both laboratory and field conditions and are likely capable of social learning [26–29]. Within a CPF context, they likely display fission–fusion dynamics, often forming groups during the day and potentially dispersing in small groups (or individually) at night to forage [21,22,30]. Mating and reproduction in reef sharks is seasonal, which influences patterns of movement, but residency on the reef can occur extensively throughout the year [24,25]. The function of sociality and central place foraging in these animals with potential diel fission–fusion dynamics are unknown. While most reef sharks are more active at night, they will also hunt during the day within their central place, potentially with multiple other individuals [22,31]. Hence, the benefits of local enhancement and social associations may persist day and night (to varying degrees), and we may expect multiyear social stability between dyadic pairs if social foraging is beneficial.

Grey reef sharks (*Carcharhinus amblyrhynchos*) are CPF that can show high residency to coral reefs but are also capable of longer range dispersal [22,24]. They can form daytime aggregations but disperse more widely at night when they are more active, although they will forage opportunistically during the day [22]. At Palmyra Atoll, in the Pacific Ocean, 80% of grey reef shark diet is estimated to be pelagic prey, and sharks have been seen feeding on offshore fish schools during the day ([32], electronic supplementary material, S1). Hence, prey patches are likely to be ephemeral and unpredictable in distribution, and sharks should benefit from social foraging with local enhancement. If central place foraging represents a mechanism for maintaining social associations in groups with diel fission–fusion dynamics and increases foraging success via social information sharing, then we would predict that (i) sharks form social communities assorted by patterns of space use, (ii) group size should increase throughout the day as individuals (or subgroups) return to the central place, (iii) social associations between community members should be stable over multi-year periods and (iv) groups of individuals using social information to forage (local enhancement) and sharing a central place will outperform non-CPF social foragers in computer simulations. We test these predictions with a population of grey reef sharks at Palmyra Atoll, using a combination of acoustic telemetry, biologgers, dynamic social networks and individual-based models.

2. Methods

(a) Study population and location

Palmyra Atoll (5°54' N 162°05' W) is located at the northern end of the Line Island chain, in the Central Pacific Ocean, and has been a US Federal Wildlife refuge since 2001, with only a research station on the island. Consequently, the atoll has large numbers of upper level predators, including grey reef sharks (*Carcharhinus amblyrhynchos*), with approximately 8000 grey reef sharks distributed heterogeneously around the forereef, with average densities of 21 sharks km⁻² [33].

(b) Quantifying movements and community assignment

Grey reef sharks were caught on hook and line and had a uniquely coded V16 (69 kHz, semi-randomized delay 60–180 s, Vemco Ltd, Nova Scotia) acoustic transmitter surgically implanted into their body cavity. Individual animals ($n = 41$) were detected and tracked across a network of 65 VR2W acoustic receivers, which were attached to the reef and retrieved and downloaded annually. Receivers that were overlapping in their detection ranges (specifically in the SW of the atoll) were reduced in number to avoid detections being recorded multiple times simultaneously, a prerequisite for the mixture model analysis (see below). This resulted in the exclusion of 18 receivers but did not reduce the total area under acoustic surveillance. Receiver detection range varied between forereef and backreef habitats but was approximately 300 m at forereef sites (where grey reef sharks spend most of their time, [22,25]).

Weighted, undirected movement networks were constructed from the departure and arrival profile of the acoustic data, with receivers treated as nodes and movements between receivers as edges in a movement network [34]. Prior to quantifying social behaviour we wanted to understand how tagged individuals were organized based on their space use. Therefore, ‘communities’ were derived from the collective movement network across all individuals using the Fast-Greedy algorithm,

implemented in the R package *igraph*, revealing statistically significant clusters of movement [35–37]. The extent of the movements made by individuals in different communities across the whole atoll is shown in electronic supplementary material, S2. Community modularity within the movement network was high ($Q=0.589$), suggestive of area restricted movements, and resulted in the formation of five distinct movement communities. Note that movement communities do not consist of individual sharks, but rather receivers that showed significantly higher movements within than between locations, despite occasional visits to many other receivers, supporting our case for social rather than spatial drivers of network structure (electronic supplementary material, S2). We then calculated a residency index (RI) for each individual across each location before assigning individual sharks to movement communities based on their most resident receiver location (i.e. the receiver with the highest RI). RI for each individual per location can be defined as

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

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

(c) Dynamic social networks

We produced dynamic social networks using a ‘gambit of the group’ approach, where animals co-occurring in time and space are assumed to represent social associations after controlling for individual spatial preferences [38]. Shark social networks were inferred directly from the detection data stream using the Gaussian mixture modelling approach, *GMMEvents* [39,40]. Clusters of detections, produced by visits of multiple individuals to the same place at the same time, varied temporally to reflect the variation expected in the temporal distribution of animal aggregations and were determined using a variational Bayesian mixture model. From these clusters, associations were assigned to an adjacency matrix. Randomization of the individual-by-location bipartite graph, a procedure built in to the *GMMEvents* model, excludes random associations attributable to purely spatial drivers of aggregation, leaving only significant associations to populate the adjacency matrix [40]. Importantly, this constrained the randomization procedure by the detection frequency of individuals and the number of clustering events in which they occurred.

Networks were constructed in this way for each of the 4 years of tracking data separately and tested for weighted assortative mixing (r_d^{wv}) by spatial community membership for each year using the ‘*assortment.discrete()*’ function in the R package ‘*assortnet*’ [41]. Each annual network was then tested for significant assortment by spatial community and sex against 10 000 networks in which interactions were randomized. Constraining the number of individuals per community and the number of associations measured that particular year, edge weights were randomly assigned and r_d^{wv} calculated for each permutation. The observed assortativity coefficient was then compared to the posterior distribution from the null model. We tested for social stability between years using Mantel tests reflecting the correlation in strength of dyadic relationships year on year when individuals were present across 2 consecutive years (1&2, 2&3, 3&4) and finally for those dyads that remained at liberty for the duration of the study (years 1&4). There were far fewer detections at night [22] hence the majority of social associations described are for daytime periods.

(d) Changes in group size

To determine how the number of tagged sharks visiting the central place varied temporally, we modelled the change in the number of sharks detected throughout the day at core receivers. We performed this analysis for the two communities with large numbers of tagged sharks (the blue and red communities, figure 1), and for 1 year (2012–2013) to reduce computation times. We determined the effect of hour of day on the number of sharks detected (i.e. group size), using a Poisson generalized linear mixed model (GLMM) with an AR(1) (first-order auto-regressive) process to account for serial correlation, using the *mgcv* package [42] in R. Model fit was assessed by examining residual diagnostic plots, and Akaike’s information criterion (AIC) was used to assess model performance against a null model (intercept only), with improved model fit indicated by a minimum ΔAIC value > 3 .

To estimate minimum group sizes, we deployed animal-borne camera tags on two grey reef sharks caught off the SW region of the atoll in July 2013. Sharks had DVL400 video loggers (Little Leonardo, Japan) attached to the dorsal fin which record at 640×480 pixels at 30 frames s^{-1} and recording duration of 11 h [22]. Cameras were embedded in copolymer floats along with VHF (ATS) and SPOT satellite (Wildlife Computers) transmitters. A time release mechanism caused tags to pop-off 48–72 h later, where they would float to the surface and could be recovered via the VHF and SPOT transmitters. Cameras were programmed to turn on the day after capture at 7.00–8.30, to avoid the period of stress associated with capture and night-time periods. For each 30 min segment we produced a conservative estimate of the minimum number of sharks in a group ensuring that individuals could not be counted twice (i.e. sharks in frame or seen sequentially while swimming in a straight line), including the individual carrying the camera (i.e. minimum size = 1).

(e) Individual-based models

In order to investigate potential determinants and subsequent benefits to both sociality and central place foraging in reef sharks, we developed two-dimensional individual-based models (IBMs) to examine a range of scenarios that may have influenced the evolution of these behavioural strategies. All models were constructed in the individual-based multi-agent modelling environment Netlogo 5.5 [43], and the basic parameters of these models were previously described [25].

In brief, in all model contexts outlined below, starting conditions comprised 100 simulated individual ‘sharks’ that moved and foraged within a simple environment consisting of a fixed number of prey patches (100 or 200 depending on the specific simulation set) randomly distributed across an unbounded torus. Prey patches moved using random walks and rare long-range movement jumps, but also responded to foraging predators by increasing their probability of making longer range movements. Sharks lost energy during each movement step but gained energy if they successfully captured prey. Upon detecting prey patches, sharks swam to the patch and switched to area restricted movements. Undiscovered prey patches were only detectable at short distances of 0.3 unit radius (i.e. private information). However, following discovery and commencement of feeding by a shark, such discovered patches became visible to other individuals at a fourfold greater distance (i.e. social information). One hundred simulations were run for each combination of model parameters (number of prey patches, energetic value of prey patches), with each simulation run for 4000 time steps. The initial model included two types of individuals: (i) ‘lone’ foragers that are only able to use private information and (ii) ‘social’ foragers that are able to detect prey using both private and social information, which mimics passive social information transfer including visual and chemical cues in the water.

We then assumed all sharks were social foragers to examine whether there is any additional benefit to being a CPF, as opposed

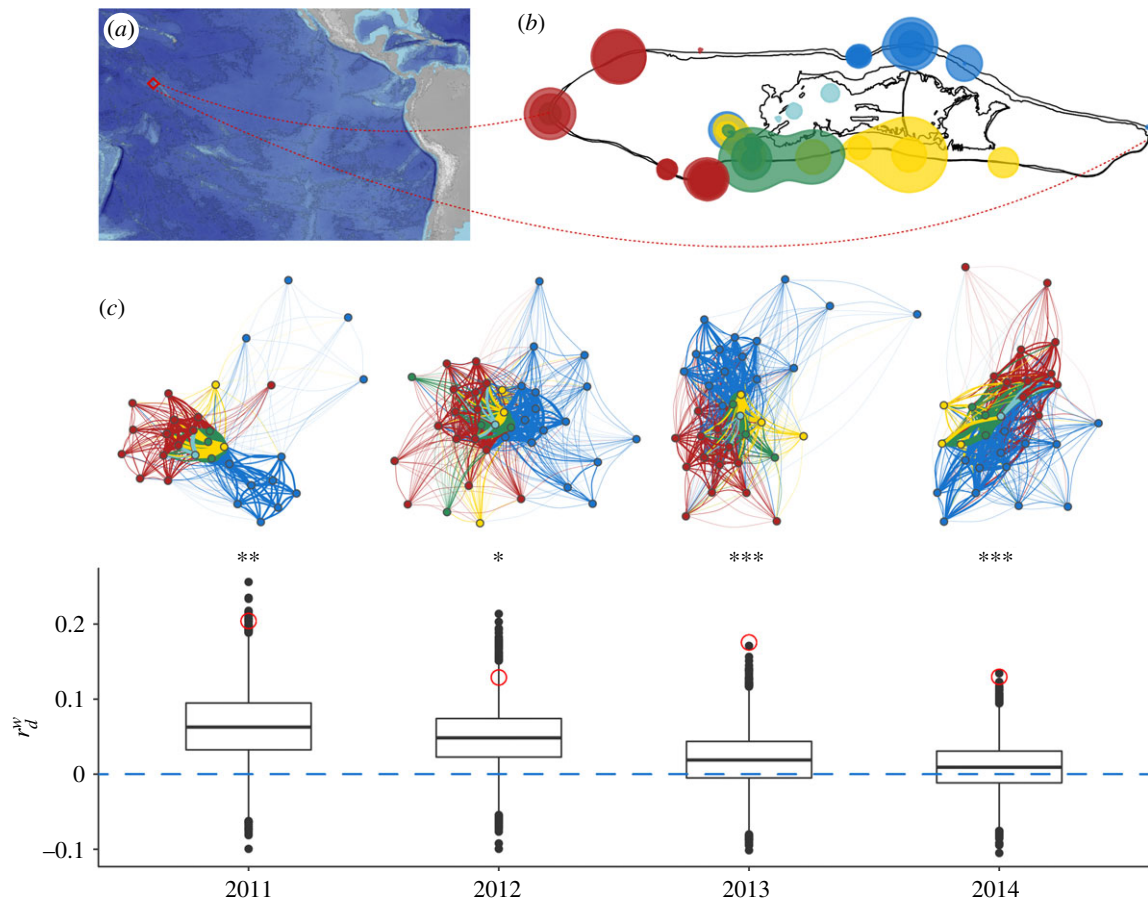


Figure 1. Spatial and social assortment. (a) Palmyra Atoll US National Wildlife Refuge (red diamond) in the Central Pacific Ocean. (b) Space use measured as the 50% UD of sharks assigned to their respective communities, which were defined using community detection of movement networks in addition to residency behaviour (colours reflect communities in c). (c) Social networks and the distribution of weighted assortativity coefficients (r_d^w) for 10,000 random networks (boxes) and observed networks (red circles) across 4 years of shark telemetry data. Each node in the network represents an individual shark, with clusters showing closely associated dyadic pairs. Networks were all significantly, positively assorted by community, represented as different coloured nodes. No assortment is illustrated by blue dashed line. ($p < 0.05^*$, $p < 0.01^{**}$ and $p < 0.001^{***}$). (Online version in colour.)

to moving freely throughout model space, under varying levels of prey patch predictability. Thus, in these simulations, a varying proportion (20, 50 or 80%) were CPF (central place), returning to a fixed spatial location at every 500th time step, with the rest starting in random positions and moving continuously through model space throughout each simulation run (wanderer). All simulations had three fixed locations positioned based on draws from a random number generator. These three fixed locations remained the same for all simulations within a model set (i.e. central places were fixed but prey patches and ‘wanderer’ starting locations changed with each simulation). Simulations were run at three different levels of prey patch predictability i.e. ‘high stability’ level (5% chance at each time step of prey patches relocating to another random position in model space), ‘medium stability’ (25% chance of a long-range prey patch movement) and ‘low stability’ (50% chance of movement at each time step). Such variation in prey patch stability simulates an increasing dependence on pelagic as opposed to reef-dwelling prey, that are less predictable in time and space. Full model details can be found in electronic supplementary material, S3.

3. Results

We tracked the movements of 41 individual grey reef sharks over 13 800 accumulative tracking days (27 female, 12 male, two unknown, total length: 142 ± 18 cm). Tagged sharks were assigned to five distinct movement communities, based on similarity of individual movement networks

(network modularity, $Q = 0.589$). Thus, individuals were organized into groups that predominantly only used small, sub-sections of the available reef. Community members had 50% utilization distributions ranging in area from less than 1 to 7.53 km^2 (mean \pm s.e., $1.26 \pm 0.32 \text{ km}^2$, figure 1b). Although movements of individuals between areas were limited, there was some spatial overlap between movement communities, suggesting that subsequent social patterns were not simply artefacts of animals having restricted and non-overlapping home ranges (particularly as spatial preferences were also controlled for in our inference models; see Methods, electronic supplementary material, S2).

(a) Dynamic social networks

Controlling for spatial preferences, the mixture model retrieved a total of 972 significant social clustering events ($Y1 = 209$; $Y2 = 227$; $Y3 = 277$; $Y4 = 259$). Calculating a weighted assortativity coefficient for each annual network revealed significant social assortment by spatial community membership (r_d^w : $Y1 = 0.204$; $Y2 = 0.129$; $Y3 = 0.176$; $Y4 = 0.130$) when tested against a null model of 10 000 random networks (figure 1c). However, there was no evidence for assortment based on sex (r_d^w (SE): $Y1: -0.074$ (0.065), $Y2: 0.129$ (0.015), $Y3: 0.177$ (0.025), $Y4: -0.043$ (0.042)). Mantel tests revealed that there was a strong correlation in the dyadic association strength between pairs for years 1&2 ($n = 29$, Mantel $r = 0.74$, $CI = 0.13\text{--}0.30$, $p < 0.001$), 2&3 ($n = 35$, Mantel $r = 0.85$, $CI = 0.13\text{--}0.29$, $p < 0.001$), 3&4

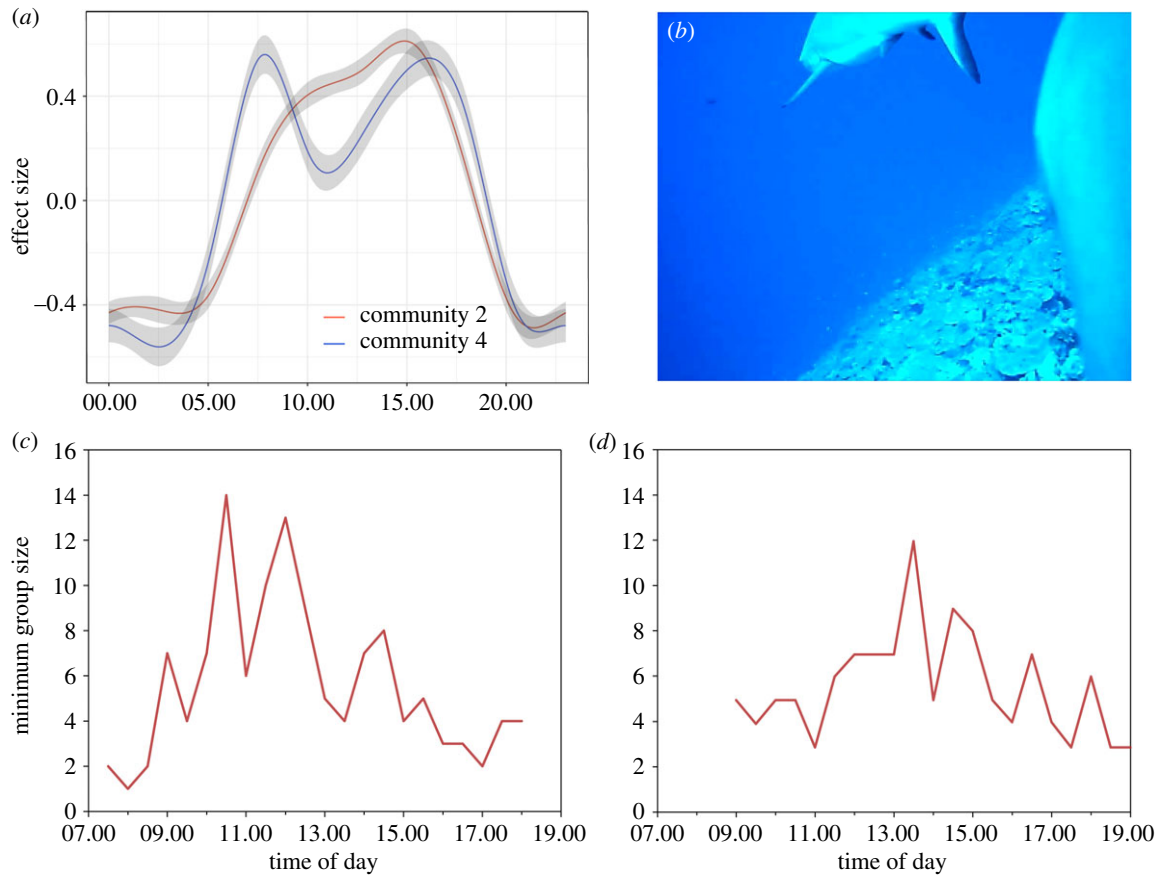


Figure 2. Diel period predicts changes in group size within the two largest communities. (a) Number of acoustically tagged sharks detected at core receivers increase significantly throughout the day for individuals within the two largest communities (red and blue, figure 1). (b) Frame capture from an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

($n = 31$, Mantel $r = 0.78$, CI = 0.13–0.27, $p < 0.001$) and finally for the duration of the study for years 1&4 ($n = 22$, Mantel $r = 0.76$, CI = 0.16–0.35, $p < 0.001$).

(b) Changes in group size

The number of tagged sharks increased throughout the morning, for both communities (blue and red), peaking about 15.00 (GLMM $R^2 = 0.18, 0.10$; $F = 244.9, 111.9$, $p < 0.001$, community 2, community 4, respectively; figure 2a). The number of tagged sharks detected then decreased, reaching a minimum by 20.00–21.00 before starting to increase at 05.00–06.00 (figure 2a). Footage from camera tags deployed on two sharks showed that group size typically varied between two and 14 individuals, with group size increasing throughout the morning and peaking in the afternoon (figure 2c, electronic supplementary material, video S4). Close following behaviour, where individuals were approximately less than 1 m from a conspecific, was commonly observed (electronic supplementary material, S4). It is likely that detection range of receivers will be reduced at night due to increased noise on the reef, which may influence our ability to detect individuals. However, the more gradual increase in shark numbers throughout the early morning as well camera footage still suggests diel changes in group size are genuine.

(c) Individual-based models

Our first IBMs showed that individuals using only private information to locate resources (loners) have much lower

fitness than those using social and private information (electronic supplementary material, S5). Under all simulated scenarios of starting ratios of prey quality (energetic reward) and patch density, the proportion of ‘loner’ individuals rapidly declined typically to extinction, unless energetic rewards were extremely high (electronic supplementary material, S5). Our second series of models (private and social info/some CPFs, others wanderers) showed that regardless of prey quality, patch density or the starting ratio of wanderers to CPFs, in all modelling scenarios CPFs had much greater survival times (figure 3, electronic supplementary material, S3 and S5). When simulations were run with less predictable spatial stability of prey patches, CPFs always had longer survival times than wandering foragers regardless of patch density or quality (figure 3c–f). However, the difference in survival time was greatest at higher patch densities and quality (figure 3, electronic supplementary material, S3 and S5).

4. Discussion

Grey reef sharks form spatially assorted social communities, with dyadic associations that can last multiple years. These stable associations persist despite sharks displaying diel fission–fusion dynamics, with individuals generally fusing within a larger group throughout the day. These results, combined with our simulations, suggest that CPF may facilitate the maintenance of fission–fusion groups, and improve foraging success via social information sharing. As such, sharks can display a degree of social complexity traditionally associated more

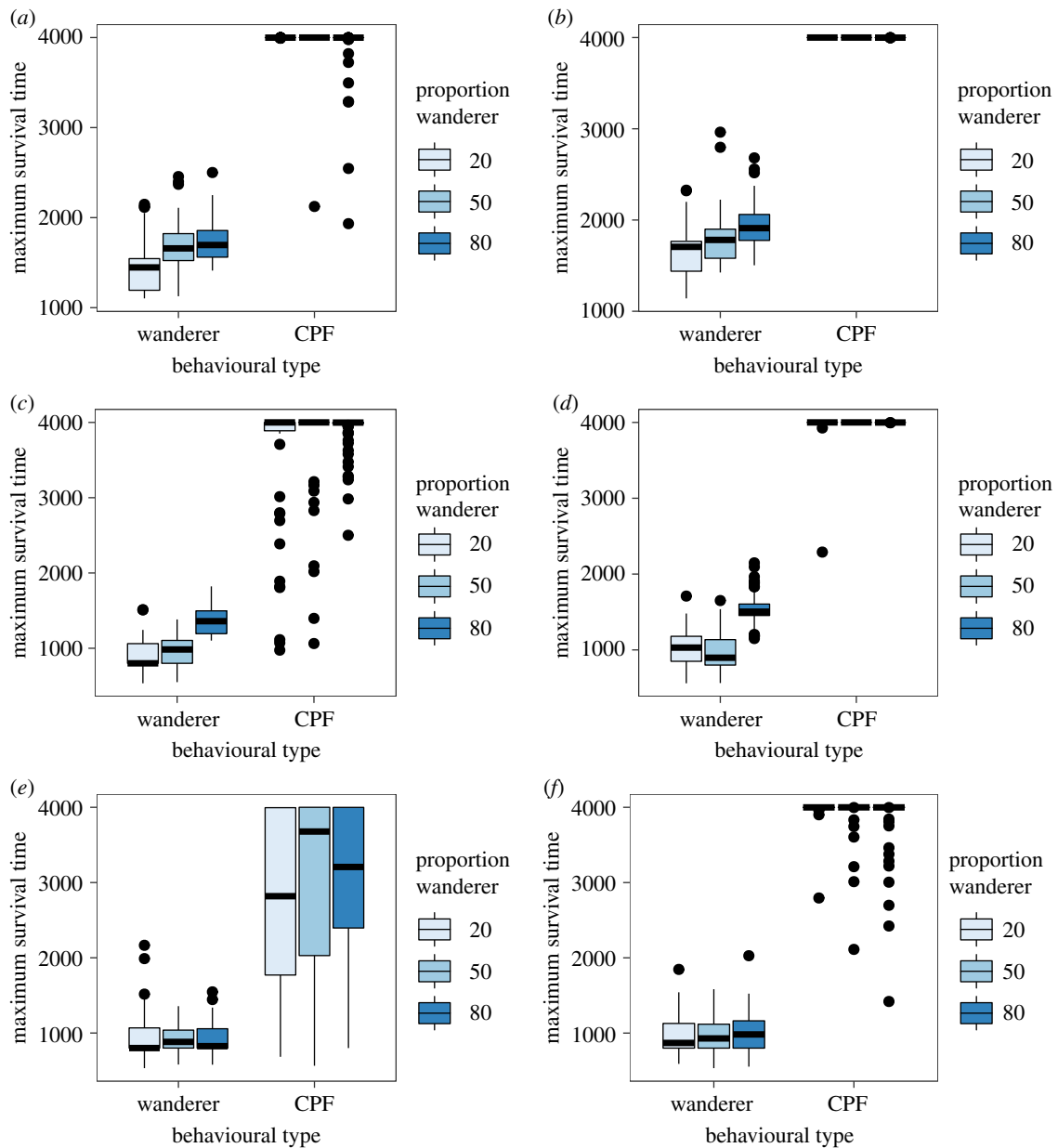


Figure 3. Strategy and survivorship modelling. Survival time of simulated sharks behaving either as central place foragers (CPF) or wanderers (do not use a central place) under different levels of food patch stability (*a,b*: 5% instability, *c,d*: 25% instability, *e,f*: 50% instability). Regardless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

with mammals and birds. Unlike other social CPFs which refuge in groups (e.g. birds, bats), we can rule out reproductive explanations for sharks as they do not display any parental care, which further highlights the potential importance of information sharing in driving the formation of social groups.

Grey reef sharks only use small regions of the available reef habitat and show low rates of movement to adjacent regions [25]. Reduced movement between neighbouring communities has been hypothesized in both seabirds and sharks to arise through density-dependent intraspecific competition in combination with sharing of social information between group members [11,25]. Here, we show that sharks also form social communities with associations assorted by patterns of space use, with social structure persisting for multiple years. Although some individuals moved between the communities defined by the movement networks, their associations with adjacent community members were weak

or random. Hence social structure was not purely due to individuals never encountering those from adjacent communities. Similar spatial assortment of social communities has also been seen in blacktip reef sharks off French Polynesia [28]. Our dynamic social network approach also showed that these dyadic associations are temporally stable, signifying that the same individuals were associating with one another over multiple years. While our data only spans a maximum of 4 years, such associations have the potential to last for much longer. Spatial assortment of social communities is relatively common in animals of higher cognitive abilities, including birds, bats, dolphins and seals (e.g. [8,9,44–46]). However, rarely is multiyear social stability detected in wild animal populations, with some examples from birds and mammals [8–10]. Unlike bats and birds, shark social communities are not seasonal, but instead occur year-round with long-term residency to central place locations [22,25].

We also show that sharks form fission–fusion groups over diel time frames with group size increasing throughout the morning as individuals return from night-time forays. Both telemetry and camera tag data suggests that sharks leave individually or in smaller groups during night-time periods, before fusing with larger groups during the day. Similarly, juvenile blacktip sharks develop larger aggregations during the day than they do at night [30]. However, individual sharks were rarely detected over consecutive days suggesting that they spend multi-day periods offshore or in other regions, before returning. The long-term social associations persist despite sharks exhibiting fission–fusion dynamics, within the confines of community membership, a pattern also documented in bats [8].

The central place itself may facilitate fusion of individuals or smaller groups, enabling the persistence of long-term social structure, often an issue for fission–fusion groups [6]. Here, we provide evidence that social information sharing, likely within a foraging context, can potentially explain social community formation for CPFs. Models of local enhancement and/or public information sharing suggest increased foraging success and benefits of group foraging, but only if prey patches are ephemerally distributed, unpredictable and short lived [2,14,17,20]. 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 [3,47]. 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 [13,48]. 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 path integration abilities [49]. 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 [11,20]. We also do not include density-dependent effects related to group size, such as increased competition.

As grey reef sharks forage on pelagic schooling fish, they will likely benefit from social information sharing, similar to predictions from seabird models [20,32]. 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 [22]. Hence, social associations should still exist even during daytime aggregations, and our model would still suggest a potential advantage of CPF behaviour over wandering. Gregariousness will likely vary spatio-temporally, with seabirds for example, showing highest levels at foraging patches but weaker levels while commuting [7,13]. We would predict that social associations in grey reef sharks may be strongest at the central place, and at offshore foraging patches, but weaker during commutes to patches.

However, we only measure associations when sharks were detected on receivers which will be primarily in reef environments. White sharks hunting seals were also thought to remain within proximity of other sharks while located off a California seal colony, presumably due to local enhancement benefits although this is likely only seasonal [50].

We measure associations via a ‘gambit of the group’ approach, and only consider time periods when sharks are within range of acoustic receivers. The distance between individuals at receivers could be a few hundred metres, although random associations should be removed by our analysis due to the long-time frame over which they are measured. While we were only tracking a small proportion of the grey reef shark population, densities per area of the forereef are relatively low [33] and our camera deployments suggest group sizes of approximately 14 individuals. Furthermore, sharks at geographic locations were generally all caught and tagged at the same time and depth, hence we are confident that we likely caught and tagged individuals within groups (for example sharks carrying camera tags actually filmed each other over different days). However, future studies should aim to quantify the distance between individuals and measure associations continuously over the diel cycle and when animals are offshore (e.g. [50]). Despite these issues, we show that shark communities display temporally stable, complex social structures comparable to seabirds and potentially even some mammals. Sharks may provide a model system to study the role of information sharing in animal gregariousness in general, as breeding related mechanisms are likely of lower importance (over annual timescales, although breeding will be of importance seasonally, [24]). Social information transfer could be a key foraging mechanism and by itself sufficient to drive central place foraging behaviour with group refuging, in animals that do not require the use of a nest or shelter, including other marine predators (e.g. carangid fishes [51]). Social information links individual behaviour to population- and community-level dynamics and can contribute to patterns of spatial separation between communities as well as changing the frequency and strength of species interactions [11,52]. While the importance of social information in colonial birds and mammals is now well established, we show that these concepts likely also apply to some species of shark. Tantalizingly, our analyses suggest a process that may be much more widespread than originally thought in free-ranging, marine animals that behave as CPF with no obvious reason for doing so.

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

Data accessibility. Raw acoustic detections are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bnzs7h47f> [53].

Authors' contributions. Y.P.P. and D.M.P.J. conceived the study. D.M.P.J., R.F. and D.B. performed the analysis. T.W.B. built the individual-based models. Y.P.P., D.B., A.M.F. and J.E.C. performed fieldwork. Y.P.P. and D.M.P.J. wrote the paper with input from all authors.

Competing interests. We declare we have no competing interests.

Funding. Field research at Palmyra was supported by funds from the Marisla Foundation. D.M.P.J. was supported by the Bertarelli Foundation and the project contributed to the Bertarelli Programme in Marine Science.

Acknowledgements. We thank K. Davis, P. Carlson, C. Lowe, and K. Weng for assistance with fieldwork, the staff of The Nature

Conservancy that run the research station at Palmyra, and USFWS. We thank Y. Watanabe for providing camera data-loggers used in the study. Finally we thank the reviewers whose comments improved the manuscript. We declare that no authors have any conflicts of

interest. This is contribution no. 156 from the Palmyra Atoll Research Consortium (PARC). This is contribution no. 206 from the Coastlines and Oceans Division of the Institute of Environment at Florida International University.

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