

Social information shapes interannual social stability in colonial reef sharks

Yannis Papastamatiou¹, Thomas Bodey², Jennifer Caselle³, Darcy Bradley⁴, Robin Freeman⁵, Alan Friedlnader⁶, and David Jacoby⁷

¹Florida International University College of Arts and Sciences

²University of Exeter College of Life and Environmental Sciences

³University of California, Santa Barbara

⁴University of California Santa Barbara

⁵Zoological Society of London

⁶University of Hawaii at Manoa

⁷Institute of Zoology of the Zoological Society of London

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Abstract

Animal societies organised as colonies gain a variety of fitness benefits, and consequently colonial behaviour has evolved amongst avian, mammalian and invertebrates species, but far less is known for fish. Using dynamic social networks, we document highly structured sociality in central place foraging grey reef sharks at a Pacific atoll, with sharks forming stable, social groups over multi-year periods. Individuals were highly assorted by their patterns of space use, with specific paired dyadic associations consistent across years. We demonstrate high within-colony reciprocity of leadership roles in departure times of dyads from core areas, relative to between colony dyadic associations. We provide evidence of colonial behaviour in elasmobranch fishes, underpinned by conditions under which we would expect foraging via social or public information exchange to persist. Our models also suggest that social foraging with information transfer could drive central place foraging and colonial behaviour without the requirement for reproductive mechanisms.

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Data accessibility: Should the manuscript be accepted, data used for analysis will be uploaded to dryad.

Introduction

Gregarious animals face a constant trade-off regarding the costs and benefits associated with group living (Krause and Ruxton 2002). This trade-off can be heavily influenced by reproductive strategy, competition, the distribution of food or predators in space and by processes that facilitate collective decision-making (Janson and Goldsmith 1995, Nowak et al. 2010, Stranberg-Peshkin et al. 2015, Gil et al. 2017). Consequently, the interplay between movement, space use and social behaviour within animal populations is complex and often difficult to disentangle (Spiegel et al. 2015, 2017). Colonial animals are defined by multiple individuals sharing and showing fidelity to the same location, and traditionally benefits have been associated with breed-

ing (Evans et al. 2016). However, more recently the benefits related to social information sharing between colony members have also been highlighted (Evans et al. 2016).

Social information about foraging locations, whether intentionally communicated or otherwise, can initiate spontaneous aggregation in memory-based foragers (Lang and Farine 2017, Riotte-Lambert and Matthiopoulos 2018). Social foraging can consist of local enhancement (where animals in a group are within sensory range of other foraging individuals and can simultaneously forage and observe conspecifics, Buckley 1997), recruitment (an individual ‘recruits’ others to a patch, with foraging success increasing with group size, i.e. the recruitment hypothesis, Buckley 1997), and for central place foraging (CPF) animals, public information sharing (where uninformed individuals follow informed individuals to prey patches, Barta and Giraldeau 2001, Bijleveld et al. 2010). Public information sharing is often conceptualised using the producer-scrounger game, where individuals either search for prey (producers) or follow other individuals to prey patches (scroungers), but within this framework no individual can both forage and observe other individuals simultaneously (Vickery et al. 1991, Barta and Giraldeau 2001). The transmission of public information has even been proposed as being responsible for driving the evolution of colonial behaviour (i.e. the information centre hypothesis (ICH)), with or without the added benefits of local enhancement and recruitment (Barta and Giraldeau 2001, Bijleveld et al. 2010).

While the ICH remains controversial (Barta and Giraldeau 2001), evidence for social foraging with public information sharing has been found in seabirds, non-breeding roosting vultures, and bats (Wakefield et al. 2013, Harel et al. 2017, Egert-Berg et al., 2018). Furthermore, public information sharing can have ecological implications by contributing to spatial separation between colonies, as seen in seabirds (Wakefield et al. 2013). While models demonstrate the collective advantage of information sharing amongst colony members, they have all assumed that CPF itself, is a necessary requirement for animals returning to nests or shelters (Buckley 1997, Barta and Giraldeau 2001). However, there are examples of CPF animals that form social groups unrelated to breeding (e.g. non-breeding roosting vultures, large fish, Meyer et al. 2007, Harel et al. 2017), where there is no obvious need for them to return to a central place.

Within a producer-scrounger game, the scrounger strategy will be negatively frequency dependent (either as a fixed strategy or for animals that switch between producer/scrounger roles). Consequently, an evolutionarily stable strategy (ESS) would predict approximately equal frequencies of each role (Giraldeau and Beauchamp 1999). In simpler information sharing models (local enhancement), predictions include social associations between individuals with assortment related to foraging abilities (Giraldeau and Beauchamp 1999). Under scenarios where social or public information plays an important role in colony formation (or at least subsistence) then we might expect reciprocity in terms of how often individuals behave as leaders or followers when leaving the colony, without the requirement of reciprocal altruism (Vickery et al. 1991, Giraldeau and Beauchamp 1999, Barta and Giraldeau 2001). Non-breeding roosting vultures for example, show no preference overall for leadership or follower roles when searching for carcasses, suggesting individuals adopt both roles in equal measures (Harel et al. 2017).

Many shark species are upper level predators that can form large aggregations and maintain social associations under both laboratory and field conditions (Schilds et al. 2019, Mourier et al. 2012, 2018). They are also known to be able to learn socially via observation of conspecific behaviours (Guttridge et al. 2009). Mating and reproduction in reef sharks is seasonal, which influences patterns of movement, but residency on the reef can occur extensively throughout the year leading to frequent aggregation (Heupel and Simpfendorfer 2014). Tropical reef sharks will often behave as central place foragers, with multiple individuals sharing the same central place on small regions of the reef, but the reasons behind this behaviour are unclear (Papastamatiou et al. 2018a, 2018b). We hypothesize that grey reef sharks (*Carcharhinus amblyrhinchos*) at an isolated Pacific atoll, display colonial like behaviour by forming long term social associations, assorted by patterns of space use. We further hypothesize that a key driver of social associations are social information sharing between colony members and that this could provide an explanation for the evolution of CPF colonial behaviour in large fishes. To test these ideas we use dynamic social networks from movements of individuals over a four year period, combined with simulation models of social foraging.

METHODS

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 grey reef sharks (*Carcharhinus amblyrhinchos*), with approximately 8000 individuals distributed heterogeneously around the forereef, with average densities of 21 sharks/km² (Bradley et al. 2017).

Quantifying movements and colony assignment. Grey reef sharks were caught on hook and line and had a uniquely coded V16 (69 kHz, Vemco Ltd, Nova Scotia) acoustic transmitter surgically implanted into their body cavity. Individual animals (n = 41) were tracked across a network of 65 VR2W acoustic receivers which were attached to submerged moorings on the reef, and retrieved and downloaded annually. Receiver nodes 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. Movement networks were constructed from the departure and arrival profile of the acoustic data (i.e. a shark was detected at one receiver and then subsequently detected at another, Jacoby et al. 2012). Community detection of the resultant movement network was implemented in the R package *igraph* using the Fast-Greedy algorithm, to reveal statistically significant clusters of movement (Clauset et al. 2004, Casardi and Nepusz 2006, Finn et al. 2014). Community modularity within the movement network was high ($Q = 0.589$), suggestive of restricted movements, and resulted in the formation of five distinct communities. Individual sharks were then assigned to communities, forming groups that we refer to as ‘colonies’. Colony membership was determined based on calculating residency indices (RI) for each individual across each location and assigning an individual to a colony based on its 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.

Social stability and leadership. 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 (Franks et al. 2010). Shark social networks were inferred directly from the detection data stream using the Gaussian mixture modelling approach, GMMEvents (Psorakis et al. 2012, Jacoby et al. 2016). Clusters of detections, produced by visits of multiple individuals to the same place at the same time, varying temporally to reflect the variation expected in the temporal distribution of animal aggregations, were determined using a Variational Bayesian mixture model. From these clusters, associations were assigned to an adjacency matrix. Randomisation of the individual-by-location bipartite graph, a procedure built in to the GMMEvents model, excludes non-random associations attributable to purely spatial drivers of aggregation, leaving only significant associations to populate the adjacency matrix. Social duration matrices and leadership matrices were extracted from the model, reflecting the cumulative time (in seconds) dyadic pairs spent together, and determined by the order with which individuals within a pair arrived (leader = 1, follower = 0) respectively, within significant social clustering events.

Networks were constructed in this way for each of the four years of tracking data and tested for weighted assortative mixing (rw_d) by colony membership using the R package ‘*assortnet*’ (Farine 2014). Each annual network was then tested for significant assortment by colony against 10,000 networks in which interactions were randomised. Constraining the number of individuals per colony and the number of associations measured that particular year, edge weights were randomly assigned and rw_d 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 two 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).

While we could calculate leadership/follower roles between dyadic pairs based on when they arrived or departed spatial-temporal clusters, we could not calculate the frequency of leader/follower roles, because we do not know the total number of individuals from the population departing or arriving, or group sizes. However, we hypothesise that under a social foraging scenario (public or social information), with social associations between colony members, relative reciprocity in leadership between dyadic pairs within colonies, should be higher than those between colonies (controlling for the number of times individuals associate). From the leadership matrix, pairs of individuals were assigned a normalised, dyadic reciprocity index reflecting the probability of leadership behaviour being reciprocated between associates (Wang et al. 2015). This index takes the form

$$R_{ij} = |\ln(p_{ij}) - \ln(p_{ji})|$$

with

$$p_{ij} = \frac{w_{ij}}{w_{i+}}$$

where w_{ij} is the raw, directed edge weight between nodes i and j and w_{i+} is the strength of the i th node given by Barrat et al. 2004, and Wang et al. 2015 as

$$w_{i+} = \sum_{j \in N(i)} w_{ij}$$

in which $N(i)$ is the set of nodes that immediately neighbour i via outgoing edges. An index of 0 represents full reciprocity (mutual leader-follower behaviour) and increasing values from 0 represent increasingly more unbalanced ties. Crucially, this index quantifies the normalized weighted difference (i.e. probability of reciprocal leadership), rather than raw edge weights, accounting for the fact that some dyads simply associate more than others (e.g. within colonies as opposed to between colonies). A Welch's two-sample t -test was used to compare the distributions of within colony and between colony reciprocity and a negative binomial GLM to explore the relationship between reciprocity and the cumulative duration dyads were in association.

Group size. To estimate minimum group sizes, we deployed two animal-borne camera tags on grey reef sharks caught off the SW region of the atoll. Sharks had DVL400 video loggers (Little Leonardo, Japan) attached to the dorsal fin which record at 640x480 pixels at 30 frames/second and recording duration of 11 h (Papastamatiou et al. 2018a). 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 48-72h 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 AM, to avoid the period of stress associated with capture. For each 30-minute 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. shark in frame or seen sequentially while swimming in a straight line), including the individual carrying the camera (i.e. minimum size=1).

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

(Wilensky 1999), and the basic parameters of these models were previously described (Papastamatiou et al. 2018b).

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, 200 or 300 depending on the specific simulation set) randomly distributed across an unbounded torus. Simulated individuals moved at a constant speed of 0.6 m/s (Papastamatiou et al. 2018a) and initially used a naive random search pattern. On discovering a prey patch, individuals remained there until the prey moved, at which point the predator commenced a more restricted search pattern based on a tighter turn angle for 300 time-steps. Simulated shark lifespans were constrained by an energy term, with all individuals starting with 800 energy units, losing one unit per time step while searching for prey patches, and dying if this reached zero. Successfully locating a prey patch resulted in an energy gain for the shark (150, 300 or 450 units depending on the specific set of simulations). If individuals gained sufficient energy (individual energy score > 1000 units) then they could potentially reproduce, with the probability of reproduction of a single offspring drawn from a log-normal distribution (reflecting the low reproductive rates of this species). Prey patches (i.e. shoals or individual reef fishes) are likely semi-predictable in space as a result of diel and tidally influenced movements (e.g. Meyer et al. 2010), as well as specific territoriality and habitat requirements, so prey patches followed a random walk within model space with step length drawn from a normal distribution (mean = 0, SD = 2). In addition, to incorporate less predictable prey movements, at each time step there was a 5% chance of prey patches relocating to another random position in model space. Finally, following discovery and the commencement of foraging, prey patches had an increased probability of dispersing, mimicking predator avoidance and escape behaviour. These movements could be either localized or larger jumps as described above, and were made more likely through a doubling of the acceptability threshold for movement from a random draw made at each time-step. 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. A burn-in of 1000 time-steps at the start of each simulation allowed individuals to explore their environment so that they were not completely naive, and some degree of prey patch knowledge was established.

The first set of models were devised to examine the importance of using both social and private information during foraging, in this case the ability to both find prey oneself and the ability to identify and join foraging aggregations. This model set therefore included two types of individual: i) ‘social’ foragers that are able to both discover prey for themselves (i.e. private information), and to observe successful feeding in others and aggregate around prey patches, mimicking passive social information transfer including visual and chemical cues in the water; and ii) ‘lone’ foragers that are only able to find prey for themselves and do not recognize and move towards other foraging individuals. In these models, undiscovered prey patches were only detectable at short distances (0.3 unit radius). However, following discovery and commencement of feeding by either a ‘lone’ or ‘social’ individual, such discovered patches became visible to other ‘social’ individuals at a four-fold greater distance. ‘Lone’ individuals could also join discovered patches, but would only locate them through moving to close proximity as described above. One hundred simulations were run for each combination of food patch density (100 or 200 patches) and energy gain (150, 300 or 450 units per successful forage), with the proportion of ‘social’ and ‘lone’ individuals recorded through model time.

The second set of models then examined whether, if all individuals are able to use both public and private information sources, there is any additional benefit to being a central place forager under these circumstances. Thus, in these simulations all individuals behaved as ‘social’ individuals described above in terms of their ability to forage. However, a varying proportion (20, 50 or 80%) were central-place foragers (‘central place’), returning to a fixed spatial location at every 500th timestep, 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). As in the previous model, 100 simulations were run for each combination of food patch density (100 or 200 patches) and energy gain (150, 300 or 450 units

per successful forage), with the length of model time the ‘central place’ and ‘wanderer’ individuals survived recorded for each simulation.

Results

We tracked the movements of 41 individual grey reef sharks (*Carcharhinus amblyrhinchos*) over 13,800 accumulative tracking days (26 Female, 13 Male, 1 unknown, Total Length: 142 ± 18 cm). Tagged grey reef sharks were assigned to five distinct movement communities, based on similarity of individual movement networks (network modularity, $Q = 0.589$). Thus, individuals were organised into groups that predominantly only used small, sub-sections of the available reef. Colony members had 50% utilization distributions ranging in area from <1 to 7.53 km² (mean \pm SE = 1.26 ± 0.32 km², Fig. 1b). Although movements of individuals between areas were limited, there was some spatial overlap between colonies, suggesting that observed 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).

Calculating a weighted assortativity coefficient for each annual network revealed significant social assortment (rwd : Y1 = 0.204; Y2 = 0.129; Y3 = 0.176; Y4 = 0.130) when tested against a null model of 10,000 random networks (Fig. 1c). Each year, social associations were positively assorted by colony membership with no evidence for assortment based on sex (rwd (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=0.13-0.30, $p<0.001$), 2&3 ($n=35$, Mantel $r=0.85$, CI=0.13-0.29, $p<0.001$), 3&4 ($n=31$, Mantel $r=0.78$, 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, $p<0.001$). While we were only tracking a small proportion of the grey reef shark population, densities per area of the forereef are relatively low (Bradley et al. 2017) and our camera deployments suggest group sizes of approximately 20 individuals (see below). 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. Footage from camera tags deployed on two sharks showed that group size typically varied between 2-16 individuals, with group size increasing throughout the day and peaking in the afternoon (Supplementary material Fig. S1). Close following behaviour, where individuals were approximately less than 1 m from a conspecific, was commonly observed (Fig. S1, Movie 1).

From the leadership-follower matrix, the distribution of R_{ij} differed significantly for dyads within rather than between colonies (Welch’s two-sample t -test, $t(2416) = 8.938$, $P < 0.001$; Fig. 2a), suggesting leader-follower behaviour is more reciprocal at the colony level than between individuals outside of colony affiliates. Furthermore, those dyads that were relatively more reciprocal also spent more time together with a significant negative effect of R_{ij} on association duration across all four years (negative binomial GLM, $F = -0.804$, $P < 0.001$, Fig. 2b).

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 (social, Fig. 3a, b). 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 (Fig. 3a, b, Fig. S2). Our second series of models assumed that all individuals use both private and social information to find prey patches, with some individuals exhibiting random movement within a home range (wanderers) and others consistently returning to a central place within the home range (central place foragers, CPFs). Again, regardless of prey quality, patch density, or the starting ratio of wanderers to CPFs, in all modelling scenarios, CPFs had much greater survival times (Fig. 3c, d, Fig. S3, Table S1).

Discussion

Grey reef sharks form social communities akin to colonies formed by other species, with social structure assorted by patterns of space use and with associations persisting interannually. Furthermore, our dynamic social network approach showed that dyadic associations were stable, signifying that the same individuals were associating, in some cases for up to four years. Spatial assortment of social communities is relatively common in animals of high cognitive abilities, including birds, bats, dolphins, and seals (e.g. Wolf et al. 2007, Kerth et al. 2011, Shizuka et al. 2014, Titcomb et al. 2015). Although across-year social associations have been recorded in some birds and mammals, they are rarely quantified in animal communities, highlighting that sharks form relatively complex social communities over long time periods (Kerth et al. 2011, Shizuka et al. 2014, Ilany et al. 2015). These long-term associations persist despite sharks exhibiting fission-fusion dynamics where group membership will change, within the confines of colony membership, as is also the case in bats (Kerth et al. 2011). However, unlike bats and birds, shark social communities are not seasonal but occur year-round. To the best of our knowledge this is the first documentation of similar interannual social associations in fish.

Given that grey reef sharks do not need to return to a nest site or shelter area, why would social communities and central place foraging evolve in these predators? Here, we provide evidence that social information sharing, potentially within a foraging context, can explain both social associations and the broader advantage of CPF behavior. We show that there is greater reciprocity in leadership roles between dyadic pairs within a colony compared to dyadic associations between colony members. Regardless of whether social foraging is the product of simple information sharing (e.g. local enhancement) or public information where sharks follow other individuals to patches, we would expect some degree of reciprocity in leadership roles for stable social groups (Barta and Giraldeau 2001, Giraldeau and Beauchamp 2001). For example, vultures use public information to find carcasses but individuals do not show an overall preference for leader or follower roles (Harel et al. 2017). Such reciprocity would not require reciprocal altruism but could instead represent an evolutionary stable strategy of the frequency of scroungers in a producer-scrounger games, or sharks socially assorting with individuals with similar foraging traits and abilities (Vickery et al. 1991, Barta and Giraldeau 2001, Giraldeau and Beauchamp 1999). In addition, the duration of social associations between dyadic pairs was a positive function of reciprocity; simply put, pairs that switched leader-follower roles spent more time together. This would suggest benefits of spending time with individuals that are unlikely to cheat in terms of leadership roles.

The benefits and evolutionary significance of group foraging are well known and studied using both empirical and modelled data (Clarke and Mangel 1984, Buckley 1997, Barta and Giraldeau 2001, Kraus and Ruxton 2002). 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 the home range. Hence, regardless of whether social communities act as information centers, multiple individuals sharing a central place and sharing social information will outperform random walkers. Although group formation will also lead to increased competition, the negative effect of competition on information sharing within the group may be minimised if travel times to patches are short, resources are distributed heterogeneously, and patch locations are unpredictable (Sernland and Olsson 2003, Smolla et al. 2015). Models of local enhancement by foraging seabirds suggest that group foraging is only advantageous if prey patches are ephemeral, scarce, and of little future value (Buckley et al. 1997). Empirical support for these predictions can be found in bats where social foraging is only seen in species foraging on ephemeral prey (Egert-Berg et al. 2018).

These prey conditions are likely met by our focal sharks that regularly prey on fish schools situated offshore, whose location in time and space are extremely unpredictable (McCauley et al. 2012, Papastamatiou et al. 2018a). Over 80% of grey reef shark diet at Palmyra is estimated to consist of pelagic prey, and sharks have been observed foraging on fish baitballs offshore (McCauley et al. 2012, Y. Papastamatiou pers. comm.). In addition to meeting model criteria set above, these prey schools would also likely support the recruitment hypothesis, as multiple sharks are needed to successfully forage on schooling baitballs (Thiebault et al. 2016).

In addition, foraging also takes place during the day on the reef where roaming fish shoals are also dynamically distributed in time and space (Papastamatiou et al. 2018a). Hence social information sharing, underpinned by a stable social structure, is likely to be an advantageous strategy for grey reef sharks.

To our knowledge, this is the first evidence to suggest that elasmobranchs are capable of colonial behaviour, spatially structuring themselves within restricted areas of a small reef ecosystem and forming long-term social associations between colony members, comparable to birds and mammals. Social information transfer can be a key foraging mechanism, and by itself, may be sufficient to select for CPF behaviour in animals that do not require the use of a nest or shelter, including many fishes (e.g. Meyer et al. 2006). Social information is important for linking individual behaviour to population- and community-level dynamics and can enable positive, density-dependent growth of populations, as well as change the frequency and strength of species interactions (Gil et al. 2015). Information sharing in combination with density-dependence competition, is also thought to drive spatial separation between seabird colonies (Wakefield et al. 2013). The grey reef shark population around Palmyra Atoll appear to show similar patterns with limited movement of individuals between colonies. As with seabirds, the mechanism behind spatial separation may include intra-specific competition and information sharing by sharks within colonies (Papastamatiou et al. 2018b). While the importance of social information in colonial birds and mammals is now well established (Evans et al. 2016), we show that these concepts likely also apply to some species of shark. Tantalisingly, our analyses may be suggestive of a process (colonial behaviour) that may be much more widespread than originally thought in free-ranging, marine animals.

Ethics statement: 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).

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Figures

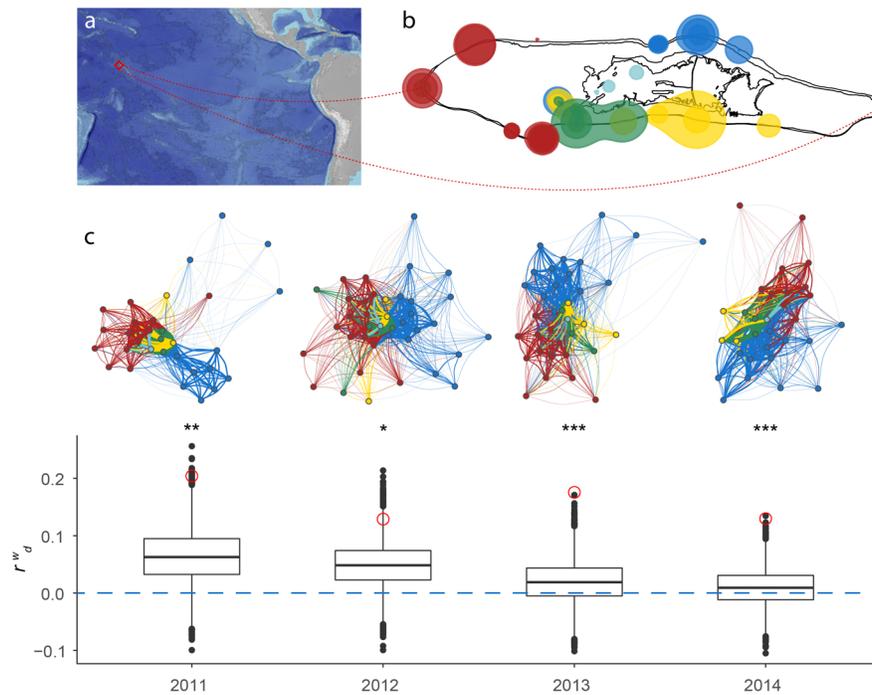


Figure 1. **Spatial and social assortment** . **a** , Palmyra Atoll Marine Reserve (red diamond) in the Central Pacific Ocean. **b** , Space use measured as the 50% utilisation distribution (UD) of sharks assigned to their respective colonies which were defined using community detection of individual movement networks (colours reflect colony groups 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 four 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 colonies, represented as different coloured nodes. No assortment is illustrated by blue dashed line. ($p < 0.05^*$, $p < 0.01^{**}$ and $p < 0.001^{***}$).

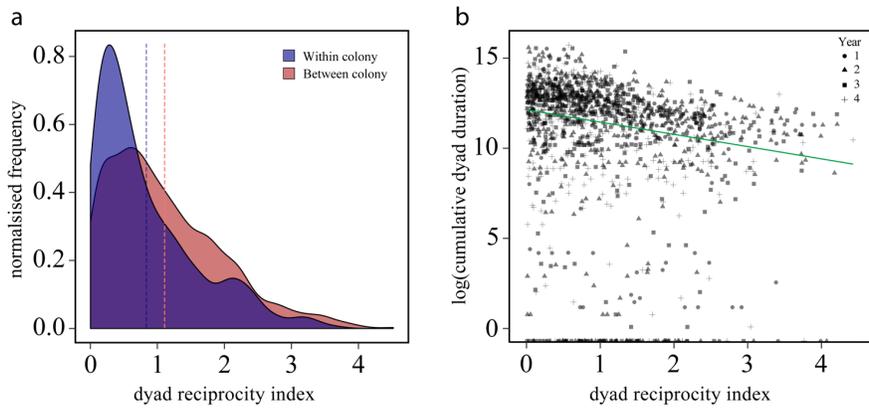


Figure 2. **Leadership, reciprocity and the potential for information exchange** . **a** , Normalised frequency distribution of dyadic reciprocity indices between all possible pairs of sharks within and between colonies indicates significantly higher reciprocity within colony (lower dri). **b** , Those dyads with higher reciprocity also spend significantly more time together (higher cumulative association).

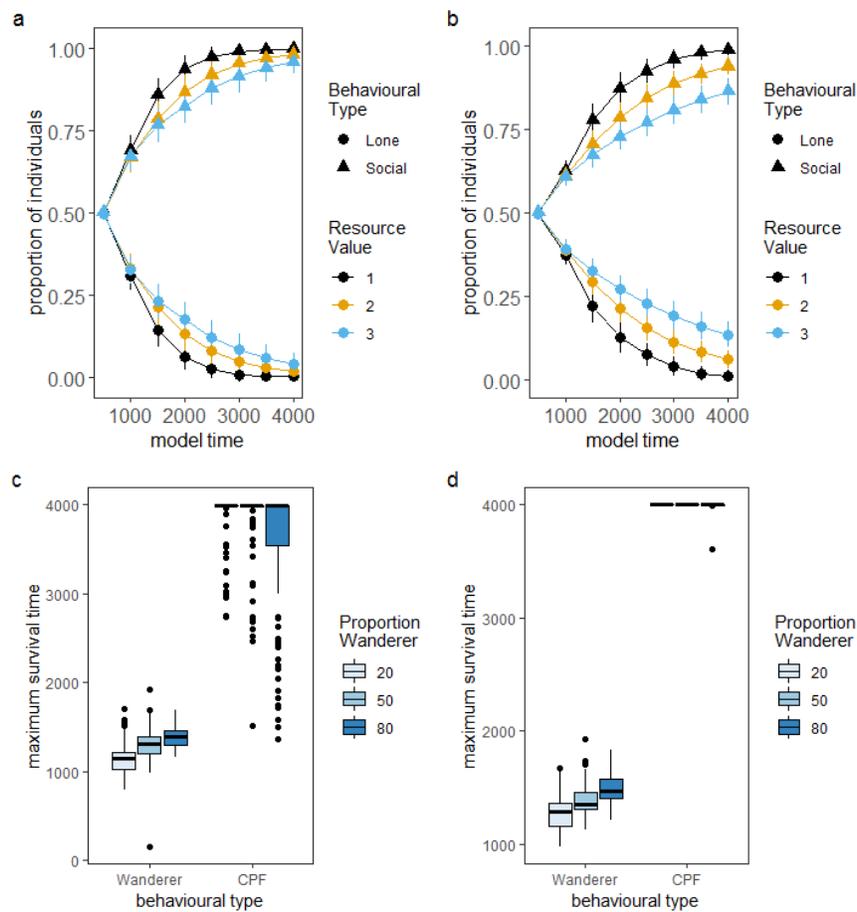


Figure 3. **Strategy and survivorship modelling** . **a, b** , Proportion of simulated individual sharks surviv-

ing through model time. Those pursuing ‘lone’ foraging strategies (using only private information to locate prey patches) declined rapidly compared to ‘social’ foragers (using both private and social information), regardless of the energetic reward obtained from locating resources (**a** : 100 prey patches, **b** : 200 prey patches, for further reward ratios and patch densities see Fig S1). **c** , **d** , Survival time of simulated sharks behaving either as wandering or central-place foragers (CPF), assuming all individuals can use both private and social information to locate prey patches. Regardless of prey abundance (**c** : 100 prey patches, **d** : 200 prey patches), the reward obtained from foraging events (Fig S2), or the starting ratio between the two foraging strategies, under all conditions only CPF individuals successfully survive for the full duration of model time. Once prey density is sufficiently high, there is no variation in likelihood of survival of CPF **d** .