

Research



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Animal behaviour

Social dynamics and individual hunting tactics of white sharks revealed by biologging

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Social foraging, where animals forage in groups, takes many forms but is less studied in marine predators as measuring social associations in the wild is challenging. We used biologging (activity, cameras and telemetry receivers) sensors to measure social associations and simultaneous behaviour, in white sharks (*Carcharodon carcharias*) off Guadalupe Island, Mexico. Animal-borne telemetry receivers revealed that sharks varied in the number of associations they formed and occurred most often when sharks were swimming in straight paths or when they were turning frequently. While many associations were likely random, there was evidence of some stronger associations. Sharks varied in the depths they used and their activity, with some individuals more active in shallow water while others were more active 200–300 m deep. We propose that white sharks associate with other individuals so they can inadvertently share information on the location or remains of large prey. However, there may be a wide range of individual variability in both behaviour and sociality. Biologging now enables social associations of animals to be measured, concurrent with measures of their behaviour, so that social foraging of large marine predators can be quantified in the wild.

1. Introduction

Social foraging, where animals hunt in groups, can take many forms and range from simple sharing of information via local enhancement (where individuals can simultaneously forage and observe other animals foraging) to more complex cooperative hunting [1]. While social foraging of marine predators has been studied in animals across a wide range of sizes, it has generally only been measured during the foraging event itself (e.g. [2]). Far less is known about the social associations between marine predators while hunting in the wild, mostly due to the difficulties in measuring associations in free-ranging animals. Animal-borne telemetry receivers enable social associations of free-ranging animals to be directly recorded [3,4]. Animal-borne telemetry receivers have been used with some marine predators in captive and field settings but from a largely descriptive standpoint [5–9].

Measuring social foraging requires more than just quantifying associations with other individuals, but also considering the behaviour of individuals

during associations [8,10]. Measuring individual behaviour in relation to social networks is important as an increasing number of studies are showing that individual variability in hunting tactics exist in wild populations [11,12]. Furthermore, individual behaviour (e.g. bold versus shy personalities) can influence social network position which may also reflect how or if individuals benefit from social foraging [13]. Currently available animal-borne sensors can be combined to simultaneously measure social associations and interactions, individual behaviour, and habitat use of marine predators in the wild.

White sharks (*Carcharodon carcharias*) are large (up to 6 m) migratory predators found in tropical and temperate waters and form well-known seasonal aggregations at pinniped colonies, which are prey for adult sharks and often ambushed at the surface [12,14–17]. There is evidence that white sharks form non-random social associations and may remain in proximity to each other to take advantage of pinniped kills [18–20]. They can also show quite specialized hunting tactics that vary by sex and individual [12,21]. Guadalupe Island (GI), Mexico, is a seasonal aggregation site where white sharks likely forage on pinnipeds and deeper water squid [14,22,23]. However, the clear water at GI makes it difficult to ambush prey on the surface, and it is thought that hunting takes place at depth where light levels are lower [23,24]. Here we use novel multi-sensor biologgers to quantify the social associations and behaviour of white sharks at GI, Mexico. As previous studies suggest that white sharks at Guadalupe hunt in deeper water, we hypothesize that sharks (i) are more active and hunting at depth and (ii) form more social associations during the day and at depth.

2. Methods

(a) Tagging

We combined Customized Animal Tracking Solutions (CATS, Germany) diary dataloggers with a miniSUR acoustic receiver (Sonotronics Ltd, 190 × 16 mm) integrated into a custom-designed syntactic foam float. The CATS diary consisted of a three-dimensional accelerometer, three-dimensional gyroscope, three-dimensional magnetometer (all sampling at 20 Hz), light, depth and water temperature sensor (sampling at 1 Hz) and a HD video camera that could record for 5 h (2017) or 8 h (2018). The miniSUR was programmed to sample the environment at 69 kHz, and all acoustic detections were stored to memory (detection ranges up to 30 m, [9]). Our social dataloggers were attached using clamps to the dorsal fins [25] of white sharks at GI, either from subsurface cages or by using free divers. A 5-day galvanic release caused the datalogger to release from the clamp and float to the surface, where we recovered them via embedded VHF and satellite transmitters (SPOT, Wildlife Computers). Pole spears were used to attach acoustic transmitters (V16, Innovasea, 69 kHz) via arrowheads to free-swimming white sharks (details in [23]). An array of 11 underwater listening stations (VR2W, Innovasea) were also deployed along the eastern side of GI, which could detect acoustically tagged sharks anytime they swam within range [23].

(b) Associations

For each miniSUR deployed on a white shark, detections of other tagged sharks were considered the contacts of the focal shark within a radius of approximately 30 m [9]. Social association matrices were constructed based on co-occurrences (i.e. simultaneous detection) of individuals within the detection range of the focal shark

and within an arbitrary pre-defined 10-min bin. Association strength for each dyad was calculated using the simple ratio index with *asnipe* R package [26], where associations are scaled between 0 (never observed in the same group) and 1 (always occurred in the same group, [27]). We also calculated the duration of detections, diel patterns and tested for an assortment of social associations by sex. We fitted mixture distributions to the association strength values data from the focal sharks, with the R package *mixtools* [28] to see if we could identify clusters of stronger connections. Further details in electronic supplementary material, A.

(c) Customized Animal Tracking Solutions diary

For each shark, we calculated overall dynamic body acceleration (ODBA) from three-dimensional acceleration data (as a proxy for shark activity) and heading from the three-dimensional magnetometer data. The number of sharks detected each hour (encounter rate) by the miniSURs was calculated and paired with data from CATS diaries. From these data, mean ODBA, depth and heading standard deviation (s.d.; as a proxy for periods of tortuous (indicative of area-restricted searching, ARS) or straight movement) were also calculated in hourly bins. Gaussian generalized additive mixed models (GAMMs) with an identity-link function were fit to test the effects of encounter rate with other white sharks (no. of unique IDs), time of day and depth, on ODBA values, including individual as a random effect. Similarly, Poisson GAMs with a log-link function were fit to test the effects of time of day, depth and movement metrics (ODBA, heading s.d.) on no. of unique IDs, including individual as a random effect. Further details of GAMMs are in electronic supplementary material, A.

3. Results

We deployed the biologging package on six white sharks (3M: 3F; 3.5–4.5 m total length) in 2017–2018 (table 1) for 1–4 days (52 ± 28 h, range: 27–100 h). Four animals had a combined CATs diary/video/miniSUR (although the video failed on one shark), while two animals had a CATS diary/video only. Between 2015 and 2017, 30 white sharks were fitted with acoustic transmitters, while an additional seven were tagged with acoustic transmitters from 2017 to 2018 (a total of 37 sharks).

(a) Associations

The four focal sharks showed a remarkably large number of associations with their surrounding tagged congeners (figure 1). WS1 and WS2 (illustrated in figure 1e and figure 1f) had the highest number of associations with, respectively, 19 and 12 individual tagged sharks in 2017. WS3 and WS4 had a lower number of associations with, respectively, six and four tagged sharks (electronic supplementary material, B and figure S1). There was high variation in the duration of associations between white sharks with a mean \pm s.d. of 7.64 ± 10.55 min (maximum ranged from 32 min (WS3) to 73 min (WS2), electronic supplementary material, B, table S1 and figure S2). Assortment by sex was variable with only WS2 showing a clear assortment ($r_{WS2} \pm$ s.e. = 0.413 ± 0.129 ; figure 1f) while assortment was only apparent between males for WS1 and between females for WS3 and WS4 (electronic supplementary material, B and figure S1). Among the 98 associations, two distinct clusters were identified in the distribution of association strength values by the mixture model, including low associations (92%) and stronger associations (8%, only for WS1 ($n = 3$) and WS2 ($n = 5$)) (figure 1b). Diel

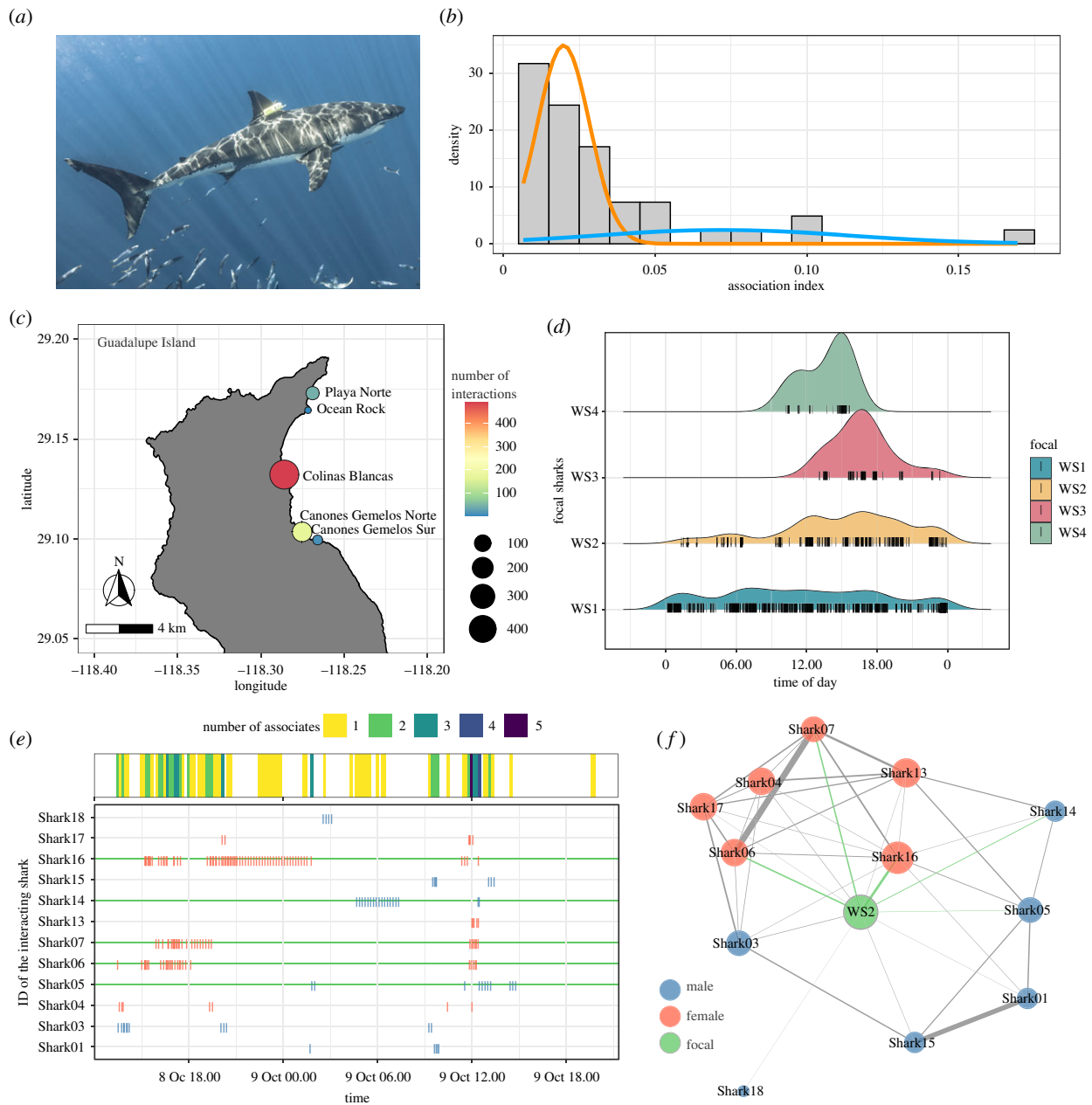


Figure 1. Social associations for free-ranging white sharks at Gl. (a) A white shark with a biologging social tag on the dorsal fin (photo: A. Voyer) and (b) the frequency distribution of association index strength for all four focal sharks. Most associations were weak (orange) but there were a small number of strong associations (blue). (c) The spatial location of associations were determined from acoustic detections on underwater listening stations for all four focal sharks. (d) Diel patterns of associations for all four sharks fitted with biologgers. (e) Temporal patterns and number of associations for WS2 and (f) the social network for WS2. Red individuals are female and blue males for (e) and (f) and green edges represent the stronger associations.

Table 1. Details of white sharks fitted with biologging tags at Gl. Receiver tag is a miniSUR acoustic telemetry receiver.

shark no.	date	sex	size (m)	duration (h)	depth (max, mean \pm s.d.)	tag
1	Oct 2017	M	3.5	67	236 m (40 \pm 35)	diary/video/receiver
2	Oct 2017	M	3.5	27	260 m (34 \pm 29)	diary/video/receiver
3	Oct 2018	F	4.5	49	332 m (89 \pm 91)	diary/video/receiver
4	Oct 2018	M	3.0	100	285 m (47 \pm 29)	diary/receiver
5	Dec 2018	F	4.0	40	302 m (35 \pm 25)	diary/video
6	Dec 2018	F	4.0	29	353 m (45 \pm 73)	diary/video

patterns in associations were found for WS3 and WS4 in 2018 with most associations occurring during the day, while associations were homogeneously distributed across a 24 h period

for WS1 and WS2 (figure 1d). Most associations were recorded at Colinas Blancas (68%) where most of the cage diving activity takes place, followed by the seal colony at Cañones

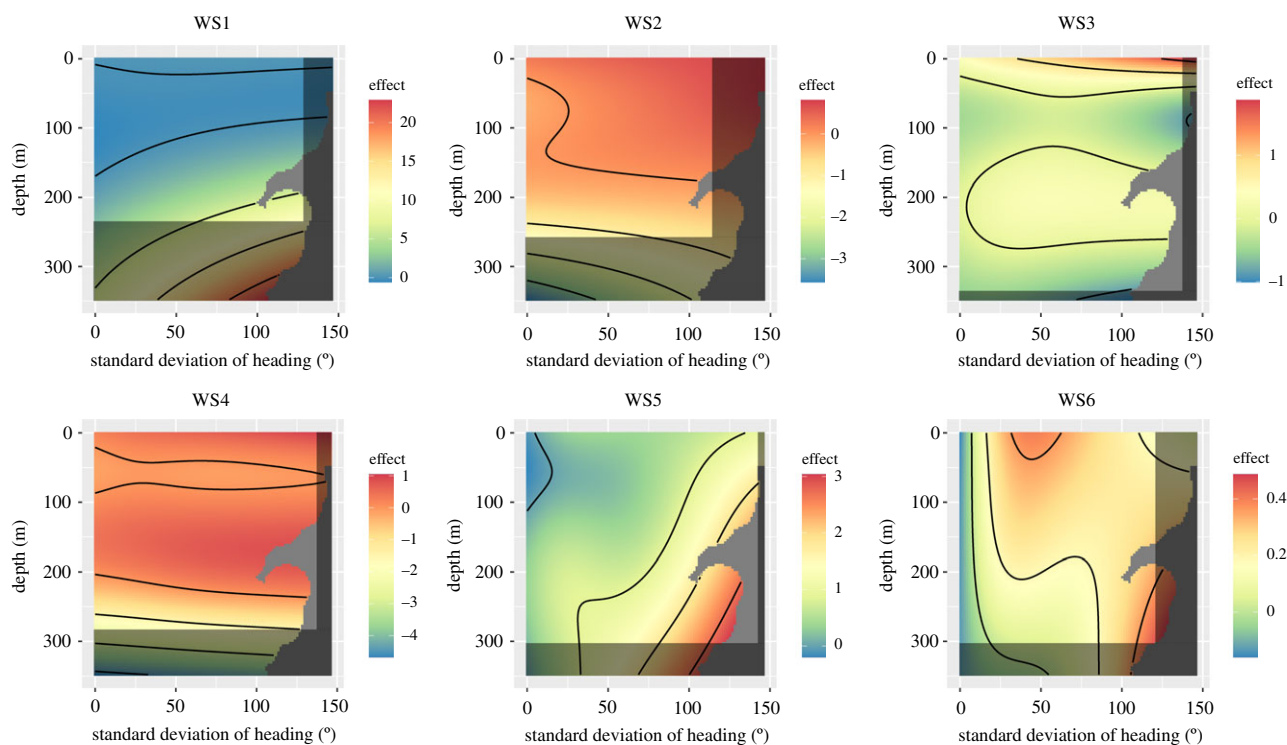


Figure 2. Results from GAMM of the effect of and interaction between swimming depth and heading s.d. (a proxy for tortuosity) tensor product smooths, on white shark activity (ODBA). Colour ramps represent the additive effect of tensor products on ODBA values. Note that additive effect varies across individual smooths and range of colour ramps. Grey shaded areas represent values beyond sampling extent of either predictor for individuals (shaded rectangles) and all sharks combined (solid grey irregular polygons).

Gemelos Norte (24%, figure 1c; electronic supplementary material, B and figure S3). Additional details in electronic supplementary material, B.

(b) Associations and behaviour

Sharks spent the majority of their time < 100 m although there was a large amount of individual variability (table 1; electronic supplementary material, B and figure S5). No significant relationship was observed between ODBA and the presence of other white sharks (no. of unique IDs, $F_{1,226} = 0.65$, $p = 0.419$; electronic supplementary material, B and table S2). ODBA values were greatest when near the surface, and during the afternoon hours (approx. 16.00 h), decreasing significantly with increasing depth ($F_{1,226} = 20.44$, $p < 0.001$), and in the early morning (approx. 05.00 h; $F_{1,226} = 10.56$, $p < 0.001$). The presence of other sharks was significantly related to time of day ($F_{1,226} = 33.03$, $p < 0.001$), peaking in the early afternoon (approx. 13.00 h) and decreasing until approximately midnight. Number of unique IDs was lowest when heading s.d. (a proxy for tortuosity) values were moderate ($F_{1,226} = 22.05$, $p < 0.001$, electronic supplementary material, B and figure S5d-e). Heading s.d. decreased slightly with depth ($F_{1,226} = 12.62$, $p = 0.005$; electronic supplementary material, B and figure S5i), and increased when encounter rates were high (greater than six unique IDs, $F_{1,226} = 2.54$, $p = 0.035$; electronic supplementary material B, figure S6). Heading s.d. also increased slightly in the early afternoon hours and was lowest through the evening and early morning hours ($F_{1,226} = 7.62$, $p < 0.001$), likely in concert with the presence of other sharks.

(c) Activity

Although sharks spent most their time < 100 m, there was a wide range of individual variability in vertical habitat use

(electronic supplementary material, B and figure S5). ODBA varied significantly with depth and heading s.d. (electronic supplementary material, B, table S2 and figure S5), though the sign and magnitude of this variation differed substantially among individuals (figure 2). Half the sharks (WS2, WS3, WS4) showed a negative relationship between ODBA and depth, while ODBA values increased with depth for WS1, WS5 and WS6 (figure 2; electronic supplementary material, B and table S2). The majority of sharks displayed high levels of variation in heading (i.e. heading s.d.) in tandem with high ODBA values, indicating rapid, tortuous movements occurred primarily near the surface (WS2, WS3 and WS4), and between approximately 200–300 m (WS1, WS5 and WS6).

We obtained a total of 34.3 h of video footage from five sharks (table 1). Sharks 5 and 6 encountered other sharks within the video which were not associated with cages, at depths of 18–80 m. One of those encounters included the tagged shark following another individual and encountering that individual multiple times over a 20 min period (electronic supplementary material, C). Sharks 1, 5 and 6 approached potential prey items including turtles (eight encounters), a California sea lion *Zalophus californiensis* (one encounter in shallow water) and electric rays *Tetronarce californica* (three events).

4. Discussion

Predation on pinnipeds at GI has been observed (and inferred from stable isotopes), but an ambush has never been witnessed at the surface, and it is thought the ambushing takes place in deeper water where visibility is reduced [23,24,29]. We found some white sharks to be highly active at depth, sometimes greater than 300 m deep, while others were

more active in shallow water (e.g. the interactions with the sea lion was at 10 m depth). White shark hunting behaviour appears very different from other areas with murkier water where pinnipeds are ambushed on the surface [12,15–17]. While white sharks at GI use patrolling behaviour to search for prey similar to other locations, diel patterns of behaviour differ [12,19]. White sharks at a South African seal colony are more likely to perform ARS behaviour early in the morning as conditions at sunrise are optimal for ambushing prey on the surface [12,15]. At GI, ARS is highest during the day (although for short periods of time), potentially partially induced by baited cage diving [12,30].

While white sharks form lots of likely random associations with other individuals, they also form longer (up to 70 min) associations with certain sharks. These results add to growing evidence that white sharks may form non-random social associations [18,20]. While some of these associations may be driven by sharks being attracted to cage diving activities, we found associations that occurred at night (when no chumming takes place) and many associations occurred at a seal rookery at the south of the bay, where cage diving boats are absent. We also found evidence that associations may be more likely to form when sharks are patrolling or frequently turning (suggesting ARS), but not at intermediate levels of turning. There was also evidence of sexual assortment (for some individuals), similar to white sharks in Australia [20]. However, we also found large individual differences in the number and extent of social associations by tagged sharks. WS2 had the shortest tag deployment, but the highest number of strong associations, while WS4 had the longest deployment and the least number of associations (despite spending most of its time >100 m depth). Future studies should investigate what drives social network position and how it may relate to individual differences in activity and behaviour [13].

By remaining in proximity to other individuals, white sharks may be able to acquire social information on the location of prey or recent kills [19,31]. Our video footage provides some support for this, with a white shark orienting to and following another individual for a short period of time. Additional evidence for this includes the location of some of these associations (the pinniped rookery) and because associations may be more likely to occur while

sharks are patrolling and potentially searching for natural prey. Finally, one of us (M.H.-P.) made an observation of an elephant seal carcass floating to the surface, with two white sharks at the carcass (electronic supplementary material, D). We were likely on site of the kill within a few minutes of its arrival at the surface, suggesting both sharks were in close proximity of the kill when it occurred.

The use of biologging to measure social dynamics of free-ranging animals is a relatively new field which has been mostly confined to terrestrial environments [3,4]. However, here we use these tools to simultaneously quantify social associations with animal behaviour and habitat use and show that white sharks form some short duration (but strong) associations, with a wide range of individual variability in their sociability, behaviour and vertical habitat use. These tools will provide new opportunities to generate hypothesis-driven questions on marine predator sociality (also see [10]).

Ethics. All shark tagging was approved by the Florida International University Animal Care Committee, IACUC no. 200998. Research at GI was performed under permits General Wildlife Administration SPGA/DGVS/06673/17 and 004284/18.

Data accessibility. R code of social association matrices and raw acoustic detections have been uploaded to Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.2v6wwpzq9> [32].

Authors' contributions. Y.P.P.: conceptualization, funding acquisition, investigation, methodology, project administration and writing—original draft; J.M.: formal analysis and writing—review and editing; T.T.: formal analysis and writing—review and editing; S.L.: formal analysis, investigation and writing—review and editing; S.H.: formal analysis and writing—review and editing; O.S.-M.: investigation and writing—review and editing; M.H.-P.: conceptualization, funding acquisition, investigation, methodology and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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References

- Lang SDJ, Farine DR. 2017 A multidimensional framework for studying social predation strategies. *Nat. Ecol. Evol.* **1**, 1230–1239. (doi:10.1038/s41559-017-0245-0)
- Herbert-Read JE *et al.* 2016 Proto-cooperation: group hunting sailfish improve hunting success by alternating attacks on grouping prey. *Proc. R. Soc. B* **283**, 20161671. (doi:10.1098/rspb.2016.1671)
- St Clair JJ, Burns ZT, Bettaney EM, Morrissey MB, Otis B, Ryder TB, Fleischer RC, James R, Rutz C. 2015 Experimental resource pulses influence social-network dynamics and the potential for information flow in tool-using crows. *Nat. Comm.* **6**, 7197. (doi:10.1038/ncomms8197)
- Ripperger SP *et al.* 2019 Vampire bats that cooperate in the lab maintain their social networks in the wild. *Curr. Biol.* **29**, 4139–4144. (doi:10.1016/j.cub.2019.10.024)
- Holland KN, Meyer CG, Dagorn LC. 2009 Inter-animal telemetry: results from first deployment of acoustic 'business card' tags. *End. Spec. Res.* **10**, 287–293. (doi:10.3354/esr00226)
- Haulsee DE, Fox DA, Brece MW, Brown LM, Kneebone J, Skomal GB, Oliver MJ. 2016 Social network analysis reveals potential fission–fusion behavior in a shark. *Sci. Rep.* **6**, 34087. (doi:10.1038/srep34087)
- Guttridge TL, Gruber SH, Krause J, Sims DW. 2010 Novel acoustic technology for studying free-ranging shark social behavior by recording individual interactions. *PLoS ONE* **5**, e9324. (doi:10.1371/journal.pone.0009324)
- Barkley AN, Broell F, Pettitt-Wade H, Watanabe YY, Marcoux M, Hussey NE. 2020 A framework to estimate the likelihood of species interactions and behavioral responses using animal-borne acoustic telemetry transceivers and accelerometers. *J. Anim. Ecol.* **89**, 146–160. (doi:10.1111/1365-2656.13156)
- Mourier J, Bass NC, Guttridge TL, Day J, Brown C. 2017 Does detection range matter for inferring social networks in a benthic shark using acoustic telemetry? *R. Soc. Open Sci.* **4**, 170485. (doi:10.1098/rsos.170485)

10. Wilson DM, Brownscombe JW, Krause J, Krause S, Gutowsky LFG, Brooks EJ, Cooke SJ. 2015 Integrating network analysis, sensor tags, and observation to understand shark ecology and behavior. *Behav. Ecol.* **26**, 1577–1586. (doi:10.1093/beheco/arv115)
11. Tinker MT, Benthall G, Estes JA. 2008 Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proc. Natl Acad. Sci. USA* **105**, 560–565. (doi:10.1073/pnas.0709263105)
12. Towner AV, Leos-Barajas V, Langrock R, Schick RS, Smale MJ, Kaschke T, Jewell OJD, Papastamatiou YP. 2016 Sex-specific and individual preferences for hunting strategies in white sharks. *Funct. Ecol.* **30**, 1397–1407. (doi:10.1111/1365-2435.12613)
13. Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, Sheldon BC. 2013 Individual personalities predict social behavior in wild networks of great tits (*Parus major*). *Ecol. Lett.* **16**, 1365–1372. (doi:10.1111/ele.12181)
14. Domeier ML, Nasby-Lucas N. 2008 Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico and identification of an eastern Pacific shared offshore foraging area. *Mar. Ecol. Prog. Ser.* **370**, 221–237. (doi:10.3354/meps07628)
15. Martin RA, Hammerschlag NH, Collier RS, Fallows C. 2005 Predatory behavior of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J. Mar. Biol. Assoc. UK* **85**, 1121–1135. (doi:10.1017/S002531540501218X)
16. Semmens JM, Kock AA, Watanabe YY, Shepard CM, Berkenpas E, Stehfest KM, Barnett A, Payne NL. 2019 Preparing to launch: biologging reveals the dynamics of white shark breaching behavior. *Mar. Biol.* **166**, 95. (doi:10.1007/s00227-019-3542-0)
17. Watanabe YY, Payne NL, Semmens JM, Fox A, Huveneres C. 2019 Hunting behavior of white sharks recorded by animal-borne accelerometer and cameras. *Mar. Ecol. Prog. Ser.* **621**, 221–227. (doi:10.3354/meps12981)
18. Anderson JM *et al.* 2021 Non-random co-occurrence of juvenile white sharks (*Carcharodon carcharias*) at seasonal aggregation sites in southern California. *Front. Mar. Sci.* **8**, 688505. (doi:10.3389/fmars.2021.688505)
19. Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Van Sommeren S, Kelly JT. 2001 The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar. Biol.* **138**, 617–636. (doi:10.1007/s002270000489)
20. Schilds A, Mourier J, Huveneres C, Nazimi L, Fox A, Leu ST. 2019 Evidence for non-random co-occurrences in a white shark aggregation. *Behav. Ecol. Sociobiol.* **73**, 138. (doi:10.1007/s00265-019-2745-1)
21. Huveneres C, Holman D, Robbins R, Fox A, Endler JA, Taylor AH. 2015 White sharks exploit the sun during predatory approaches. *Am. Nat.* **185**, 562–570. (doi:10.1086/680010)
22. Becerril-García EE, Bernot-Simon D, Arellano-Martínez M, Galván-Magaña F, Hoyos-Padilla EM. 2020 Evidence of interactions between white sharks and large squids in Guadalupe Island, Mexico. *Sci. Rep.* **10**, 17158. (doi:10.1038/s41598-020-74294-4)
23. Hoyos-Padilla EM, Klimley AP, Galván-Magaña F, Antoniou A. 2016 Contrasts in the movements and habitat use of juvenile and adult white sharks (*Carcharodon carcharias*) at Guadalupe Island, Mexico. *Anim. Biotelem.* **4**, 14. (doi:10.1186/s40317-016-0106-7)
24. Skomal GB, Hoyos-Padilla EM, Kukulya A, Stokey R. 2015 Subsurface observations of white shark *Carcharodon carcharias* predatory behavior using an autonomous underwater vehicle. *J. Fish Biol.* **87**, 1293–1312. (doi:10.1111/jfb.12828)
25. Chapple TK, Gleiss AC, Jewell OJD, Wikelski M, Block BA. 2015 Tracking sharks without teeth: a non-invasive rigid tag attachment for large predatory sharks. *Anim. Biotelem.* **3**, 14. (doi:10.1186/s40317-015-0044-9)
26. Farine DR. 2013 Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods Ecol. Evol.* **4**, 1187–1194. (doi:10.1111/2041-210X.12121)
27. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* **84**, 1144–1163. (doi:10.1111/1365-2656.12418)
28. Benaglia T, Chauveau D, Hunter DR, Young D. 2009 *mixtools*: An R package for analyzing finite mixture models. *J. Stat. Soft.* **32**, 1–29. (doi:10.18637/jss.v032.i06)
29. Jaime-Rivera M, Caraveo-Patino J, Hoyos-Padilla M, Galván-Magaña F. 2014 Feeding and migration habits of white shark *Carcharodon carcharias* from Isla Guadalupe inferred by analysis of stable isotopes $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. *Rev. Biol. Trop.* **62**, 637–647. (doi:10.15517/rbt.v62i2.7767)
30. Aquino-Baleyto M *et al.* 2021 Diving deeper into the underlying white shark behaviors at Guadalupe Island, Mexico. *Ecol. Evol.* **11**, 14 932–14 942. (doi:10.1002/ece3.8178)
31. 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. (doi:10.1098/rspb.2020.1063)
32. Papastamatiou YP, Mourier J, TinHan T, Luongo S, Hosoki S, Santana-Morales O, Hoyos-Padilla M. 2022 Data from: Social dynamics and individual hunting tactics of white sharks revealed by biologging. Dryad Digital Repository. (doi:10.5061/dryad.2v6wvpzq9)