

*Habitat-specific inter and intraspecific
behavioral interactions among reef sharks*

**Maria A. Sabando, Guillaume Rieucau,
Darcy Bradley, Jennifer E. Caselle &
Yannis P. Papastamatiou**

Oecologia

ISSN 0029-8549

Volume 193

Number 2

Oecologia (2020) 193:371-376

DOI 10.1007/s00442-020-04676-y

Your article is protected by copyright and all rights are held exclusively by Springer-Verlag GmbH Germany, part of Springer Nature. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



Habitat-specific inter and intraspecific behavioral interactions among reef sharks

Maria A. Sabando¹ · Guillaume Rieucou² · Darcy Bradley³ · Jennifer E. Caselle⁴ · Yannis P. Papastamatiou¹

Received: 16 September 2019 / Accepted: 28 May 2020 / Published online: 4 June 2020
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

Abstract

Behavioral interactions such as dominance are critical components of animal social lives, competitive abilities, and resulting distribution patterns with coexisting species. Strong interference competition can drive habitat separation, but less is known of the role of interference if agonistic interactions are weak. While most theoretical models assume interference abilities to be constant in an environment, few consider that the extent of interference can vary by habitat and change model predictions. Using baited underwater cameras, we show a consistent dominance status between two sympatric reef sharks at an uninhabited Pacific atoll. Blacktip reef shark (*Carcharhinus melanopterus*) and gray reef shark (*Carcharhinus amblyrhynchos*) relative abundance showed an inverse relationship to each other but the strength of this relationship varied by habitat. Reef shark relative abundance declined more rapidly in the presence of heterospecifics on forereef habitats as opposed to backreefs. In all habitats, gray reef sharks were more likely to bite bait cages than blacktips when both species were present, and appeared to be the dominant species. Intraspecific interactions were also apparent, with individual willingness to bite bait decreasing as the number of conspecifics increased. Gray reef sharks may exert differential control over blacktip foraging success in different habitats. Habitat-specific behavioral interactions may partially explain patterns of spatial separation between competing species where interference is weak.

Keywords Blacktip reef shark · Grey reef shark · BRUV · Competition · Dominance

Introduction

Spatial separation between and within species is seen throughout animal phyla, with drivers including both interference (including intraguild predation and territoriality) and

exploitation competition (Case and Gilpin 1974; Wakefield et al. 2013; Rebollo et al. 2017). While intraguild predation and strong interference competition (e.g., where one competitor attacks or kills another) plays an important role in spatial separation between species, the role of exploitation competition and/or weak interference is less clear. The predictions of ideal free distribution models where competitors are not equal differ based on the mechanisms by which competitive advantages manifest themselves (e.g., dominance, prey search times, or handling times, Holmgren 1995). When species differ in dominance, models predict that competitors will distribute themselves between a two patch system according to a (semi) truncated distribution, where the superior competitor is found in good habitats, while subordinate competitors can be found across habitat types, or only in low quality habitats (Holmgren 1995). There are many examples of dominance-driven habitat separation in birds and mammals, but these generally involve a high degree of interference or agonistic interactions (Robinson and Terborgh 1995; Pasch et al. 2013; Rebollo et al. 2017). However, when interference and agonistic interactions are

Communicated by Aaron J Wirsing.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-020-04676-y>) contains supplementary material, which is available to authorized users.

✉ Yannis P. Papastamatiou
ypapastamatiou@gmail.com

- ¹ Department of Biological Sciences, Florida International University, Miami, FL, USA
- ² Louisiana Universities Marine Consortium, Chauvin, LA, USA
- ³ Bren School of Environmental Science, University California Santa Barbara, Santa Barbara, CA, USA
- ⁴ Marine Science Institute, University California Santa Barbara, Santa Barbara, CA, USA

weak, dominance alone may not be sufficient for separation to occur (Papastamatiou et al. 2018). Instead, habitat separation may require dominance (or some other competitive ability) to vary by habitat, where different species have a habitat-specific competitive advantage (Cresswell et al. 2001; Humphries et al. 2001; Papastamatiou et al. 2018). However, rarely are dominance and/or behavioral interactions measured across habitat types.

There will also be intraspecific interactions and a key prediction of competition theory is that coexistence can occur if levels of intraspecific competition are greater than interspecific competition (Case and Gilpin 1974). Density-dependent intraspecific competition can also shape spatial separation between colonies and communities (Wakefield et al. 2013; Papastamatiou et al. 2018). While the contribution of intraspecific interactions to exploitation competition are clear, the dynamics of interactions between individuals may be more variable and range from positive social associations to strong interference. These interactions are again rarely considered or compared across habitats and generally considered to be constant within an ecosystem.

Sharks are common upper and meso-level predators in marine ecosystems. Habitat separation between sympatric species is often reported, but little is known about the mechanisms driving separation (Lea et al. 2016; Heupel et al. 2018; Papastamatiou et al. 2018). Studies of dominance between sharks are also rare, although interspecific comparisons suggest that dominance status may be determined by size or social cues, and that agonistic interactions are generally weak (Myberg and Gruber 1974; Ritter 2001; O'Shea et al. 2015; Papastamatiou et al. 2018; Brena et al. 2018). Two reef shark species at an uninhabited Pacific atoll demonstrate a semi-truncated distribution between habitat types, with larger gray reef sharks (*Carcharhinus amblyrhynchos*) primarily using forereef habitats (FR), while the smaller blacktip reef sharks (*Carcharhinus melanopterus*) are found across multiple

habitat types but more abundant in backreefs (BR). There is further spatial separation within the habitat they share, with gray reefs using deeper FR habitats than blacktips (Papastamatiou et al. 2018). A simulation model suggested that these distribution patterns could be driven by habitat-specific competitive advantages and/or dominance between the two species, with gray reef sharks having an advantage in the FR and blacktip reef sharks in the BR and lagoons (Papastamatiou et al. 2018). While there was evidence of gray reef sharks being dominant over blacktips, the dynamics of their interactions between habitats were not explored. As habitat-specific behavioral interactions may be a critical component of competition models, we explore the differences in behavior separated by habitat. Our goals were to (1) determine how one species influenced the behavior or presence of the other, (2) evaluate how these interactions differed by habitat, (3) evaluate if intraspecific interactions occur and if they vary by habitat. We predict that gray reef sharks will be dominant in FR habitats, while blacktips will show dominance or competitive advantages in the BR.

Methods

Study site

Palmyra Atoll (N 5°53', W 162°05') is located in the central Pacific Ocean and is uninhabited other than a small research station. Palmyra has been a US Federal Wildlife Refuge since 2001 with minimal human impacts, and consequently, large shark populations (Bradley et al. 2017a). The atoll consists of four basic marine habitat types; steep forereefs (FR) which lead to pelagic waters, shallower backreefs (BR) with high coral cover, and deep and murky lagoons which are surrounded by sandflats (Fig. 1).

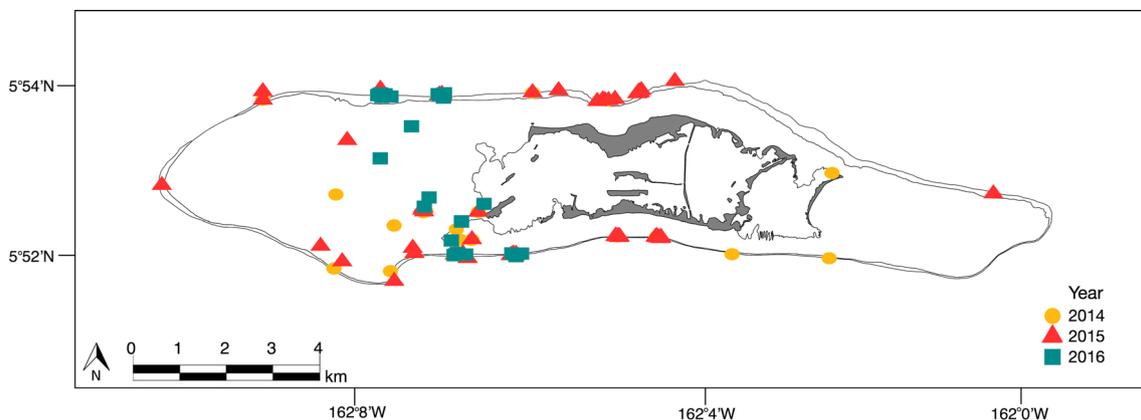


Fig. 1 A map of Palmyra atoll, showing the location of BRUV deployments, colored by year

Behavioral observations

Behavioral interactions and relative abundance were quantified using baited remote underwater video (BRUVs), consisting of a PVC frame and GoPro camera. An arm connects to a canister of bait ($0.5 \text{ kg survey}^{-1}$) that is within frame of the video. BRUVs were deployed throughout the FR, BR, and lagoons each summer from 2014–2016. Each BRUV was deployed for 90-min, with only the first 60 min of footage analyzed. We used the first hour of footage because shark (and other predators) interest in bait has been shown to decline greatly after an hour of soak time (Mclean et al. 2011). Survey depths ranged between 1 and 30 m. No gray reef sharks were ever seen on lagoon BRUVs so these were removed from analysis. BRUVs were deployed throughout the day, but each location was originally sampled at multiple times of day to test for diel effects, which were not present in the data (Bradley et al. 2017b). Relative shark abundance was measured as MaxN (maximum number of sharks in one frame of each 10 min period during the 60 min video; Cappo et al. 2004), to account for repeat observations of the same individuals. Additional behaviors recorded included biting of the BRUV and actively chasing away other sharks. Videos were analyzed using JWatcher 1.0 (Blumstein et al. 2006).

Data analysis

The relative abundance of the two species between the habitat types was compared using nonparametric Kruskal–Wallis tests as the assumption of the homogeneity of variance was violated. We determined how the number of gray reef sharks in both habitat types influenced blacktip reef shark MaxN, using a linear mixed effects model (LME) with habitat type, gray reef shark MaxN and the interaction between these two included as fixed effects. Date of the deployment was included as a random effect in the LME to control for pseudo-replication. We tested whether the two species differed in their propensity to bite the BRUV in each habitat type using a Pearson Chi-square test. Here we calculated the percentage of observations where a shark bit the bait. An “observation” consists of any time when a shark is observed in frame. Observations are then further classified as “monospecific observations” (i.e., a single shark species), “heterospecific observations” (i.e., at least two sharks of different species observed in the same frame), and “biting events” (i.e., a shark of either species bites the BRUV, with species identity recorded). We explored interspecific interactions by testing whether the likelihood of a shark biting the BRUV differed when only a single species was present (monospecific) vs. if heterospecific individuals were present at the same time, and how this varied by habitat type, using a Pearson Chi-square test. LMEs were performed using the

nlme package in R 3.12 (The R Foundation for Statistical Computing; www.r-project.org).

Results

In total, we deployed BRUVs at 74 sites (80 h analyzed, $N_{\text{observations}} = 748$) within the forereefs (FR) and 22 sites (22 h analyzed, $N_{\text{observations}} = 193$) within the backreefs (BR). The two species of sharks used the two habitats differently, with MaxN of blacktips relatively higher on the BR than on the FR (Kruskal–Wallis test: $\chi^2 = 26.78$, $df = 1$, $P < 0.0001$; BR = 1.44 ± 0.06 ; FR = 0.98 ± 0.03 ; mean \pm SE), while the opposite was true for gray reef sharks (Kruskal–Wallis test: $\chi^2 = 35.04$, $df = 1$, $P < 0.0001$; BR = 0.25 ± 0.49 ; FR = 0.59 ± 0.71 ; mean \pm SE). Overall, MaxN for blacktip reef sharks on the FR was higher than that for gray reef sharks on the FR. There was a significant inverse relationship between blacktip reef and gray reef shark MaxN; with decreasing values for one species as the other increased ($F = 35.59$; $P < 0.0001$, Fig. 2a). However, the strength of the relationship differed between the two habitats, with a stronger negative relationship observed on the FR (number of gray reef sharks \times habitat: $F = 6.56$; $P = 0.01$; Fig. 2a).

If only one species was present (monospecific situation), gray reef sharks bit the BRUVs more often than blacktips when on the FR (51.75%, $n_{\text{observations}} = 228$ and 17.57%, $n_{\text{observations}} = 387$, respectively), and when on the BR (gray reef sharks: 37.5%, $n_{\text{observations}} = 16$; blacktip reef sharks: 20.95%, $n_{\text{observations}} = 148$). When the propensity to bite the bait was compared under heterospecific conditions (i.e., both species present), there was an effect of species ($\chi^2 = 8.86$, $P = 0.003$) but no effect of habitat ($\chi^2 = 0.77$, $P = 0.38$) or an interaction between the two ($\chi^2 = 1.89$, $P = 0.17$). When both species were present, gray reef sharks bit the BRUVS more often than blacktip reef sharks in both habitats (BR: gray reef sharks: 85%, $n_{\text{observations}} = 20$; blacktip reef sharks: 33.33%, $n_{\text{observations}} = 6$; FR: gray reef sharks: 60.87%, $n_{\text{observations}} = 69$; blacktip reef sharks: 39.29%, $n_{\text{observations}} = 28$). Observed behavioral interactions consisted of one shark approaching the bait, but then ‘giving-way’ to another approaching individual. As previously reported, this interaction was only observed on 17 occasions, and in 75% of those, blacktips gave way to gray reef sharks (Papastamatiou et al. 2018).

Within an intraspecific context (i.e., only one species present), for both species, an increase in the number of conspecifics reduced the chance of sharks biting the bait (Fig. 3). The percentage bites on the BR by blacktips decreased from 24.8% ($n = 22$) to 12.5% ($n = 2$) as the number of conspecifics present increased from 1 to 3. On the FR, the percentage bites decreased from 19.5% ($n = 51$) to 9.1% ($n = 3$) as the number of blacktips increased from 1 to 3. Similarly, for gray reef sharks, the percentage bites on the BR decreased from 37.5% ($n = 6$)

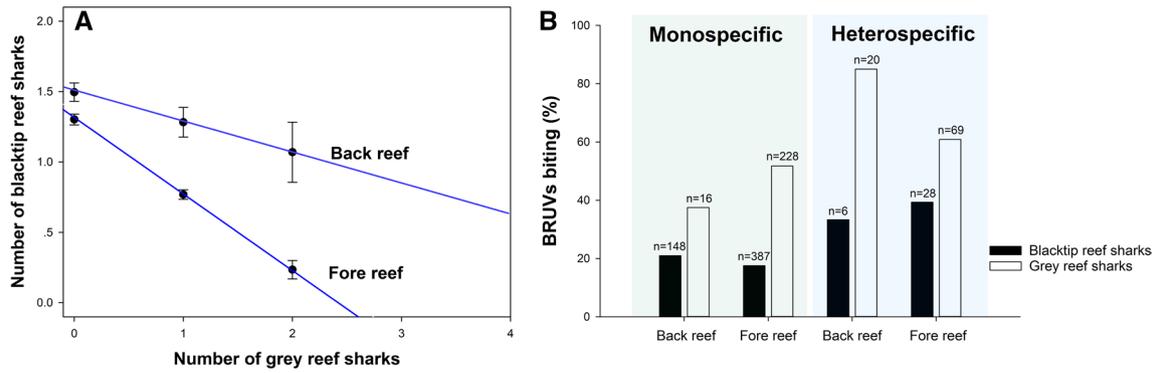


Fig. 2 a Relationship between relative abundance of gray reef sharks and blacktip reef sharks seen on BRUV deployments, in both forereef and backreef habitats. Error bars are standard errors. Data is based on MaxN. b Percentage of observations which were classified

as ‘biting events’ when there were no heterospecifics present (monospecific) and when the other species were present (heterospecific), for both habitat types. Blacktip reef sharks = black bars, gray reef sharks = white bars

Discussion

Intra and interspecific competitive interactions influence reef shark relative abundance, but the strength of these relationships are dependent on habitat type. While there were minimal agonistic interactions between sharks, the presence of other individuals was enough to reduce the propensity to remain within observable range of the bait, but not to bite the bait. There were several lines of evidence that there are interspecific interactions between the species, with gray reefs dominant over blacktip reef sharks, through weak interference. We previously showed that although rare, when individuals of both species approached the bait at the same time, blacktips would primarily ‘give-way’ to gray reefs (75% of interactions, Papastamatiou et al. 2018). While there was no observed aggression between the species, gray reef sharks were more likely to bite the bait in general, and may be more aggressive or bold (see also Hobson 1963). Here we also show that there is an inverse relationship between the relative abundance of blacktip and gray reef sharks observed via BRUVs, although the strength of this relationship varies by habitat. Similar patterns of dominance between species, where agonistic interactions are weak (or not observed) but one species’ foraging rate decreases in the presence of the other, have been seen in a wide range of animals including between sharks and dolphins (Acevedo-Gutiérrez 2002), wolves and bears (Tallian et al. 2017), and sympatric ant species (Sanders and Gordon 2003).

Under monospecific conditions (only one species was present), an increase in conspecifics caused a decline in biting propensity, for both blacktip and gray reef sharks. These results are different than those for non-social lemon sharks, where the rate of agonistic interactions and time spent adjacent to an artificial bait station increased as shark numbers increased (Brena et al. 2018). Lemon sharks appeared to use social cues to assess other individuals and decide to

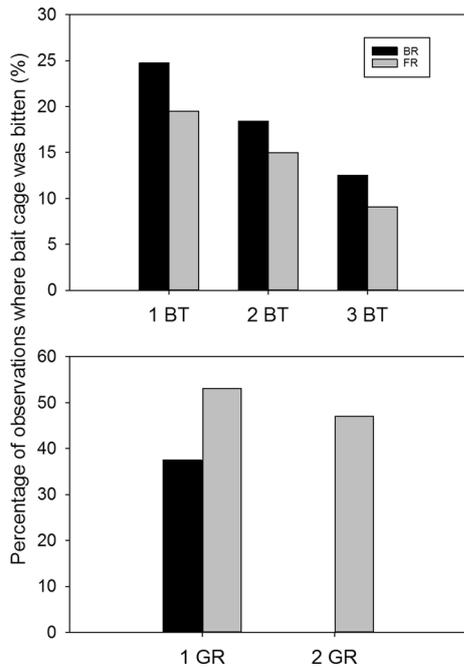


Fig. 3 Intraspecific observations highlighting the effects of blacktip reef (BT, a) or gray reef shark (GR, b) numbers on propensity to bite cages. Shown are the percentage of observations classified as biting events when a single individual was present vs. with 2–3 conspecifics, in backreef (BR) and forereef (FR) habitats

to 0% as the number of conspecifics increased from 1 to 2. On the FR, percentage bites decreased from 53% (n=96) to 47% (n=16) as the number of gray reef sharks increased from 1 to 2 (Fig. 3).

concede or perform agonistic behaviors (Brena et al. 2018). High levels of intraspecific competition have been inferred for both species of reef shark at Palmyra, based on the large population sizes, slow individual growth rates, and patterns of space use (Papastamatiou et al. 2009, 2018; Bradley et al. 2017c). Here we show one potential mechanism by which intraspecific competition may manifest itself, in addition to exploitation competition, through weak interference interactions. Our small sample sizes preclude a rigorous statistical analysis of these relationships or how they may also vary with habitat type, although they also appeared to be present, particularly for gray reef sharks on the BR. Both species of shark show evidence of being gregarious, hence there must be other benefits to sharks being in groups, likely related to social foraging of some form (Mourier et al. 2012; Jacoby et al. 2016).

In both species, the propensity to bite bait appeared to increase when heterospecific individuals were present, although the change was more pronounced for gray reef sharks, and there was little effect of habitat. Hence, blacktip reef shark propensity to bite bait does not differ between the two habitats, but they are significantly more resistant (in terms of relative numbers) to increasing gray reef shark numbers when on the BR. Previous simulations predicted that even small differences in habitat-specific dominance or competitive advantages, are enough to drive habitat separation between the species (Papastamatiou et al. 2018). However, our initial hypothesis was rejected as gray reef sharks were still apparently the dominant species on the BR, hence additional factors must also play into observed habitat separation (e.g., gray reef foraging success may be reduced in BR habitats). At Kingman Reef, 60 km north of Palmyra, blacktip reef sharks are absent and gray reefs are still most abundant on the FR but are found in larger numbers in BR and lagoon habitats relative to those in Palmyra (Papastamatiou et al. 2018). Habitat properties alone clearly play an important role in resulting distribution patterns, but competitive interactions appear additive. Habitat-specific differences in competitive advantages may be driven by habitat features (e.g., colors, visibility, vertical relief) or may relate to other aspects such as risk effects (predation risk from larger species of shark may be higher on the FR).

Studies often assume that dominance relationships or competitive interactions are fixed within an ecosystem, whereas they may depend on prey type or habitat (Sanders and Gordon 2003; Humphries et al. 2001). Ant colonies have shown interspecific dominance rankings that are resource-dependent and vary based on the food type (e.g., dead insects vs. seeds) for which they are competing (Sanders and Gordon 2003). Captive and semi-natural experiments have provided evidence that the response to interference could be dependent on habitat resource density (Dolman 1995; Cresswell et al. 2001). Here, we show that the magnitude

of the response to interference between marine predators in a natural environment can also be habitat-specific. Exploitation competition or weak interference (i.e., competitors rarely engage in fights or kill each other) may not be enough to drive habitat separation between competing species without habitat-specific interactions or additional factors (e.g., abiotic preferences Randall 1978). Measuring behavioral interactions in large marine predators is difficult yet may be critical for understanding observed distribution patterns.

Acknowledgements We thank K. Davis and P. Carlson for assistance in the field and the entire staff of the Palmyra Atoll research station, TNC, and USFWS for their support. We also thank the two reviewers whose comments improved the manuscript. Research was conducted under US Fish and Wildlife permits #12533-14011 and #12533-15011. All animal surveys were approved by the IACUC of University California Santa Barbara (#856). This is contribution #193 from the Coastlines and Oceans Division of the Institute of Environment at Florida International University. This is publication number PARC-157 from the Palmyra Atoll Research Consortium (PARC).

Author contribution statement YPP, GR, and DB designed the study. MS and GR analyzed the data. YPP, MS and GR wrote the manuscript with input from DB and JEC. YPP, DB, JEC performed the fieldwork.

Funding Funding was provided by Save Our Seas Foundation (to DB), Marisla Foundation grant (to JEC), and MARC U*STAR and the FIU Ronald E. McNair Post-Baccalaureate Achievement Program (to MS).

References

- Acevedo-Gutiérrez A (2002) Interactions between marine predators: dolphin food intake is related to number of sharks. *Mar Ecol Prog Ser* 240:267–271
- Blumstein DT, Daniel JC, Evans CS (2006) JWatcher 1.0. <http://www.jwatcher.ucla.edu>
- Bradley D, Conklin E, Papastamatiou YP, McCauley DJ, Pollock K, Pollock A, Kendall BE, Gaines SD, Caselle JE (2017a) Resetting predator baselines in coral reef ecosystems. *Sci Rep* 7:43131
- Bradley D, Papastamatiou YP, Caselle JE (2017b) No persistent behavioral effects of SCUBA diving on reef sharks. *Mar Ecol Prog Ser* 567:173–184
- Bradley D, Conklin E, Papastamatiou YP, McCauley DJ, Pollock K, Kendall BE, Gaines SD, Caselle JE (2017c) Growth and life history variability of the gray reef shark (*Carcharhinus amblyrhynchus*) across its range. *PLoS ONE* 12:e0172370
- Brena PF, Mourier J, Planes S, Clua EE (2018) Concede or clash? Solitary sharks competing for food assess rivals to decide. *Proc R Soc B* 285:20180006
- Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *J Exp Mar Biol Ecol* 302:123–152
- Case TJ, Gilpin ME (1974) Interference competition and niche theory. *Proc Natl Acad Sci* 71:3073–3077
- Cresswell W, Smith RD, Ruxton GD (2001) Absolute foraging rate and susceptibility to interference competition in blackbirds varies with patch conditions. *J Anim Ecol* 70:228–236
- Dolman PM (1995) The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenax nivalis*. *Oecologia* 102:511–514

- Heupel MR, Ledee EJI, Simpfendorfer CA (2018) Telemetry reveals spatial separation of co-occurring sharks. *Mar Ecol Prog Ser* 589:179–192
- Hobson ES (1963) Feeding behavior in three species of sharks. *Pac Sci* 17:171–194
- Holmgren N (1995) The ideal free distribution of unequal competitors: predictions from a behavior-based functional response. *J Anim Ecol* 64:197–212
- Humphries S, Ruxton GD, Van der Meer J (2001) Unequal competitor ideal free distributions: predictions for differential effects of interference between habitats. *J Anim Ecol* 70:1062–1069
- Jacoby DMP, Papastamatiou YP, Freeman R (2016) Inferring animal social networks and leadership: applications for passive monitoring arrays. *J R Soc Interface* 13:20160676
- Lea JSE, Humphries NE, von Brandis RG, Clarke CR, Sims DW (2016) Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *Proc R Soc B* 283:20160717
- Mclean DL, Harvey ES, Meeuwig JJ (2011) Declines in the abundance of coral trout (*Plectropomus leopardus*) in areas closed to fishing at the Houtman Abrolhos Islands, Western Australia. *J Exp Mar Biol Ecol* 406:71–78
- Mourier J, Vercelloni J, Planes J (2012) Evidence of social communities in a spatially structured network of a free-ranging shark species. *Anim Behav* 83:389–401
- Myberg AA, Gruber SH (1974) The behavior of the bonnethead shark, *Sphyrna tiburo*. *Copeia* 2:358–374
- O'Shea OR, Mandelman J, Talwar B, Brooks EJ (2015) Novel observations of an opportunistic predation event by four apex predatory sharks. *Mar Fresh Behav Physiol* 48:374–380
- Papastamatiou YP, Caselle JE, Friedlander AM, Lowe CG (2009) Distribution, size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus* at Palmyra Atoll: a predator-dominated ecosystem. *J Fish Biol* 75:647–654
- Papastamatiou YP, Bodey TW, Friedlander AM, Lowe CG, Bradley D, Weng K, Priestley V, Caselle JE (2018) Spatial separation without territoriality in shark communities. *Oikos* 127:767–779
- Pasch B, Bolker BM, Phelps SM (2013) Interspecific dominance via vocal interactions mediates altitudinal zonation in neotropical singing mice. *Am Nat* 182:161–173
- Randall JA (1978) Behavioral mechanisms of habitat segregation between sympatric species of *Microtus*: habitat preference and interspecific dominance. *Behav Ecol Sociobiol* 3:187–202
- Rebollo S, Martinez-Hestekamp S, Garcia-Salgado G, Perez-Camacho L, Fernandez-Pereira JM, Jennes J (2017) Spatial relationships and mechanisms of coexistence between dominant and subordinate top predators. *J Avian Biol* 48:1226–1237
- Ritter EK (2001) Food-related dominance between two carcharhinid shark species, the Caribbean reef shark (*Carcharhinus perezi*) and the blacktip shark (*Carcharhinus limbatus*). *Mar Fresh Behav Physiol* 34:125–129
- Robinson SK, Terborgh J (1995) Interspecific aggression and habitat selection by Amazonian birds. *J Anim Ecol* 64:1–11
- Sanders NJ, Gordon DM (2003) Resource-dependent interactions and the organization of desert ant communities. *Ecology* 84:1024–1031
- Tallian A et al (2017) Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proc R Soc B* 284:20162368
- Wakefield ED et al (2013) Space partitioning without territoriality in gannets. *Science* 341:68–70