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Commentary on: dominance and subordination in the smooth dogfish, *Mustelus canis* (Allee & Dickenson, 1954)

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Abstract

In, 1954, Warder C. Allee and Joshua C. Dickinson decided to establish that "dominance-subordination" hierarchies are present in the Chondrichthyan phylogenetic line. To do so, they confined sixteen fished smooth dogfish (*Mustelus canis*) in tanks and observed their behaviour. They found neither competition over food, in spite of starving the animals for up to six days at times, nor any clear example of aggression, though it is through aggressive actions that such hierarchies are, by definition, established. They therefore used collision avoidance to support their hypothesis that the sharks had established a rigid size-dependent dominance-subordinate hierarchy, and claimed to have established that such hierarchies are present in Chondrichthyans. However, ethological studies since then have not identified the hierarchies in elasmobranchs that this study claims to be present, but they have found that smaller sharks tend to avoid colliding with larger individuals, which is the simplest explanation for their observations.

Keywords

sharks, shark behaviour, shark dominance-subordination hierarchies, shark social behaviour.

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1. Introduction

In, 1954, Warder C. Allee & Joshua C. Dickinson (1954) decided to test a shark species to see if dominance-subordination hierarchies, which are common in the Osteichthyan phylogenetic line, are present in the Chondrichthyan line of vertebrates. At the time, little was known about shark behaviour, so no evidence had been gathered that might oppose their idea. The experiment they performed failed to produce the expected results, but they concluded that they had found a "dominance-subordinance [sic] hierarchy" in Chondrichthyes, anyway, with neither further testing nor analysis.

The dominance-subordination hierarchy is defined as: "...an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation. The status of the consistent winner is dominant and that of the loser subordinate." (Drews, 1993).

Thorleif Schjelderup-Ebbe (1922) first described such a society in chickens (*Gallus gallus*) and thus the chicken is the model for the dominance-subordination hierarchy (Drews, 1993). But, far from providing a generalized example of animal behaviour, chickens are highly specialized, heavy-bodied birds that evolved to walk through the predator-filled jungles of Asia. They display complex territorial behaviour (Porcher, 2020) and the aggression that comes with it (Lorenz, 1963).

Territorial behaviour appears to have developed as a way for life forms to successfully occupy and share finite habitats and resources (Lorenz, 1963). It involves the establishment of a safe place to rest and raise young, and a border, where invaders are repelled. However, Chondrichthyans neither sleep to rest like other vertebrates, nor give their young post-natal care. Their phylogenetic line diverged from ours at least 440 000 000 years ago (Coates et al., 2018; Andreev et al., 2020), before the common ancestor of fish, birds, reptiles and mammals appeared, and their behavioural repertoire evolved in a three dimensional environment in which territory presumably lacked the significance it holds for so many terrestrial species. Indeed, researchers including Allee & Dickinson (1954), have repeatedly noted the absence of territorial behaviour in those species under study (Myrberg & Gruber, 1974; Fallows et al., 2013; Papastamatiou et al., 2018; Zemah-Shamir et al., 2022). Further, though a variety of context-specific agonistic displays have been documented in many shark species (Martin, 2007; Klimley et al., 2023, this issue), to date there has been no account of sharks fighting (Porcher, 2023, this issue).

However, as a result of the claim of Allee & Dickinson (1954), their experiment has been cited since as having established dominance-subordination hierarchies in sharks (e.g., Myrberg & Gruber, 1974; Gauthreaux, 1978; Ritter, 2001; Martin, 2007; Maljkovic & Coté, 2011; Brena et al., 2015; Pini-Fitzsimmons et al., 2021).

The idea has spread to the general public, shark divers, aquarium employees, and others who work with sharks. Though most wild shark observation is now done through remote sensing, and their social networks are interpreted and generated by computer software (Mourier et al., 2019), the idea remains that a rigid social structure and dominance-subordination hierarchies are well-established in sharks.

Yet as of this writing, no remotely convincing demonstration of a true size-dependent dominance-subordination hierarchy in any species of Chondrichthyan has been presented.

2. The experiment claiming to have established dominance-subordination hierarchies in sharks

Allee & Dickinson (1954) began their paper by stating that before their experiment on the smooth dogfish, they had asked John S. MacGregor, former curator of the Marine Studios at St. Augustine, whether he had seen evidence for such a hierarchy among the several sharks on display in their aquarium. He reported that he had seen no evidence of dominance-subordination reactions among them.

To support their hypothesis, Allee & Dickinson chose sixteen fished dogfish, put them in two tanks, each $366 \times 366 \times 168$ cm and recorded their behaviour during 26 observation sessions totalling 26 h. The sharks varied in size between 54.5 to 121.8 cm in total length, so the large ones were more than twice the length, and several times the volume of the small ones, which, at that size, were juveniles.

The smooth dogfish moves in packs or schools (Murdy et al., 1997) and is an active bottom feeder. It is found on the western continental shelves of both the North and South Atlantic Oceans and ranges from shallow inshore waters to about, 200 m, though it has been found as deep as 579 m (Compagno, 1984).

The water depth in the tanks was kept at a depth of 122 and at times lowered to 46 cm for easier viewing, so the environment into which the wild sharks were put was extremely confined, especially for such active animals. The length/breadth of the tanks were just 3 times the length of the largest sharks, and when the water level was lowered, the depth would scarcely allow them to pass over and under each other. Yet this unnatural confinement in shallow water, and the severe reduction of the volume available to the sharks when the depth was reduced, was not taken into consideration in the experiment.

Studies of a variety of species of sharks in the field including spiny dogfish (*Squalus acanthias*) (Rago et al., 1998) as well as scalloped hammerheads (*Sphyrna lewini*) (Klimley, 1981, 1987), white sharks (*Carcharodon carcharias*) (Robbins, 2007), the shortfin mako (*Isurus oxyrinchus*) (Mucientes et al., 2009), sandbar (*Carcharhinus plumbeus*) and dusky (*Carcharhinus* obscurus) sharks (Zemah-Shamir et al., 2022), and blacktip reef sharks (*Carcharhinus melanopterus*) (Papastamatiou et al., 2009; Mourier et al., 2012; Porcher, 2023 this issue) have found that species across at least three out of the eight existing orders of sharks display segregation according to sex, size, and age. Thus, it is reasonable to speculate that these fished animals, who do live naturally in aggregations (Murdy et al., 1997), likely came from different, segregated fractions of the population, which would not interact closely in nature.

Further, in a small tank, no shark who wanted to escape the proximity of another could do so, and no shark who wanted to establish a region for him or herself, could be rid of the others. In a species with a dominance-subordination hierarchy, such a situation would facilitate high levels of aggression, yet, in spite of active efforts by the researchers to provoke competition for food among the sharks, they were unable to do so.

They wrote: "On no occasion did we see any action that we felt could be objectively described as active competition, although in several instances the fish were starved for 1–6 days." They saw no signs of territorial behaviour and described only six incidents they believed to involve aggression.

One was a feeding incident in which a small dogfish snatched up a squid and was followed by a larger individual. As the smaller shark swam off with its food, it became entangled in some cords in the tank, and there was a "flurry of activity". In spite of this difficulty, it was still in possession of its squid when it got free. So the larger shark failed to get the squid from the small one, in spite of its entanglement with the cords. This alone provides evidence of a lack of dominance-subordination among the sharks.

A second incident involved some of the smaller sharks at the food. It seemed to the observer that the smallest one physically pushed a larger one away. This observation, too, directly contradicts the idea that larger sharks were dominating smaller ones.

Another of the ‘aggressive incidents’ involved a shark shaking its head, which is common among feeding sharks (Klimley et al., 2023 this issue). While the Lateral head-shake has been seen to be used as an agonistic display, (Myrberg & Gruber, 1974; Klimley, 2023a; Klimley et al., 2023 this issue) it is the usual method sharks use to saw out a mouthful from a piece of food too large to swallow (Klimley et al., 2023 this issue). The observer said that at the same moment, a shark in front of the head-shaker moved away. Maybe the other shark moved away because head-shaking is usually followed by forward acceleration in feeding sequences. Maybe not. But the gesture was seen only once, and its categorization as an aggressive incident, though no subsequent conflict took place, was unconfirmed by any other similar observations (Allee & Dickinson, 1954).

Another of the ‘aggressive incidents’ involved one of the sharks lying on the bottom of the tank “trying to make contact with” another shark as it swam overhead. However, it did not make contact with the other shark, so the categorization as an aggressive incident is questionable.

The other two incidents involved a head-on collision in which neither shark gave way to the other, and a moment in which two sharks jostled against each other.

In nearly every case, the observer mentioned being unsure as to what he had seen, or what had actually taken place. Not one clear incidence of aggression involving dominance-subordination was seen, though the stated purpose of the experiment was to establish just such behaviour.

The situational predicament of the sharks, who had recently been able to soar in a straight line as far as they wished, and were now compelled to continuously turn, with many other individuals, in a small tank to avoid bodily harm, was mentioned by the researchers in descriptions of the way the animals often swam along the walls. They stated that several of the fish lived until the end of the experiment in apparently good condition, which suggests that quite a few did not, so confinement in these tanks represented a life-threatening, and in some cases lethal, experience for the animals. In spite of this, no competitive behaviour was observed.

The researchers seemed surprised by the dogfishes' willingness to touch each other. They stated: "We did not even try to record all the large number of graceful mutual evasions whose pattern makes a vivid memory in thinking over our observations. The dogfish turned so smoothly in keeping away from one another that the avoidances were not always obvious. Fish often approached and by-passed each other without noteworthy turning by either. Sometimes two dogfish do touch each other."

They wrote that much of the time the sharks avoided collisions with each other mutually, without any sign of deference, submission, or dominance: "Quite often, as two fish came near each other from opposite directions, both animals would turn aside slightly and pass without touching. Judgement of such turnings is made difficult however, in that the animals are continually making spontaneous turns in swimming and the possibility exists that the turns would have occurred in the absence of the other animal."

And: "In some 50–75 man-hours of observation we saw and dictated comments concerning 374 instances in which we thought one dogfish made greater effort to avoid contact than did the other of a possible contact pair, whereas we saw literally thousands of examples of graceful, curving swimming patterns by means of which each fish swam along an unobstructed course."

Their specification that many "mutual evasions" were not counted throws doubt on the fraction of evasions that they did count. Their decision to include, or not to include, an observation in their counts of evasions was therefore subjective, not objective, which could well have slanted their results. Indeed, the way the sharks mutually avoided collisions with each other much of the time, without any sign of deference, submission, or dominance, contradicts the idea of a dominance-subordination hierarchy affecting the shark assemblage.

However, Allee & Dickinson finished their article by reminding the reader that their experiment was done to provide information to back up the "logical expectation of dominance-subordination in the smooth dogfish,' and concluded that their experiment had established that dominance-subordination hierarchies are present in Chondrichthyes.

They state: "The data clearly show that in the great majority of instances when two fish of unequal size approach each other on courses that would result in collision if maintained, the smaller individual turns and avoids the larger much more frequently than the larger avoids the smaller."

Thus in collision avoidance, usually, but not always, the smaller individual turned aside. In one assessment, they found that in 14% of cases, it was the larger individual who turned aside to avoid a smaller one. Such a high proportion should indicate that while there seems to be a tendency for smaller sharks to avoid colliding with larger ones, that is by no means certain. In dominance-subordination hierarchies, the place in the hierarchy holds true for all encounters, not just some of them. Neither is there an explanation of how the researchers made the leap from collision avoidance to dominance and subordination, since the mechanism by which the dominance was enforced was not identified.

The findings of Allee & Dickinson, therefore, suggest that dogfish do *not* spontaneously establish a dominance-subordination hierarchy, yet they made no further studies to try to determine what sort of society these small, cold-water sharks might actually have.

3. Subsequent studies

Subsequent studies of elasmobranchs have repeatedly noted the almost complete lack of intra-specific aggression (Springer, 1967; Myrberg & Gruber, 1974; Sperone et al., 2010, 2012; Fallows et al., 2013; Porcher, 2023 this issue) and to this date there is no report of sharks fighting (Porcher, 2023 this issue).

Myrberg & Gruber (1974) studied the behaviour of wild-caught bonnethead sharks (*Sphyrna tiburo*), also suddenly confined in an enclosure, although the aquarium they used was much larger than the tanks used by Allee & Dickenson (1954). They, too, should have seen the formation of the alleged dominance-subordination hierarchy through repeated agonistic interactions among the bonnethead sharks but they did not. They wrote: "preliminary observations pointed to some social organization among the bonnethead sharks, but its characterization appeared, at first, to be impossible."

They eventually used the same method as Allee & Dickinson (1954), noting which shark Gave-way to avoid a collision, and found that smaller sharks usually Gave-way first. They noted no signs of territorial behaviour and qualified: "Our meagre knowledge forces caution, however, in assigning causation of such movements to intervening variables such as aggression, flight, food deprivation, maintenance or courtship. Quantitative and comparative data must be gained in the majority of cases before reasonable interpretations can be derived from hypothetical correlates."

Their speculations veered off-topic when they suggested that a reason that the big females might Give-way to smaller males was due to suffering their bites during mating. As noted above, it has been found in species from three out of eight orders of sharks that male/female individuals naturally segregate (Klimley, 1981, 1987; Rago et al., 1998; Robbins, 2007; Mucientes et al., 2009; Papastamatiou et al., 2009; Zemah-Shamir et al., 2022), so the bonnethead sharks' behaviour might have been altered by their close confinement with members of the opposite sex. Further, the absence of any observed tactic that enforced the supposed dominance-subordination was not explained.

Klimley's (1981) pioneering observations of the tight swirling of an immense school of hammerhead sharks around a sea-mount provide a glimpse of wild sharks socializing in nature. He wrote: "Aggression is very common in schools of hammerheads; most individuals are females which compete for a position at the center of the school. Larger females perform two approach-type behaviors, Hit and Cork-screw, within the schools and force smaller sharks to the edge as they perform two withdrawal-type behaviors, Acceleration and Head-shake. Males are rare and enter the schools, performing Torso-thrust. The differences between schools of hammerheads and those of small tcleosts are consistent with schooling in hammerheads functioning not to confer protection from predation, but to permit conspecifics to interact socially during the resting phase of their die1 cycle." Klimley (1981, 1987) provides a tantalizing glimpse of a shark society that researchers are yet to understand and fully describe.

There have been few ethological long-term observational studies of wild shark behaviour done, partly because the animals are considered too dangerous (Klimley, 2023a this issue) and partly because of the difficulties of observing large, swiftly moving animals underwater (Castro, 2016), so the details of their social lives remain virtually unknown (Mourier et al., 2019). Remote technology has been used increasingly in the past ten years to study their behaviour (Mourier et al., 2019). Some studies have found dyads with a variety of acquaintances as the basis for a social system: e.g., in bull sharks identified during eco-tourism in Fiji (Thibault et al., 2021), in juvenile lemon sharks (Gruber et al., 2011), around feeding aggregations in white sharks off

South Africa (Findlay et al., 2016) and in blacktip reef sharks (Porcher, 2023 this issue). Blacktips were observed to display the opposite behaviour to that seen in animals that form dominance-subordination hierarchies (Porcher, 2010, 2022b, 2023 this issue). They displayed neither territoriality nor conflict (including in the presence of food) and were repeatedly observed to be attracted to visitors to their ranges. Travelling dyads, triads, and gatherings paused to pursue high-velocity socializing with conspecifics they encountered along the way. Each individual had its preferred range and knew the other sharks in the vicinity, of which one or more were usually, but not always, travelling companions. Though in feeding situations they became more competitive as their numbers increased their density, no matter how much they accelerated in their efforts to get a crumb of food, they neither attacked each other, nor fought over it (Porcher, 2023 this issue). Other researchers have reported that when food is scarce, competition among the sharks present intensifies (Springer, 1967; Myrberg & Gruber, 1974; Brena et al., 2018). Their velocity increases (Myrberg & Gruber, 1974) and agonistic gestures are displayed more often in some species (Brena et al., 2018). The author was told (by dive monitors who fed sharks on the fore-reef of the study lagoon (2023)) of the intense competition among the blacktips and lemon sharks (*Negaprion acutidens*) for the few scraps of food they brought after more than two decades of feeding sharks daily in the same places (Boumedian Boucef, Philippe Molle, pers. commun., 2002). But such competition among animals from surrounding ranges, when meeting in dense numbers, provides no evidence of a rigid hierarchy of individuals in the community. Brena et al. (2018) recorded and analysed the agonistic interactions among many of the same sicklefin lemon shark individuals, and specified that the dominance and submissive behaviour displayed in the incidental competition within and in the vicinity of feeding aggregations is neither size nor sex dependent. Some of the more dominant individuals studied were unwilling to submit to each other. The researchers felt that the word 'heterarchy' is more appropriate to use to describe the relationships between the sharks than 'hierarchy.' (In a heterarchy, any unit can govern or be governed by others, depending on circumstances, and, hence, no one unit dominates the rest.) Shark morphology could not predict the outcome of interactions and individuals established relatively stable relationships, apparently using social cues. This was particularly true of sharks who displayed similar agonistic and deferential actions. Brena et al (2018) noted that individuals that spent most time together displayed greater tolerance to each other and performed less agonistic behaviour. They considered it likely that the sharks had developed their relationships through interactions that started in the nursery, and that they were responding to each other as individuals. Firth et al. (2017) found that individual differences and inter-individual differences in social behaviour can explain the apparently complex organization of what is interpreted as social networks, which Brena et al (2018) considered to be probable. Porcher (2023) found the same type of situation among blacktip reef sharks; (2022a) provides a specific example of individuals influencing each other in a community over a period of several months.

Pini-Fitzsimmons et al. (2021) documented a complex heterarchy in the Smooth Stingray (*Bathytoshia brevicaudata*), the first study showing social organization in batoids. Social network analysis of the interactions of the stingrays around a food source showed that the social network was dominated by one individual who gained most access to the resource. In this case too, size did not predict dominance.

Studies at multi-species dive sites where sharks are fed daily have found that over long periods of time, certain species, such as bull sharks, tend to become more numerous, and that others tend to be pushed out (Ritter, 2001; Mourier & Planes, 2015). Such observations involve inter-specific shark competition in areas in which extra food appears over long periods of time, and though they do argue for better management of the largely unmonitored practise of using ‘shark feeding’ for commercial gain, they do not provide evidence of dominance-subordination hierarchies in shark communities. Such shark behaviour is likely correlated to the natural segregation of sharks of different species in a given habitat, studies of which have found complex interactions among the animals but neither rigid hierarchies nor territorial behaviour (Frisch et al., 2016; Heupel et al., 2018; Papastamatiou et al., 2018; Sabando et al., 2020; Zemah-Shamir et al., 2022).

4. Discussion

The establishment of a dominance-subordination hierarchy among sixteen sharks (Allee & Dickinson, 1954) would, by definition (Chase, 1982, Drews, 1993), have involved several agonistic incidents per shark as it established its place in the said hierarchy, but not one was seen. No mechanism by which the presumed dominance was enforced was found. Therefore, the criteria for such a hierarchy was not met by Allee & Dickinson's (1954) experiment. The observation that when tightly confined together, sharks of different sizes mutually avoid colliding with each other, and that smaller sharks make more effort to do so, by no means establishes dominance and subordination as it is defined in the literature.

This leads to the question of why, in the absence of aggression, the sharks would avoid each other. Avoiding collisions is to be expected in animals with their streamlined design, for, due to their mass and momentum, sharks are subject to high impact on collision. There were sixteen wild sharks of very different sizes confined in a tank in which the length and width was only three times the length of the largest sharks. Thus, the crowded animals, obliged to perpetually advance most of the time due to ram ventilation (Piiper et al., 1977) were forced to pay continuous attention to their swim-ways in order to avoid collisions. The laws of physics governing speed, mass, and momentum dictate that a small shark runs a much greater risk of bodily harm than a larger shark in any given collision, particularly since their vital organs are not protected by a bony skeleton. As the length of an animal increases, its mass increases as a function of its linear measurements *cubed*. Thus, a dogfish 50 cm long will weigh approximately 0.43 kg, while one 120 cm long will weigh 7.28 kg (wikifish). Although less than 2.5 times its length, the larger shark weighs 17 times what the small shark weighs. This point was not addressed by Allee & Dickinson (1954).

Near collisions are the usual cause of the Startle Response in blacktip reef sharks (Porcher, 2023 this issue), especially juveniles, and any close observation of wild sharks confronted with obstacles will swiftly reveal their care in collision avoidance.

The small sharks in this experiment were juveniles. Myrberg & Gruber (1974) noted that smaller sharks move more swiftly and actively than larger ones, stating that whenever lemon sharks (*Negaprion brevirostris*), silky sharks (*Carcharhinus falciformis*), and Caribbean reef sharks (*Carcharhinus perezi*), were seen, either in captivity or in nature, smaller individuals were more unpredictable in their activities than the larger sharks. They would rapidly approach and withdraw from a strange object, had higher rates of turning, swerving and manoeuvring compared to larger members of the species, and more swiftly changed speed and direction. Porcher (2023 this issue) observed through long-term study that shark juveniles of several species are extremely vigilant and nervous in unknown situations, always ready to flee. They have a faster reaction time as well as a self-protective instinct to stay out of the way of larger predators (Guttridge et al., 2012).

The principal of Occam's razor states that the simplest explanation is the most likely. The wish to avoid bodily harm by smaller sharks — self protection — is a basic instinct that fully explains Allee & Dickinson's observations, and is much more plausible than the idea that a complex analysis about its place in society is taking place in the mind of the smaller shark. Indeed, how each shark understood that the size of its own body was smaller than that of an approaching shark is not addressed, and would necessarily involve a level of self-awareness (Lage et al., 2022) as well as the capacity to treat other sharks as individuals. Neither of these were established.

4.1. Conclusions

A tendency to associate with others of about the same size and age has been documented in a variety of shark species including dogfish (Rago et al., 1998) since Allee & Dickinson performed their experiment seventy years ago. Thus, in tightly confining many dogfish of different ages, the researchers took their natural behaviour out of its context. Regardless, they saw no territorial behaviour and no identifiable, repeated, agonistic behaviour. Not only does this indicate that the animals did not establish a dominance-subordinate hierarchy (Chase, 1982; Drews, 1993), but it suggests that the dogfishes, and likely other species too, have very different societies from those with which we are familiar in terrestrial species, as other researchers (Brena et al, 2018; Mourier et al., 2019; Pini-Fitzsimmons et al., 2021; Porcher, 2022a) have begun to document. The study of wild shark societies is likely, therefore, to be richly rewarding for future researchers.

References

Allee, D.G. & Dickenson, J.C. (1954). Dominance and subordination in the smooth dogfish, *Mustelus canis* (Mitchell). — Physiol. Zool. 27: 356-364.

Andreev, P.S., Zhao, W., Wang, N.-Z., Smith, M.M., Li, Q., Cui, X., Zhu, M. & Sansom, I.J. (2020). Early Silurian chondrichthyans from the Tarim Basin (Xinjiang, China). — PLoS ONE 15: e0228589. DOI:10.1371/journal.pone.0228589.

Brena, P.F., Mourier, J., Planes, S. & Clua, E.E. (2015). Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales. — Mar. Ecol. Prog. Ser. 538: 273-283.

Brena, P.F., Mourier, J., Planes, S. & Clua, E.E. (2018). Concede or clash? Solitary sharks competing for food assess rivals to decide. — Proc. Roy. Soc. Lond. B: Biol. Sci. 285: 20180006. DOI:10.1098/rspb.2018.0006.

Castro, J.I. (2017). The origins and rise of shark biology in the, 20th century. — Mar. Fish. Rev. 78: 14-33.

Chase, I.D. (1982). Dynamics of hierarchy formation: the sequential development of dominance relationships. — Behaviour 80: 218-239. DOI:10.1163/156853982X00364.

Coates, M.I., Finarelli, J.A., Sansom, I.J., Andreev, P.S., Criswell, K.E., Tietjen, K., Rivers, M.L. & La Riviere, P.J. (2018). An early chondrichthyan and the evolutionary assembly of a shark body plan. — Proc. Roy. Soc. Lond. B: Biol. Sci. 285: 20172418. DOI:10.1098/rspb.2017.2418.

Compagno, L.J.V. (1984). FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes. — FAO Fish. Synop. 125: 251-655.

Drews, C. (1993). The concept and definition of dominance in animal behaviour. — Behaviour 125: 283-313.

Fallows, C., Gallagher, A.J. & Hammerschlag, N. (2013). White sharks (*Carcharodon carcharias*) scavenging on whales and its potential role in further shaping the ecology of an apex predator. — PLoS ONE 8: e60797. DOI:10.1371/journal.pone.0060797.

Firth, J.A., Sheldon, B.C. & Brent, L.J.N. (2017). Indirectly connected: simple social differences can explain the causes and apparent consequences of complex social network positions. — P. Roy. Soc. B-Biol. Sci. 284: 20171939. DOI:10.1098/rspb.2017.1939.

Frisch, A.J., Ireland, M., Rizzari, J.R., Lönnstedt, O.M., Magnenat, K.A., Mirbach, C.E. & Hobbs, J.-P.A. (2016). Reassessing the trophic role of reef sharks as apex predators on coral reefs. — Coral Reefs 35: 459-472. DOI:10.1007/s00338-016-1415-2.

Gauthreaux Jr, S.A. (1978). The ecological significance of behavioral dominance. — In: Social behavior (Patrick, P., Bateson, G. & Klopfer, P.H., eds). Springer, New York, NY, p. 17-54.

Guttridge, T., Gruber, S., Franks, B., Kessel, S., Gledhill, K., Uphill, J., Krause, J. & Sims, D. (2012). Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. — Mar. Ecol. Prog. Ser. 445: 279-291. DOI:10.3354/meps09423.

Heupel, M.R., Lédée, E.J.I. & Simpfendorfer, C.A. (2018). Telemetry reveals spatial separation of co-occurring reef sharks. — Mar. Ecol. Prog. Ser. 589: 179-192.

Klimley, A.P. (1987). The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. — Environ. Biol. Fish. 18: 27-40. DOI:10.1007/BF00002325.

Klimley, A.P. (2023). A historical approach to describing the complex behaviour of a large species of carnivorous shark. Case study no. 1: the scalloped hammerhead, *Sphyrna lewini*. — Behaviour 160: 1081-1102. DOI:10.1163/1568539X-bja10211.

Klimley, A.P. & Nelson, D.R. (1981). Schooling of the scalloped hammerhead shark, *Sphyrna lewini*, in the Gulf of California. — Fish Bull. 79: 356-360. DOI:10.1111/j.1095-8649.2009.02230.x.

Klimley, A.P., Clua, E.E., Porcher, I.F. & Pratt, H.L. (2023). A review of the behaviours of the Chondrichthyes: a multi-species ethogram for the chimaeras, sharks, and rays. — Behaviour 160: 967-1080. DOI:10.1163/1568539X-bja10214.

Lage, C.A., Wolmarans, W. & Mograbi, D.C. (2022). An evolutionary view of self-awareness. — Behav. Process. 194: 104543. DOI:10.1016/j.beproc.2021.104543.

Lorenz, K. (1963). Das Sogenannte Böse, Zur Naturgeschichte der Aggression. — Dr Borotha-Schoeler, Vienna.

Maljkovic, A. & Côté, I.M. (2011). Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. — Biol. Conserv. 2: 859-865.

Martin, R.A. (2007). A review of shark agonistic displays: comparison of display features and implications for shark–human interactions. — Mar. Freshw. Behav. Physiol. 40: 3-34.

Mourier, J. & Planes, S. (2015). Les requins et raies des îles Australes, espèces emblématiques de la conservation. — In: Environnement marin des îles Australes, Polynésie française. Institut Récifs Coralliens Pacifique (Salvat, B., Bambridge, T., Tanret, D. & Petit, J., eds). CRIOBE et The Pew Charitable Trusts Polynésie française, Tahiti, p. 113-119.

Mourier, J., Vercelloni, J. & Planes, S. (2012). Evidence of social communities in a spatially structured network of a free-ranging shark species. — Anim. Behav. 83: 389-401. DOI:10.1016/j.anbehav.2011.11.008.

Mourier, J., Lédée, E., Guttridge, T. & Jacoby, D.M.P. (2019). Network analysis and theory in shark ecology–methods and applications. — In: Shark research: emerging technologies and applications for the field and laboratory (Carrier, J.C., Heithaus, M.R. & Simpfendorfer, C.A., eds). CRC Press, FL, Boca Raton, p. 337-356.

Mucientes, G.R., Queiroz, N., Sousa, L.L., Tarroso, P. & Sims, D.W. (2009). Sexual segregation of pelagic sharks and the potential threat from fisheries. — Biol. Lett. 5: 156-159.

Murdy, E.O., Birdsong, R.S. & Musick, J.A. (1997). Fishes of Chesapeake Bay. — Smithsonian Institution Press, Washington, DC.

Myrberg Jr., A.A. & Gruber, S.H. (1974). The behavior of the bonnethead shark, *Sphyrna tiburo*. — Copeia: 358-374.

Papastamatiou, Y.P., Caselle, J.E., Friedlander, A.M. & Lowe, C.G. (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. DOI:10.1111/j.1095-8649.2009.02329.x.

Papastamatiou, Y.P., Bodey, T.W., Friedlander, A.M., Lowe, C.G., Bradley, D., Weng, K., Priestley, V. & Caselle, J.E. (2018). Spatial separation without territoriality in shark communities. — Oikos 127: 767-779. DOI:10.1111/oik.04289.

Piiper, J., Meyer, M., Worth, H. & Willmer, H. (1977). Respiration and circulation during swimming activity in the dogfish *Scyliorhinus stellaris*. — Resp. Physiol. 30: 221-239. DOI:10.1016/0034-5687(77)90032-9.

Pini-Fitzsimmons, J., Nathan, A., Knott, N.A. & Brown, C. (2021). Heterarchy reveals social organization of a smooth stingray (*Bathytoshia brevicaudata*) population in a provisioned food context front. — Front. Mar. Sci. 8. DOI:10.3389/fmars.2021.641761.

Porcher, I.F. (2010). The shark sessions: my sunset rendezvous. — Strategic Book Publishing, Traverse City, MI.

Porcher, I.F. (2020). Outwitted by chickens: the bird who killed the tiger. — Independent publication.

Porcher, I.F. (2022a). Commentary on emotion in sharks. — Behaviour 159: 849-866. DOI:10.1163/1568539X-bja10145.

Porcher, I.F. (2022b). *C. melanopterus* behaviour at Session 304. — www.youtube.com/watch?v=_Wi7Q0rlYk8.

Porcher, I.F. (2023). Ethogram for blacktip reef sharks (*Carcharhinus melanopterus*). — Behaviour 160: 1167-1204. DOI:10.1163/1568539X-bja10213.

Rago, P.J., Sosebee, K.A., Brodziak, J.K., Murawski, S.A. & Anderson, E.D. (1998). Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (*Squalus acanthias*). — Fish. Res. 39: 165-181. DOI:10.1016/S0165-7836(98)00181-7.

Ritter, E.K. (2001). Food-related dominance between two carcharhinid shark species, the Caribbean reef shark, *Carcharhinus perezi*, and the blacktip shark, *Carcharhinus limbatus*. — Mar. Freshw. Behav. Physiol. 34: 125-129.

Robbins, R.L. (2007). Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South Australia. — J. Fish Biol. 70: 1350-1364. DOI:10.1111/j.1095-8649.2007.01414.x.

Sabando, M.A., Rieucau, G., Bradley, D., Caselle, J.D. & Papastamatiou, Y.P. (2020). Habitat-specific inter and intraspecific behavioral interactions among reef sharks. — Oecologia 193: 371-376. DOI:10.1007/s00442-020-04676-y.

Schjelderup-Ebbe, T. & Katz, D. (1921). Beiträge zur Sozialpsychologie des Haushuhns. — Z. Psychol. 88: 225-252.

Sperone, E., Micarelli, P., Andreotti, S., Spinetti, S., Andreani, A., et al. (2010). Social interactions among bait-attracted white sharks at Dyer Island (South Africa). — Mar. Biol. Res. 6: 408-414. DOI:10.1080/17451000903078648.

Sperone, E., Micarelli, P., Andreotti, S., Brandmayr, P., Bernabò, I., Brunelli, E. & Tripepi, S. (2012). Surface behaviour of bait-attracted white sharks at Dyer Island (South Africa). — Mar. Biol. Res. 8: 982-991. DOI:10.1080/17451000.2012.708043.

Springer, S. (1967). Social organization of shark populations. — In: Sharks, skates, and rays (Gilbert, P.W., Mathewson, R.F. & Rail, D.P., eds). Johns Hopkins University Press, Baltimore, MD, p. 149-174.

Thibaut, B., Nicolas, L., Adam, B., Marosi, N.D. & Brunnschweiler, J.M. (2021). Companions and casual acquaintances: the nature of associations among bull sharks at a shark feeding site in Fiji. — Front. Mar. Sci. 8. DOI:10.3389/fmars.2021.678074.

Zemah-Shamir, Z., Mourier, J., Ilany, A., Bigal, E., Scheinin, A. & Tchernov, D. (2022). Preliminary insights of a mixed-species shark aggregation: a case study of two carcharhinids from the Mediterranean Sea. — Environ. Biol. Fish 105: 623-634. DOI:10.1007/s10641-022-01280-2.