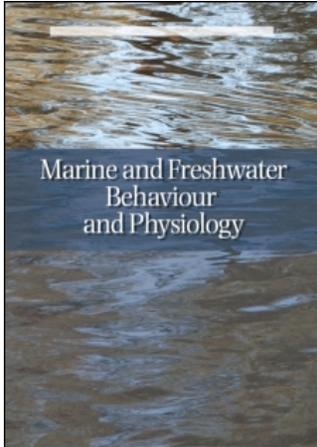


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A review of shark agonistic displays: comparison of display features and implications for shark–human interactions

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Abstract

Agonistic displays in 23 species of sharks of six families are described and illustrated. These displays are reviewed in terms of ethological concepts and shark hydrodynamic models. Shark agonistic displays feature many common elements rendering them readily distinguishable from normal swimming and pseudodisplays caused by shark-sucker irritation. Shark agonistic displays are most readily elicited by rapid, direct diver approach when food is absent and potential escape routes restricted. Such displays appear to be motivated by defence of self or the immediately surrounding space rather than defence of territory or resources. Costs and benefits of display *versus* attack in shark–shark and shark–diver contests are evaluated using payoff matrices and optimal strategies are identified. Shark–human interactions are modelled in terms of a system of nested critical approach distances. For divers faced with a displaying shark, responses which may decrease the likelihood of defensive attack are suggested. Recommendations for future work on shark agonistic behaviour are offered.

Keywords: *Sharks, social behaviour, animal communication, territoriality, agonism, signal convergence, game theory, shark attack, diver safety*

Introduction

Agonism is a class of behaviour that occurs in competitive contexts and is important to the social dynamics and evolutionary fitness in animals of many taxa (Hall and Halliday 1998). For example, individuals displaced or defeated in agonistic contests often disperse into adjacent habitats that are frequently suboptimal, thus reducing their feeding and reproductive success (Reese 1978). Agonistic behaviour is widespread among animals,

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including crustaceans, insects, spiders, mammals, birds, reptiles, amphibians, and fishes (see Bradbury and Vehrencamp 1998, for a recent review). Agonistic displays have been recorded in many teleost species, representing numerous families and orders (Fine et al. 1977; Colgan 1993; Guthrie and Muntz 1993; Helfman et al. 1997; Reeks 2001). Many shark species exhibit a variety of social behaviours, yet agonistic displays have rarely been reported in this group (Bres 1993).

Shark agonistic displays are best known in the grey reef shark (*Carcharhinus amblyrhynchos*), which exhibits a distinctive, highly stereotyped “hunch display” (named for the characteristic raised snout-arched back posture, resembling a sustained shrug) in response to persistent crowding or oriented pursuit by divers or submersibles (Johnson and Nelson 1973; Doak 1975; Stark and Anderson 1978; Nelson et al. 1986). This display features four postural elements, (1) a prominently raised snout, (2) bilaterally (to \pm the same angle) depressed pectoral fins, (3) arched back, and (4) lateral flexure of the body (Figures 1a and b), combined with two locomotory elements, (1) laterally exaggerated swimming, and (2) rolling and/or spiral looping (Johnson and Nelson 1973). The hunch display of the grey reef shark is a graded response (Figures 1b and c), increasing in intensity with speed and directness of diver approach as well as degree of restriction of the shark’s escape route (Johnson and Nelson 1973; Video clips 1–3, see below for details). If a pursuing diver or submersible persists, the hunch display rapidly escalates to either a rapid withdrawal or a lightning-fast, open-mouthed slashing attack (Johnson and Nelson 1973; Nelson et al. 1986) Thus, the hunch display of the grey reef shark is an accurate predictor of more intense defensive behaviours (Fellows and Murchison 1967).

Displays evolve from non-communicative source behaviours ritualised *via* a five-step process shaped by natural selection (Tinbergen 1952). Barlow (1974) proposed that the hunch display of the grey reef shark, like that of other predatory animals, was derived from movements associated with subjugating prey (Figure 1d). Accurate signalling of an animal’s motivation or state (“display honesty”) can be ensured by being costly, such as handicapping the signaller by diverting resources that would otherwise increase its fitness (Zahavi 1993). However, accurate signalling must have benefits that exceed the costs for such behaviour patterns to be retained rather than eliminated through natural selection

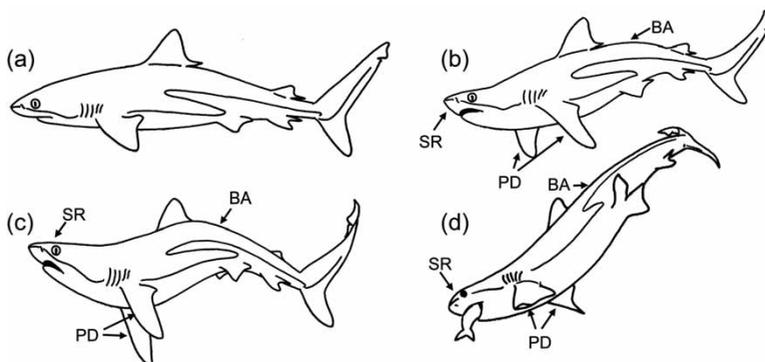


Figure 1. Elements of the agonistic display and feeding posture in the grey reef shark (*C. amblyrhynchos*); (a) non-display, (b) mild display, (c) strong display, (d) feeding posture, the probable source behaviour of the agonistic display. BA = back arch, PD = pectoral depression, SR = snout raise. See text for further details.

(Krebs and Davies 1993; Cuthill and Houston 1997). Costs and benefits of agonistic displays in the grey reef and other sharks have not been analysed.

The hunch display is most often elicited in situations where food is not present, such as close approach to a shark by an underwater photographer not using bait as a lure, and probably plays a role in normal social encounters among grey reef sharks (Johnson and Nelson 1973; Nelson and Johnson 1980). This species is widespread throughout the tropical Indo-Pacific region and, despite its modest size (most individuals are <1.5 m long), is avoided by or actively displaces most sympatric shark species, including solitary heterospecifics larger than itself (Johnson 1978; Compagno 1984). Myrberg (1991) suggested that distinctive fin markings in whaler and hammerhead sharks (Carcharhinidae and Sphyrnidae, respectively), especially on the relatively mobile pectoral and caudal fins, may serve as species recognition badges and/or accentuate signals, both social (intraspecific) and extrasocial (interspecific). The ventral apices of the grey reef shark's pectoral fins are dusky and its caudal fin bears a distinct black rear margin (Last and Stevens 1994; Figure 2); in western Pacific and Indian Ocean representatives, the first dorsal fin features a conspicuous pale apex (Compagno 1984). Intriguingly, western Pacific and Indian Ocean grey reef sharks are more timid and less likely to display than those from French Polynesia or Micronesia (personal observation). Whether such regional differences in grey reef shark behaviour and markings are causally related is unknown.

The primary literature contains descriptions of agonistic displays similar in context and execution to that of the grey reef shark in several other shark species, including the bonnethead (*Sphyrna tiburo*), scalloped hammerhead (*S. lewini*), and blacktip shark (*C. limbatus*), but none as overt as that exhibited by the grey reef shark (Myrberg and Gruber 1974; Klimley 1985; Ritter and Godknecht 2000). Putative agonistic displays in several other shark species, including the Galapagos shark (*C. galapagensis*), Caribbean reef shark (*C. perezi*), white shark (*Carcharodon carcharias*), and shortfin mako (*Isurus oxyrinchus*), have been reported in the popular literature (Hobson 1964; Stoneman 1985; Compagno et al. 1989). Confounding such anecdotal reports are recent studies showing that striped sharksuckers (*Echineis naucrates*) can induce behaviours that resemble agonistic displays in the blacktip shark, bull shark (*Carcharhinus leucas*), Caribbean reef shark (Video clip 4), and possibly other shark species (Ritter 2002; Brunnschweiler 2006). Blurring the picture further are dissimilar shark behaviours reported under competitive contexts, including tail slapping (whip-like lashing of the tail at or near the surface, hitting or directing splashes toward a receiver; Figure 3a), which has been reported in sandtiger sharks (*Carcharias taurus*) and white sharks, and breaching (leaping completely from the water; Figure 3b) and repetitive aerial gaping (RAG: rhythmic, exaggerated opening and closing of the jaws above the surface, apparently as a displacement activity; Figure 3c), which have been reported in white sharks (Compagno et al. 1989; Klimley et al. 1996; Strong 1996).

The present work reviews relevant theoretical background issues and putative shark agonistic displays from the literature, augmented and extended with opportunistic observations by the author and collected from experienced, credible divers. What constitutes an agonistic display is defined and the challenge of differentiating displays from non-displays in sharks is discussed. Previously undescribed agonistic displays or new display elements in six species of sharks are described and illustrated. All known shark agonistic displays are compared and general patterns are identified. Relative costs and benefits of shark agonistic displays in interactions with other sharks and divers are evaluated using payoff matrices. Shark-diver interaction scenarios in which sharks are most likely to exhibit agonistic displays are reviewed. A hierarchy of critical approach distances for

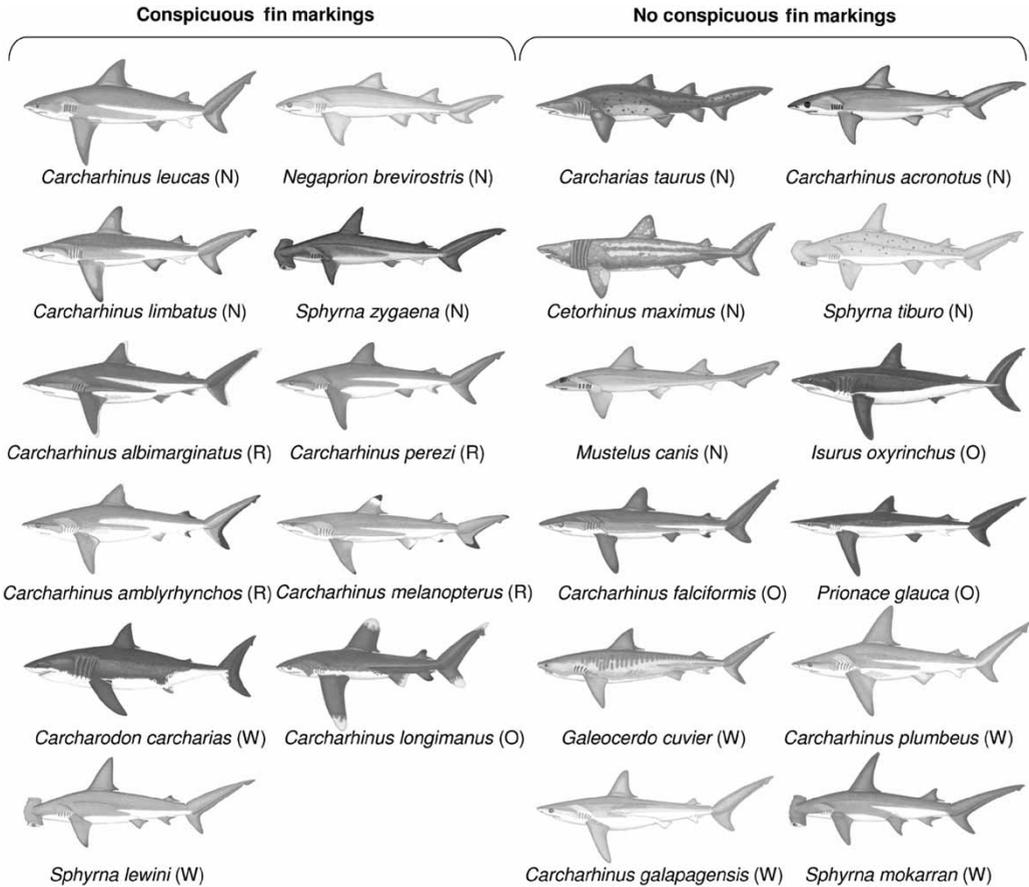


Figure 2. Distribution of conspicuous *vs.* non-conspicuous fin markings among 23 shark species in which agonistic displays are known. In whaler sharks (Carcharhinidae) and hammerheads (Sphyrnidae) known to display, distribution of conspicuous fin markings is the same as these taxa as a whole, suggesting that the presence of fin markings may not be particularly important to display evolution or form. Conspicuous markings are most common in sharks living in nearshore and reef habitats, where multiple species coexist and water is relatively clear. Habitat codes are as follows: N = nearshore, O = oceanic, R = reef, W = widespread.

sharks is hypothesised and diver responses to an agonistically displaying shark that may reduce likelihood of escalation to full attack are suggested. Recommendations for future work on shark agonistic behaviour are offered. Due to the interdisciplinary nature of this review, recurring technical terms used herein are defined in Table I. The text is augmented by video clips, which appear as supplementary material on the *Marine and Freshwater Behaviour and Physiology* website (www.informaworld.com/gmfw).

Methods

Classic and contemporary literature relevant to background theoretical issues (e.g. communication channels, signal propagation, displays, ritualisation, agonism and signal honesty), shark hydrodynamics and pigmentation (e.g. mobility of shark fins and their role

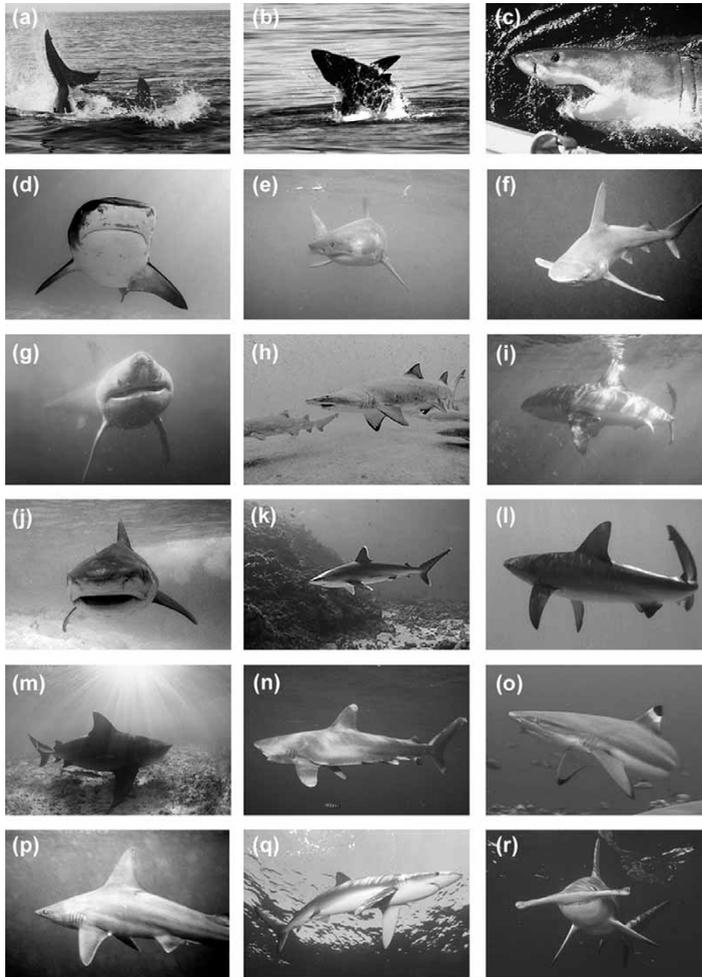


Figure 3. Non-display *versus* agonistic display in sharks; (a) tail slap, a putative agonistic behaviour, in the white shark (*Carcharodon carcharias*), (b) breach, a putative agonistic behaviour, in the white shark, (c) repetitive aerial gaping (RAG), a putative frustration-venting behaviour, in the white shark, (d) steering in the tiger shark (*Galeocerdo cuvier*) – note asymmetric use of the pectoral fins, lowering and flexing the left fin to turn toward the left, (e) steering in the white shark, featuring asymmetric use of pectoral fins, in which the left fin is lowered to turn to the right, (f) non-display in the sandbar shark (*Carcharhinus plumbeus*), featuring nearly horizontal pectoral fins, (g) agonistic display by a basking shark (*Cetorhinus maximus*), featuring strong bilateral pectoral fin depression and jaw closure (cessation of filter-feeding), (h) agonistic display in the sandtiger shark (*Carcharias taurus*) – note strong bilateral pectoral fin depression in the foreground shark *versus* non-display by the shark in the background, (i) agonistic display in the white shark (compare the relative pectoral fin angles with Figure 3e), (j) agonistic display in the tiger shark, note the open mouth and pectoral fin positions compared with Figure 3d, (k) mild agonistic display in the silvertip shark (*Carcharhinus albimarginatus*), (l) strong agonistic display in a juvenile Galapagos shark (*C. galapagensis*), (m) agonistic display in the bull shark (*C. leucas*), crowded by the photographer against the shallows (distortion due to fisheye camera lens), (n) agonistic display in the oceanic whitetip shark (*C. longimanus*), featuring head shaking and jaw gaping, (o) agonistic display in the blacktip reef shark (*C. melanopterus*), (p) agonistic display in the sandbar shark (compare with Figure 3f), (q) agonistic display in the blue shark (*Prionace glauca*), (r) agonistic display in the great hammerhead (*Sphyrna mokarran*). See text for further details.

Table I. Definitions of recurring technical terms used throughout this review. Terms for display elements are defined in the Methods section.

Term	Definition	Reference(s)
Agonism	Any behaviour related to conflict or competition, including fighting, threat, defence, flight, freezing, avoidance, and appeasement	Scott (1971)
Breaching	Leaping completely out of the water, as by a dolphin or shark	Carwardine et al. (1998)
Competition	Active demand by two or more individuals, of the same or different species, for a common resource (food, shelter, mates) that affects fitness and is in limited supply	Wilson (1975); Krebs and Davies (1993)
Conspecific Display	A member of the same species A stereotyped behaviour pattern, modified by natural selection, to convey information, usually among conspecifics or within social groups	Wilson (1975) Wilson (1975)
Dominion	An area where an individual exhibits elevated dominance and aggression toward others, but does not attempt to expel them	Brown (1975)
Heterospecific Hunch display	A member of a different species A common form of shark agonistic display, featuring raised snout, arched back, lowered pectoral fins, and exaggerated swimming movements	Froese and Pauly (2006) Myrberg and Gruber (1974)
Idiosphere	The volume immediately surrounding an individual animal (of any species) that it will defend if broached without appropriate signalling or permission	Present review
Pseudodisplay	An agonistic-like behaviour pattern elicited in non-agonistic situations, such as a shark twitching in response to activities of sharksuckers or remoras	Present review
Releasing mechanism (RM)	The sensorimotor interface mediating between a sign stimulus and the corresponding behavioural response; RM has recognition and localisation properties and can be gated or inhibited by motivational inputs	Bolhuis and Giraldeau (2005)
Repetitive aerial gaping (RAG)	An agonistic behaviour consisting of rhythmic, exaggerated opening and closing of the jaws above the surface, apparently a displacement activity; presently known only in white sharks	Strong (1996)
Sign stimulus (SS)	A stimulus adequate to activate a releasing mechanism, which sets in motion a species-specific action pattern; SS represents a complex object, such as a conspecific or diver, by a few characteristic features	Bolhuis and Giraldeau (2005)
Tail slapping	An agonistic behaviour consisting of whip-like lashing of the tail at or near the surface, hitting or directing splashes toward a competitor; presently known only in white sharks and sandtiger sharks	Compagno et al. (1989); Klimley et al. (1996)
Tail popping	A possible agonistic behaviour consisting of loud shotgun-like reports, generated by exaggerated tail beats during rapid withdrawal, often performed in conjunction with pectoral fin depression; presently known only in sandtiger sharks	Present review
Territory	A defined geographic area controlled more or less exclusively by an individual or group by means of implied or overt aggression	Wittenberger (1981)

in locomotion, conspicuous fin markings), and studies or reports of shark agonistic displays were reviewed up to the end of June 2006. Reports of putative agonistic displays were collected from experienced, credible observers (see Table II and Acknowledgements) and only included in this analysis if data on the species involved, circumstances of interaction, and specific behaviour elements were identified clearly and supported by photo or video documentation.

New observations on agonistic displays in silvertip (*C. albimarginatus*) and Galapagos (*C. galapagensis*) sharks are based on behaviours elicited in these species through sustained, oriented pursuit using a diver propulsion vehicle (DPV) at Osprey/Marion Reef and Lord Howe Island, Australia, respectively, during October and November 1982; the DPV was used to pursue each test subject, was switched off as soon as a display commenced, and was then used as a shield. Agonistic behaviour in Caribbean reef sharks was observed on scuba under baited and unbaited conditions at Nassau, Bahamas, in June 1999. Agonistic displays were elicited in sandtiger sharks by oriented diver pursuit at the wrecks of the *Aeolis* and *Carib Sea*, off Moorehead City, North Carolina, in April 2002. Agonistic displays in sandbar sharks were observed from a shark cage under baited conditions off the north coast of Oahu, Hawaii, in December 2004. Agonistic displays in white sharks were observed using a pole-mounted underwater camera and/or from the deck of the research vessel at Seal Island, False Bay, South Africa, from June to August 2000–2005.

Shark measurements and display elements used in this review are:

- *Back arching* – a sustained (>5 s) dorsal flexure of the back, so that it forms an inverted U, measured or estimated as the angle between the dorsal surface of the head and that of the pre-dorsal back (“nape”) (Figures 1b, c, and 3i; Video clips 1–3)
- *Body length (BL)* – estimated total length, from snout tip to upper caudal fin apex
- *Body shivering* – a quivering or rapid (>5 Hz) shaking of the entire body, usually combined with a lateral display (Figures 4b and c)
- *Body tilting or rolling* – an exaggerated, sustained (>5 s) roll of the body around its longitudinal axis, up to $\pm 45^\circ$ from vertical, either as a single action (tilt) or an oscillation (roll) (*sensu* Johnson and Nelson 1973; Klimley 1985; Ritter and Godknecht 2000) (Video clips 1–3)
- *Charging* – rapid (2 to 3+ BL/s) approach toward a receiver, often terminated by veering away on a perpendicular course within a distance of 1–2 BL (Figure 3j)
- *Clasper flexion* – rotation of a clasper (elasmobranch intromittant organ) anterolaterally, mimicking its erect state during copulation (*sensu* Myrberg and Gruber 1974)
- *Corkscrewing* – rapid burst swimming into a tight looping trajectory while rotating the longitudinal body axis through nearly 180° (*sensu* Klimley 1985)
- *Flank displaying* – a sustained (>5 s) perpendicular bodily orientation of signaller’s body toward a receiver, displaying its lateral surface (Figures 3h, i, and k–p)
- *Follow–give way* – an agonistic interaction in which one animal follows another, which deviates from its course, implying social precedence of the following individual (*sensu* Myrberg and Gruber 1974)
- *Gill pouch billowing* – a sustained (>5 s) conspicuous, spinnaker-like expansion of the branchial region (Figure 4a); equivalent to “gill-puff” of Myrberg and Gruber (1974)
- *Give way* – an agonistic interaction in which one animal deviates from its course at the approach of another, implying social precedence of the undeviating individual (*sensu* Myrberg and Gruber 1974)

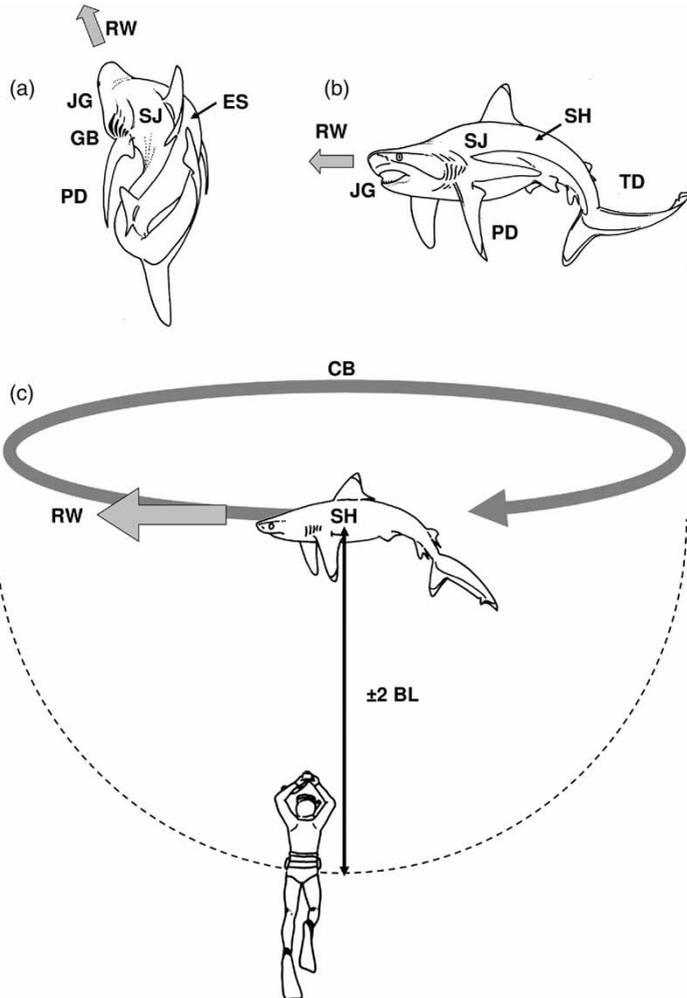


Figure 4. Agonistic displays of, (a) Galapagos shark (*C. galapagensis*) and (b) the silvertip shark (*C. albimarginatus*), (c) diagram of locomotor aspects of silvertip shark agonistic display. BL = body length; CB = circle back; ES = exaggerated swimming; GB = gill billowing; JG = jaw gaping; RW = rapid withdrawal; SH = shiver; SJ = stiff or jerky movements; TD = tail depression. See text for further details.

- *Head shaking* – rhythmic, exaggerated lateral shaking of the head, usually rapid (>2 Hz) and through an arc of >30° (Figure 3n)
- *Jaw closing* – a non-forceful bringing together the upper and lower jaws in an agonistic context (as compared to a bite, which is a forceful jaw closure during feeding) (Figure 3g)
- *Jaw gaping* – a slow, exaggerated opening of the jaws ($\pm 30\text{--}90^\circ$, measured or estimated as the angle formed at the mouth commissure), conspicuously wider than during ram ventilation and in an agonistic context, resembling a yawn (Figures 3c and n)

- *Laterally exaggerated swimming* – sustained (>5 s), eel-like swimming motion (Figure 4a; Video clips 1–3)
- *Looping* – swimming in a spiral loop (*sensu* Johnson and Nelson 1973)
- *Open jawed tooth raking* – a forceful strike with the upper jaw teeth causing injury to a receiver
- *Palatoquadrate protrusion* – forward extension of the upper jaw, causing it to separate from the cranium, and which may bare the upper dentition; categorised as present or not
- *Pectoral fin angle (PFA)* – is measured or estimated from a horizontal plane perpendicular to the body axis at the level of the chord formed by a straight-line from pectoral fin origin to pectoral free rear tip (which is often easier to discern than the pectoral insertion in free-swimming sharks); equivalent to the “dihedral angle” of Wilga and Lauder (2000)
- *Pectoral fin depression* – a sustained (>5 s), bilateral lowering of the pectoral fins from their usual position during swimming, quantified as pectoral fin angle (Figures 3g–r, 6b and c; Video clips 1–3, 8, 9)
- *Ramming with snout* – a signaller using its rostrum to forcefully strike a receiver, often causing it to recoil or retreat; synonymous with “hit” of Myrberg and Gruber (1974)
- *Rapid withdrawal* – movement of a signaller away from a display receiver at ≥ 3 BL/s.
- *Rapid, tight pattern swimming* – fast swimming marked by sudden and frequent changes in direction (Video clips 1–3)
- *Reduced swimming efficiency* – conspicuous reduction in forward locomotion, from almost normal swimming speed to nearly stationary in the water column, despite exaggerated swimming movements (Johnson and Nelson 1973)
- *Ritualistic jaw snapping* – rhythmic (± 1 Hz), exaggerated opening and closing of the jaws, (± 30 – 90° , measured or estimated as the angle formed at the mouth commissure) (Figure 3c, n)
- *Snout elevation* – a sustained (>5 s) raising of the snout from the resting position, measured or estimated as the angle between the dorsal surface of the rostrum and that of the epibranchial region (surface of the back above the gill slits) (Johnson and Nelson 1973; Figures 1b, c, and 3m; Video clips 1–3)
- *Stand back* – an agonistic interaction in which two oncoming animals deviate from their courses simultaneously, making it impossible to infer social precedence (*sensu* Compagno 2001)
- *Stiff or jerky movement* – a conspicuous reduction or loss of fluidity of body and fin movements during locomotion, probably due to an increase in tonus of associated muscles
- *Swimming speed* – is measured in BL/s
- *Tail depression* – a sustained (>5 s) vertical bending of the caudal peduncle, stiffly holding the caudal fin downward, below the main body axis (Figures 4b, c)
- *Tail flexure* – a sustained (>5 s) lateral bending of the caudal peduncle, stiffly holding the caudal fin to one side, away from the longitudinal axis (Johnson and Nelson 1973)
- *Tail slapping* – a whip-like lashing of the tail at or near the surface, hitting or directing splashes toward a competitor (Compagno et al. 1989; *sensu* Klimley et al. 1996; Figure 3a)
- *Torso thrusting* – an exaggerated, sustained (>5 s) lateral flexure of the abdominal region into an S-shape, often accompanied by body tilting, *sensu* Klimley (1985)

Results

Signal logistics and types

Belief that animal behaviour comes in discrete, measurable units is one of the cornerstones of ethology. Choice of appropriate behavioural units to be measured is one of the most important and difficult decisions to be made (Barlow 1977). Classically trained ethologists adhered to the notion of a fixed action pattern (FAP), a complex behavioural sequence that responds to a key stimulus (KS) *via* an innate releasing mechanism (IRM) and that invariably runs to completion (Dewsbury 1978; Alcock 1993; Carew 2000). However, more recent work has shown the concepts KS, IRM, FAP to be of limiting simplicity. Instead, most modern workers prefer the term sign stimulus, which is less suggestive of key-like high specificity of the stimulus necessary to elicit a response, the term releasing mechanism, which avoids controversy among ethologists over how “innate” such mechanisms are, and the more flexible concept of a modal action pattern (MAP), which is a recognisable pattern of movement that cannot usually be further subdivided into independent subunits but is variable in intensity and duration (Barlow 1977; Bolhuis and Giraldeau 2005). Using this terminology, a general model of a behavioural chain is:

Sign stimulus → Sensory neuron(s) → Releasing mechanism → Behaviour.

Martin and Bateson (1986) stated that behaviour could be most simply described in terms of its structure (form) or consequences (effects). Four basic properties of any behavioural observation can be measured: latency (usually, delay between environmental stimulus and behavioural response), frequency, duration, and intensity (Martin and Bateson 1986). Four scales of behaviour measurement are possible, arranged from lowest to highest resolution: (1) nominal, in which behaviour is scored as mutually exclusive categories (A, B, C), (2) ordinal, in which a behaviour category is scored relative to other categories ($A < B < C$), (3) interval, in which a behaviour is scored according to an arbitrary scale, and (4) ratio, in which a behaviour is scored according to a scale for which the zero point is known (Lehner 1979). Due to the danger involved in experimentally provoking shark agonistic behaviour in the wild (Johnson and Nelson 1973), descriptions are often limited to form, and scoring of behavioural units is often limited to lower resolution scales.

The term “agonism” was introduced by Scott and Fredericson (1951) to refer to any behaviour related to fighting and competition. Agonism embraces a broad spectrum of behaviours related to animal conflict, including fighting, threat, defence, flight, freezing (remaining motionless to avoid detection), avoidance, and appeasement (Johnson 1972; King 1973; Dewsbury 1978; McFarland 1987). For all their variety, agonistic behaviours are united by occurrence during conflict situations (Scott 1971). Lorenz (1966) recognised three forms of conflict in animals: social, predatory, and antipredatory. Although Wilson (1975) recognised predation as a form of aggression on functional grounds, Hinde (1974) and Huntingford (1976) argue convincingly that predation and intraspecific fighting cannot be lumped together on grounds of proximate causation. Conflict denotes a motivational state in which tendencies to perform more than one activity are expressed simultaneously (Manning 1979). Much agonistic behaviour is characterised by motivational conflict between attack and flight, often resulting in vacillation between approach and withdrawal (McFarland 1987). A “display” is a stereotyped motor pattern involved in animal communication; displays are usually intraspecific and related species often have similar displays (McFarland 1987). Displays evolve from non-communicative source behaviours

that have been ritualised *via* a five-step process shaped by natural selection (Tinbergen 1952; Wilson 1975). For well-armed contestants, physical combat bears significant risk of injury, which could compromise the feeding or reproductive abilities of both participants (Lorenz 1964). Therefore, in conflict situations, ritualised displays may be more adaptive than combat (Reichert 1982). Display form is phylogenetically constrained and specific elements can be punctuated by conspicuous postures or pigmentation (McGregor 2005).

Due to their conservative structure and the constraints of efficient swimming, sharks have few structures available for signalling. Their only suitable appendages are the relatively highly mobile pectoral and caudal fins (Myrberg 1991) and, in males, the claspers (Myrberg and Gruber 1974; Klimley 1985). Signals are ritualised from non-communicative source behaviours *via* a process of simplification, exaggeration, decreased performance speed, repetition, and increased stereotypy (Tinbergen 1952). Eibl-Eibesfeldt (1966) noted that, while taking bait from a reef, a grey reef shark lowered and rotated the pectoral fins forward, bracing its body in the water column. Hobson (1963) reported that the jaws of an agonistically displaying grey reef shark often open and close, as in biting, while Eibl-Eibesfeldt and Hass (1959) reported that, as they swim toward a diver, whaler and hammerhead sharks often shake their heads vigorously from side-to-side, as during gouging out a mouthful of flesh. Elements of the agonistic display of grey reef and other sharks are likely derived from movements associated with subjugating prey (Barlow 1974); a typical feeding posture of a grey reef shark is contrasted with a moderate agonistic display of this species in Figures 1d and 1b, respectively. Nearly 56% of whaler and hammerhead sharks bear conspicuous fin markings (Myrberg 1991), which may emphasise display elements. Patterns of fin and body markings in all species considered in this survey of agonistic displays in sharks are illustrated in Figure 2.

Grey reef and other sharks performing hunch displays exhibit reduced forward swimming speed and manoeuvrability (Johnson and Nelson 1973; Barlow 1974). For an aquatic animal in a fight-or-flight conflict situation, sacrificing swimming efficiency in favour of displaying bears significant costs and risks (Simpson 1968; Torricelli et al. 1983), and therefore constitutes honest signalling (Zahavi 1993).

Thus, by definition, shark agonistic displays are conspicuous MAPs elicited in conflict situations, usually between or among conspecifics. The hunch display of grey reef sharks, however, is not known to be performed toward conspecifics, but is known to be directed toward humans (Johnson and Nelson 1973; Nelson et al. 1986), great hammerhead sharks (*Sphyrna mokarran*) and moray eels (Johnson 1978). Similarly, blacktip sharks have been documented displaying toward scuba divers before accelerating away (Ritter and Godknecht 2000; Stafford-Deitsch 2000). Since shark agonistic displays are unlikely to have evolved in response to diver encroachment (within the last ± 50 years), it is likely that shark species perform agonistic displays the same way toward natural predators or competitors as toward humans. This performance conservatism is useful, as it enables scientific study of shark agonistic displays.

Recognising shark agonistic displays

Complex biological structures, such as fins, are often multifunctional (Bock and von Wahlert 1998). Caudal and pectoral fins of sharks play important and active roles in shark locomotion (Bone 1988). This raises methodological questions about differentiating between use of these fins for locomotion *versus* signalling.

Biomechanics of shark locomotion are now understood to be considerably more complex than earlier models postulated (see Wilga and Lauder 2004, for a recent review).

Body form and caudal fin shape strongly influence swimming style, but in all sharks the caudal fin is the principal source of propulsion (Thomson 1976; Thomson and Simanek 1977). Contrary to classical theories of shark locomotion, recent experiments have demonstrated that the pectoral fins do not contribute significant lift during steady horizontal locomotion although, by varying angle of attack and flexure of the fin web, they can finely control manoeuvring (Fish and Shannahan 2000; Wilga and Lauder 2000). Instead, body angle most significantly affects a shark's pitch in the water column, enabling the animal to generate lift by planing on the flattened ventral surfaces of its snout and belly (Wilga and Lauder 2004). Shark pectoral fins thus do not function like fixed hydrofoils during swimming, making them available for steering and signalling.

Use of pectoral fins by sharks for turning is conspicuously different from their use during agonistic displays (Barlow 1974). Qualitatively, during turning in free-swimming sharks in the wild, the pectoral fins are flexed slowly in a fluid, short-duration (usually <1 s) motion and PFA of the left and right pectoral fins are unequal, with the fin on the side to which a shark turns usually depressed more strongly than the other (Figure 3d; Video clips 5 and 6), although this is not always the case in slow-moving sharks (Figure 3e; Video clip 7). This biased pectoral fin depression is contrary to Figure 11 in Wilga and Lauder (2000), which may reflect simplification for clarity or an artefact of inhibited steering in the confines of a laboratory tank. In contrast, during shark agonistic displays, both pectoral fins are held stiffly downward for prolonged periods (usually 5 to 120+ s), and bilaterally, as illustrated in Figures 3g–r. Such pectoral fin depression, probably derived from postures assumed by a shark bracing its body in the water column during prey dismemberment (Figure 1), would be expected to increase yaw stability and decrease agility. A non-displaying shark, with its pectoral fins unoccupied by the demands of signalling, is able to turn within 1/2 to 1/3 BL (Video clip 5); in contrast, an agonistically displaying shark is not nearly so agile, requiring >1.5 BL to negotiate a 180° turn (Video clips 1–3, 8). Quantitative studies of these differences in fin usages are beyond the scope of the present review, but would assist to define them better.

While stiffly and bilaterally depressed pectoral fins are characteristic of shark agonistic displays, their mere presence is insufficient to determine that a shark is performing an agonistic display. For example, attachment of sharksuckers (Echeneidae) to sharks can elicit behaviour patterns that resemble elements of agonistic displays, such as twitching, shaking, rolling, fin flexure, jaw gaping, and acceleration (Ritter 2002; Brunnschweiler 2006; Video clip 4). Since such behaviour patterns seem to be attempts to relieve irritation caused by contact with sharksuckers, rather than competition for a common resource or defence of "personal space", they are not, by definition, agonistic; the term "pseudodisplay" is here proposed for agonistic-like sharksucker-induced behaviour patterns in sharks. However, sustained bilateral pectoral fin depression, *performed in a conflict situation*, and accompanied by other common shark agonistic display elements (described subsequently) greatly increase the likelihood of correctly identifying a shark agonistic display.

Species in which displays are known

Agonistic displays are known in at least 23 species of sharks, representing six families (Table II). About one-third of these displays are well described in the literature and their component elements summarised in the table presented here. Observations that augment published reports of shark agonistic displays and original data on agonistic displays in additional species are included in Table II and presented below, organised by species.

Sandtiger shark. This species exhibits a variety of agonistic behaviours not reported by Compagno et al. (1989) in western Indian Ocean individuals. Among the most obvious of these in western North Atlantic individuals is pectoral fin depression accompanied by flank displaying. As in grey reef sharks, pectoral fin depression is elicited in approach-withdrawal conflict situations and is a graded response, with intensity of PFA increasing from -30° to -50° with diver proximity and degree of escape route restriction (Figure 3h; Video clip 8). This species has attacked divers off South Africa and elsewhere, delivering minimalist bites (not removing flesh) similar to those inflicted on captive conspecifics (Compagno 2001). Another putative agonistic behaviour in this species, often performed in conjunction with pectoral fin depression, is a loud shotgun-like report, generated by exaggerated tail beats during rapid withdrawal that is termed “tail popping” by North Carolina wreck divers (R. Allen, personal communication). Preliminary field tests off North Carolina suggest that likelihood of tail popping increases with speed, directness, and angle of diver approach. Rapid frontal approaches at a downward angle of $\pm 30^\circ$ from the animal’s longitudinal axis seemed to produce the strongest tail popping response. Similar sounds generated by the caudal fin of this species have also been reported from Australia, where groups of sandtigers were observed apparently herding a school of carangids (Cliff 1988). However, it is probable that sound production in this species is caused, at least in part, by cavitation in the wake of its large subterminal lobe (Figure 2), which may make it an artefact of rapid acceleration rather than a display element. Systematic testing of tail popping under agonistic and non-agonistic contexts is needed to resolve this matter. Such testing could include speaker playback of tail popping, which would allow separation of visual and other shark-related cues from the potential stimulus-specific role of popping, analogous to birdsong playback to distinguish mate-attraction from competitor-repulsion functions (e.g. Searcy and Nowicki 2000; Vehrencamp 2000).

White shark. A variety of named and described agonistic behaviours have been reported in this species, but without supporting evidence (Compagno 2001; Martin et al. 2005). A photo of a white shark hunch display featuring strong pectoral fin depression (PFA = -70°), was taken off Dyer Island, South Africa in July 2003 (Figure 3i). A possible hunch display by a white shark, apparently contesting access to speared fish and followed by an attack on the spearfisher, was reported in South Africa by Jones (1991), while Collier (2003) identifies four cases in which this species appears to have attacked humans off California in agonistic contexts. Between July 2002 and July 2005, the following agonistic behaviours were performed by white sharks toward conspecifics at Seal Island in False Bay, South Africa: 22 give ways, four follow-give ways, three hunch-give ways, and two stand backs. As these behaviours are well defined and illustrated elsewhere (Myrberg and Gruber 1974; Martin 2003; Martin and Martin 2006), they will not be further described here. However, footage of a typical hunch display by a white shark directed toward a conspecific is presented in Video clip 9. On 27 June 2005, after having been thwarted by the bait handler in repeated attempts to consume the bait, a 3.5 m male white shark twice performed RAG displays (Figure 3c) completely consistent in form and context with those described and illustrated in Strong (1996).

Silvertip shark. Encroachment by underwater photographers and pursuit by a submersible elicited a partial agonistic display in this species. This display featured slightly stiff-bodied swimming and brief pectoral fin depression (Eibl-Eibesfeldt and Hass 1959, Figure 8; Nelson et al. 1986). A mild agonistic posture by a juvenile of this species off Ribbon Reefs, Australia, is presented in Figure 3k. Diver pursuit elicited a more elaborate,

highly stereotyped agonistic display in at least five different individuals (1.4–1.8 m BL) in eight out of 28 (28.6%) trials on non-feeding animals at several offshore reefs on the Great Barrier Reef, Australia. In each successful trial, when a distance of about 2 BL was broached by a diver, the test subject accelerated away to a distance of about 15 m. Each shark then turned sharply and charged toward the observer at ± 3 BL/s. When the shark reached a distance of about 2 BL, it strongly depressed its pectoral fins, turned broadside, vertically depressed its caudal peduncle, and—while holding this posture and moving at greatly reduced speed (± 0.5 BL/s)—gaped its jaws rhythmically (± 1 Hz) and vibrated its entire body in a shiver-like motion. This shiver accentuated the white fin markings characteristic of the species (Figure 2) and was maintained until the posterior margin of the animal's pectoral fin base passed the observer's mid-line. The shark then ceased shivering, raised its caudal fin and accelerated away at ± 3 BL/s with both its pectoral fins strongly depressed (Figures 4b and c). In one trial, a 1.7 m female silvertip shark attacked before fleeing; the observer was uninjured but the nose-cone of the DPV was raked by the shark's upper teeth. Repeated attempts to approach this species for photographic purposes in the Chagos Archipelago, central Indian Ocean, elicited essentially the same display (A. Emery, personal communication).

Galapagos shark. Aspects of an agonistic display, featuring laterally exaggerated swimming, have been reported in this species (Hobson 1964). During this display, the shark's head swung through an arc of $>90^\circ$, which Hobson (1964) interpreted as an attempt by the animal to increase its visual field to maintain visual contact with the diver following it. Sustained diver pursuit elicited a more extreme version of this display on four occasions in non-feeding subadult Galapagos sharks (1.5–2 m TL) at Lord Howe Island, Australia. This display was elicited when the observer repeatedly approached from behind to within 2 BL of the shark. It featured laterally exaggerated, sub-anguilliform swimming movements, strong bilateral pectoral fin depression (PFA = -40 to -60°), gill pouch billowing, and exaggerated jaw gaping at about 0.5 Hz (Figure 4a). The display was terminated when all postural and locomotory behavioural elements ceased, except bilateral pectoral fin depression, which was sustained during rapid withdrawal at ± 3 BL/s. A partial agonistic display by a juvenile Galapagos shark, featuring flank displaying and strong pectoral fin depression (PFA = -70°) was photographed in October 2003 at Bassas da India Atoll, Mozambique Channel (Figure 3l), which may be a nursery area for this species (Hammerschlag and Fallows 2005).

Caribbean reef shark. Stoneman (1985) reported more than 450 observations of agonistic behaviour, some of which (fraction cannot be determined, since full data are not available) resulted in attacks, in what he identifies as *Carcharhinus limbatus* (blacktip sharks). However, Stoneman seems to consistently mistake Caribbean reef sharks for this species (Meltzoff 1988; Gruber 1993). Unfortunately, Stoneman has not published his observations, so they are unavailable for independent analysis. Consultation with Stoneman's scientific advisor indicated that the displays they attributed to *C. limbatus* featured brief, 1 to 1.2-second pectoral fin dips, punctuated by frequent changes in direction (A. Emery, personal communication). Diver-acclimatised Caribbean reef sharks in the Bahamas were observed in the presence and absence of bait by the author using scuba. Despite high concentrations of sharks (~ 60 animals in an area < 2500 m²), no clear agonistic behaviour was observed without baits, but repeated brief pectoral fin dips (PFA = -15° , period = ± 1 Hz) followed a second or so later by ± 90 -degree changes in direction were evident when bait was present, supporting the proposition that the behaviours attributed

by Stoneman (1985) to *C. limbatus* were performed by Caribbean reef sharks. Scharfer (2003) reported similar agonistic behaviour patterns in Caribbean reef sharks at another long-term shark feeding site in the Bahamas, noting that frequency of agonistic acts by sharks depended on feeding technique and that female sharks bumped camera ports (a possible agonistic behaviour) more frequently than males. Systematic observations, preferably of less diver-acclimatised sharks, are needed to verify agonistic behaviour patterns in Caribbean reef sharks.

Sandbar shark. Agonistic displays have not previously been reported in this species, which is a congener of the grey reef shark and ten other species from which such displays have been reported. Partial agonistic displays by subadult sandbar sharks (1.2–1.5 m BL), in mixed aggregation with Galapagos sharks (1.8–2 m BL), and in the presence of baits, were observed from a shark cage off the north shore of Oahu, Hawaii. This display appeared to be directed toward the observer/cage and featured partial flank display combined with moderately strong pectoral fin depression, increasing from an initial PFA of -5° (Figure 3f) to a final PFA of -60° (Figure 3p). In more intense versions of this display in Hawaiian waters, subadult sandbar sharks charged toward a diver in the presence of bait at 2–3 BL/s. During such charges, the pectoral fins were strongly depressed and, at a distance of ± 1.5 BL, males veered away from the diver on a perpendicular course, while females continued toward the diver and sometimes rammed him with the snout tip before withdrawing rapidly (D. Fleetham, personal communication).

None of the preceding six species exhibited palatoquadrate protrusion as a component of agonistic displays.

Discussion

Sensory channels of communication

Sharks are endowed with a battery of well-developed senses, responsive to mechanical, chemical, visual, and electrical stimuli (see Hueter et al. 2004, for a recent review). In theory, any or all of these sensory channels are available for communication (Dusenbery 1992). However, the marine operating environment imposes signal attenuation and limits signal functional range, ability to go around obstacles, transmission speed, and persistence as well as receivers' ease of locating signal source (Bradbury and Vehrencamp 1998).

Visual signals propagate at the speed of light within limits set by the optical properties of the transmission medium, are directional and non-persistent (McGregor 2005). Sharks possess a high order of visual sensitivity and acuity, with pupillary dilation and tapetal plates affording some ten times greater photic sensitivity than human eyes under scotopic conditions and at least some species exhibit a well-developed Purkinje shift and true colour vision (Gruber and Cohen 1978; Hueter et al. 2004). There is no reason to believe that sharks cannot see to the limit of underwater visibility which, depending upon habitat, may be as far as 30 m (Hueter and Gilbert 1991). Functional distance of underwater visual signals is limited by incident light intensity, wave activity, surface reflection, light scattering, absorption and polarisation in the water column as well as critical fusion frequency of receivers (McFarland 1991). At distances >15 m, vibrations and olfaction appear more important than vision to guide sharks to prey or divers; however, at distances of ≤ 15 m, depending on current strength and direction, water clarity, and light levels, vision increases in importance and, at very close range (<3 m), vision is probably the principal sense in directing sharks to food (Eibl-Eibesfeldt and Hass 1959; Gilbert 1963). Thus, at the

relatively close ranges of agonistic encounters, visual signals are an expedient sensory channel for shark communication. However, other sensory modalities may also be employed in shark communication.

Sharks possess well-developed mechanoreceptors, chemoreceptors, and electroreceptors (Heuter et al. 2004). Tail slap and breach in white sharks (Figures 3a, b) and tail popping in sandtiger sharks have been proposed as agonistic behaviours (Klimley et al. 1996; present review). Many fishes are known to use sound as a communication channel (Fine et al. 1977) and the above-named behaviours could exploit the exceptional vibration propagation properties of water (Dusenbery 1992). The number and intensity of such mechanical signals could impart information about the relative stamina and power of the signaller, which would seem reasonable indicators of its fighting ability. Although direct evidence is lacking, pheromones are probably important to shark reproductive behaviour (Bass 1978; Johnson and Nelson 1978; Demski 1990) and may extend to other shark social behaviours as well. Similarly, major histocompatibility complexes may facilitate kin recognition in sharks as they do in many other animals (Wyatt 2003). Kin recognition in agonistic contexts may avoid inflicting injuries on related combatants, which could reduce their fitness and thus violate the sociobiological principle that individuals tend to behave in ways that maximise representation of their genes, including those shared with kin, in future generations (Alcock 2001). But the mechano- and chemo-receptive experiments that could test these ideas have not yet been conducted on sharks. Electroreception in elasmobranch fishes is highly acute and known to play a role in prey detection and predator avoidance but – due to electrical “noise” in the marine environment – detection of bioelectric signals is functionally limited in ranges of <25 cm (Kalmijn 1978; Hueter et al. 2004). Such close range may be practical in certain social interactions, such as courtship (Moss 1984), but seems dangerous when faced with an unknown opponent in a competitive context. Thus, performance characteristics of non-visual senses of sharks are either too poorly known to assess their importance in signalling or of such short range they are impractical in agonistic interactions.

As highly visual creatures ourselves, we may be biased toward seeking and recognising visual displays. Vision packs an enormous amount of information into a succinct message (size, shape, speed and direction of movement) that would seem highly advantageous in agonistic contexts. At least some sharks appear to use visual cues for species recognition (see review in Myrberg 1991). Dark fin markings are most common among whaler and hammerhead sharks of nearshore and reef habitats and indistinct fin markings are more common in such sharks that range across many habitat types or inhabit turbid water (Myrberg 1991). Given that whaler and hammerhead shark diversity and abundance is greatest in nearshore and reef habitats (Compagno 1984) and such sharks tend to be residents of seasonal aggregation sites or year-round home ranges (Nelson 1990), multiple shark species with similar resource needs and exploitation capabilities may encounter one another regularly. Thus, bold fin markings may be important species recognition badges for sharks in clear waters of nearshore or reef habitats. However, the importance of such markings in agonistic encounters is not clear. Of sharks in which agonistic displays are known, conspicuous fin markings occur in 48% of all species, of which almost two thirds (64%) inhabit nearshore or reef habitats, and in 56% of whaler and hammerhead sharks (Figure 2). This latter figure agrees well with the overall occurrence of conspicuous fin markings in these two families (Myrberg 1991), suggesting that such visual cues evolved independently from agonistic signals. However, distinctive fin markings may be incorporated into agonistic displays. For example, display elements such as flank displaying, body tilting or rolling, and pectoral fin depression may reveal or accentuate distinctive

fin markings in agonistic contexts, facilitating species recognition as well as signalling agitation or defensive threat. Thus, pending further data, it is provisionally suggested that vision may be the primary sensory channel employed by sharks for agonistic signalling.

What information is conveyed?

Agonistic encounters are framed by uncertainties between or among the combatants. Agonistic displays provide information about the likely intent and level of commitment of the signaller and may provide information on relative fighting ability. For example, agonistic displays may emphasise body size, weapons, or status badges, and may also include a tactical element, placing the signaller in a better position to attack or flee (Bradbury and Vehrencamp 1998). Agonistic displays are stabilised by natural selection if the costs are borne by the signaller, in what are termed “vulnerability handicaps” (Vehrencamp 2000). Size is a good indicator of fighting ability, such that competitors of grossly dissimilar size rarely need to fight or display (Krebs and Davies 1993). If, however, combatants are similar in size, ritualised agonistic displays are likely to occur (Bradbury and Vehrencamp 1998). In assessing the validity of an agonistic display, two sources of uncertainty arise, (1) receiver estimation of signal magnitude, and (2) degree to which a display indicates the likely outcome of combat (Bradbury and Vehrencamp 1998). Agonistic displays performed at close range to the receiver are likely to be more effective, but they also bear greater risk (Zahavi 1977). Intention movements are incomplete initial phases of behaviour patterns and many threat displays, such as jaw gapes, are ritualised from attack or defensive behaviours (McFarland 1987; Hauser and Nelson 1991). Frontal and lateral agonistic displays occur as a result of motivational conflict between attacking and fleeing, with frontal displays indicative of a tendency toward attack and lateral displays of a tendency toward escape (Fine et al. 1977). Broadside or lateral agonistic displays are widespread among vertebrates (Thomas et al. 1965; Carpenter 1978; Hinde 1982), probably because they emphasise size by presenting the largest possible aspect; such displays also place the signaller at elevated risk of attack, which could signal the sender’s confidence in its fighting ability. Complicating these issues further, individual combatants may recognise a degree of relatedness or have prior experience of one another, but researchers are rarely privy to such parameters (especially in wild or free-ranging subjects), introducing much uncertainty into interpreting isolated agonistic interactions among study subjects.

A cost–benefit analysis of the hunch display in grey reef sharks provides insights into the signal reliability of this behaviour. Costs of the hunch display likely include increased cost of transport (laterally exaggerated swimming movements combined with decreased locomotory efficiency, as evidenced by reduced speed through the water) and increased risk (lateral display presents the vulnerable flank to a potential attacker and reduces manoeuvrability); benefits likely include potential discouragement of a would-be competitor or predator and decreased risk of combat (which could result in injuries that may decrease fitness). Thus, the costs to a displaying grey reef shark are actual, but the benefits are merely potential. Duration of shark agonistic displays is variable, ranging from several seconds (5+) to a few minutes; such a time frame may be short in terms of the signaller’s lifetime, but is a long time for any animal to be exposed and at risk of attack. If the cost–benefit analysis performed for the grey reef shark applies to other shark species as well, shark agonistic displays are costly in conflict situations and thus are probably honest indicators of signaller motivation (Zahavi 1993).

Motivation

Clear agonistic displays are difficult to elicit in sharks, because they require sustained (several minutes) oriented pursuit. Drawing on visual and possibly other cues, sharks in the wild use their superior swimming ability to set the preferred minimum distance between themselves and divers; if a diver attempts to approach, most simply swim away to avoid contact (Video clip 10). However, in some cases, a shark that is approached by a diver will not retreat and will attack instead.

Traditionally, it was thought that shark attacks on humans were motivated by hunger. Baldrige and Williams (1969) were the first to suggest that the character of many shark attacks seemed more consistent with fighting than feeding. Analyses of 1165 case histories archived in the International Shark Attack File concluded that 50–75% of shark attacks on humans were motivated by something other than a desire to feed (Baldrige 1974b, 1988). The hunch display of the grey reef shark appears defensive in nature and often precedes a rapid, slashing attack with little or no removal of flesh (Fellows and Murchison 1967; Johnson and Nelson 1973; Nelson et al. 1986). Agonistic displays by sharks have preceded attacks on humans in at least five other species: sandtiger (Compagno et al. 1989; Compagno 2001; and present study), white shark (Jones 1991; Collier 2003), silvertip (Nelson et al. 1986; and present study), Caribbean reef (Stoneman 1985), and smooth hammerhead (*Sphyrna zygaena*) (Miller and Collier 1981; Collier 2003). Yet the majority of agonistic displays do not result in an all-out attack. For example, in the silvertip shark, only one of eight agonistic displays resulted in forceful contact with the receiver (present study).

Nelson (1981, 1983) suggested that sharks may sometimes attack humans because they are regarded as competition for food or another resource. Shark agonistic displays are rarely elicited during feeding or in the presence of bait, which suggests that access to a food resource is not usually a precipitating factor and that divers are not regarded by sharks as competitors. However, in two attacks on divers involving white sharks and one involving a smooth hammerhead, agonistically displaying sharks appeared to contest access to speared fish (Jones 1991; Collier 2003).

One often-raised possibility is that a displaying shark is defending a geographic area and its resources (territory) for its exclusive use (Baldrige and Williams 1969; Johnson and Nelson 1973; Nelson 1981, 1983). Defining territoriality in a way that all ethologists agree upon is difficult because different workers emphasise different attributes to different degrees, depending upon their specific research questions. For purposes of the present review, territoriality will be defined following Wittenberger (1981) as more or less exclusive control of a geographic area by an individual or group of individuals by means of implied or overt aggression. Territorial animals use a variety of displays in defence of their territories, usually against conspecifics (McFarland 1987). Although many reef-dwelling sharks have well-defined home ranges through which they move in highly predictable ways (Johnson 1978; Nelson and Johnson 1980; Nelson 1990), evidence of territoriality in any shark species is equivocal (Barlow 1974; McKibben and Nelson 1986; Nelson et al. 1986). There is no record of reef-dwelling sharks agonistically displaying toward conspecifics—which, having most similar resource needs and exploitation capabilities, constitute the most intense ecological competitors (Nelson et al. 1986). D.R. Nelson (personal communication) noted that resident grey reef sharks at Rangiroa Atoll, French Polynesia, regularly tolerate conspecifics swimming—and even feeding—within their respective home ranges without responding aggressively. Grey reef sharks on the outer reef at Rangiroa undertake medium-scale location changes of up to 15 km per day (Nelson 1981). It seems unlikely that the benefits of defending such a large area warrant the costs.

Conversely, McNair (1975) reported site-dependent temperament in known individual grey reef sharks at Enewetak Atoll, Micronesia, where a given animal would be consistently aggressive on one section of reef yet docile or shy at another section a kilometre or so away. This may be an example of what Brown (1975) termed “dominion”: an area where an individual exhibits elevated dominance and aggression toward others, but does not attempt to expel them. Site-dependent aggression in sharks would be a significant discovery, but more quantitative studies are needed to test this idea.

Direct, rapid approaches by divers are most likely to elicit shark agonistic displays, especially if potential escape routes are restricted or absent. This observation is consistent with the hypothesis (Fellows and Murchison 1967; Johnson and Nelson 1973; Nelson et al. 1986) that these displays signal defensive threat. The open-mouthed, slashing attack that sometimes follows persistent movement toward a displaying grey reef shark, as well as the rapid withdrawal that terminates the agonistic display, are likewise consistent with self-defence rather than feeding. Pending further evidence on the issue of site-dependent aggression, it seems likely that, in most cases, an agonistically displaying shark is motivated by defence of self rather than of a food resource or territory.

Within shark species, agonistic displays are graded responses, suggesting that the signalling animal gauges risk to itself and modulates the intensity of its agonistic display appropriately. Modulation of a signaller’s agonistic response in proportion to perceived risk is probably mediated *via* neurological and endocrine feedback mechanisms (such as experience and motivational state), as it appears to be in other vertebrates (Huntingford 1976; Miller 1978; Toates 1998; Wingfield et al. 1999; Zupanc 2004; Wingfield 2006), but systematic experiments are needed to test this hypothesis.

Evolution

Game theory has contributed significantly toward understanding the evolution of animal behavioural strategies, including habitat usage, foraging decisions, mate choice, and spatial distribution (e.g. Sigmund 1993; Dugatkin and Reeve 1998; Giraldeau and Caraco 2000). Payoff matrices are a robust tool for modelling a wide variety of contests, from which each player’s optimal strategy is readily determined (Barash 2003). Costs (risks) and benefits (rewards) of shark agonistic displays in encounters with divers and the adaptive value of shark agonistic displays can be modelled using payoff matrices. The risks and payoffs to sharks and divers in such encounters are situation and species-dependent. From a modelling perspective, the simplest contests are symmetric, in which opponents have identical fighting ability (Maynard Smith and Price 1973), but most contests in nature are asymmetric, in which opponents differ in fighting ability or the relative value of a contested resource, and must be modelled differently (Maynard Smith and Parker 1976).

Agonistic displays provide information about the signaller, but introduce two kinds of uncertainty, (1) degree of signaller motivation (performance uncertainty) and (2) ability of signaller to inflict injury (assessment uncertainty), rendering accurate risk assessment by receivers difficult (Johnstone 1997). To a shark, a similar-sized conspecific may be more or less motivated to engage in conflict; a larger shark may be faster and more capable of inflicting serious injury than a smaller shark, but may also be less manoeuvrable; bumping or biting a diver may be less risky for a large shark than for a small one; an armed diver is likely more dangerous to attack than an un-armed one, but different weapons (which may be indistinguishable to a shark, such as a speargun *versus* a powerhead) bear different risks of injury to both shark and diver. If the consequences of under- or over-estimating a competitor’s motivation or fighting ability are severe, honest signalling would be favoured

by natural selection; the more uncertainty inherent in an agonistic contest or the more opportunities to benefit or suffer from a mistake, the longer the duration of a display (Johnstone 1997). In all agonistic contests, prudence dictates erring on the side of caution.

Evaluating the costs and benefits of displaying *versus* attacking to a shark under agonistic contexts is difficult. To do so requires knowing or estimating the caloric value of shared *versus* monopolised food items to food-limited sharks relative to the locomotory expense of fleeing *versus* displaying and attacking, weighted against risk of injury and the caloric cost of healing wounds and reduced foraging and reproductive success due to various injuries (W. Goodey, personal communication). Apart from estimates of metabolic rate and cost of transport (Carlson et al. 2004), such data or models for calculating them are not available.

Applying a simple relative scale of costs and benefits to a series of hypothetical encounters between a shark and a similar sized shark, a larger shark, and a diver were evaluated using a payoff matrix (Figure 5; see also Table S-I of supplementary material). In shark–shark encounters, flight is always an economical tactic with generally small energy expenditure, display is economical only if the other shark does not attack, and attack is always expensive (energy and potential for injury), except if the other shark is small enough to be overcome and be a potential meal. In any diver encounter, a shark’s best strategy is to flee whenever possible, as this strategy imposes low locomotor cost and low risk of injury. A shark’s next best strategy, if flight is not possible, is to display, which imposes greater locomotor cost but less risk of injury than an attack. Only as a last resort should a shark attack an unknown opponent, as this imposes low locomotor cost but high potential risk of injury. The only scenario in which a diver might benefit by approaching a fleeing shark during an encounter would be if it afforded a better view or photographic opportunity than that obtained by not approaching. However, when faced with a displaying shark, a diver’s best strategy is to withdraw, as this imposes a relatively low locomotor cost and low risk (the shark will probably flee). Approaching a displaying shark imposes greater risk of injury to a diver than

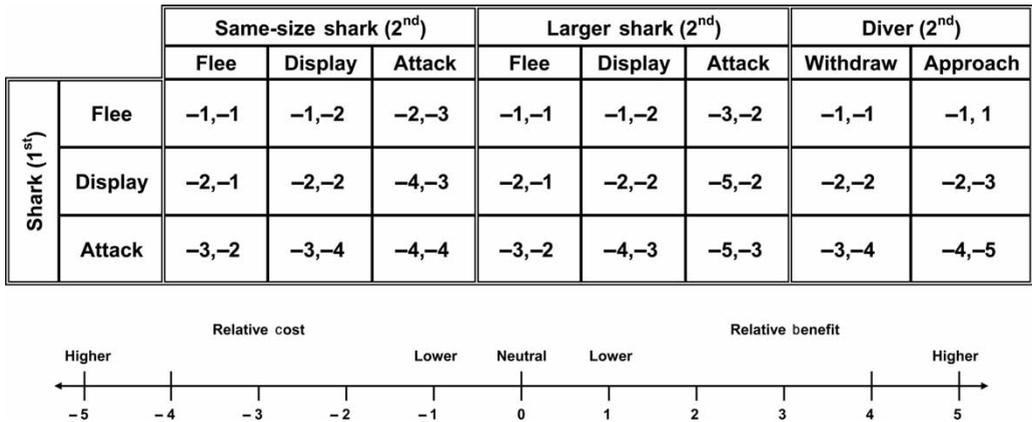


Figure 5. Payoff matrices used to model adaptive value of shark agonistic displays in shark–shark and shark–diver interactions according to a relative scale of costs (risks) and benefits (rewards) of three shark strategies and two diver strategies. Regardless of whether a diver approaches or withdraws, a shark’s best strategy is to flee when possible, display when flight is not possible, and attack only as a last resort. This optimal shark strategy is the same for any encounter with a potential threat. See text for further discussion.

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to a shark, which has greater speed, manoeuvrability, weapons, and is protected by armoured skin that heals quickly (Baldrige 1974a; Reif 1978). Thus, a shark's optimal strategy in encounters with divers is the same, regardless of whether the diver approaches or withdraws. As such, a shark's best responses in agonistic contexts with an unknown combatant can be ranked as follows:

Flee > Display > Attack.

This pattern is completely consistent with observed patterns of shark behaviour during shark–diver interactions. Deviation from this pattern would be expected to result in a suboptimal payoff and thus should be selected against. If, as argued above, divers and submersibles are regarded by sharks as potential threats or predators, this suggests a mechanism by which this anti-predator algorithm may have evolved in response to “natural” (non-human) predators. Maynard Smith (1982) defined an evolutionarily stable strategy (ESS) as a strategy such that, if all members of a population follow the rules, no other strategy could invade the population through natural selection. ESS thus proposes a possible genetic mechanism by which a shark's best response to any potential predator could become fixed within the population (see Parker 2006, for a recent review).

Common features of shark agonistic displays

Agonistic displays of a few shark species exhibit unique elements (e.g. body shiver in the silvertip or corkscrewing in the scalloped hammerhead, *S. lewini*), but a number of elements appear common to the agonistic displays of most (Table II). The seven most common features (with percentage occurrence in parentheses) include: (1) stiff or jerky movements (100%), (2) sustained bilateral pectoral fin depression (100%), (3) rapid withdrawal (83%), (4) jaw gaping (70%), (5) reduced swimming efficiency (52%), (6) flank displaying (48%), and (7) laterally exaggerated swimming movements (13%). All these elements are found in the hunch display of the grey reef shark, indicating that its highly overt agonistic display represents an extreme along a continuum of agonistic behaviours in sharks, which range from subtle (in the Caribbean reef shark) to overt (in the grey reef, silvertip, and Galapagos sharks).

Intriguingly, agonistic behaviours that resemble those of sharks in form (arched back, lowered flippers, ritualised jaw gaping, and flank displaying) and context have been reported in at least three species of cetaceans, the spinner dolphin (*Stenella attenuata*), the bottlenose dolphin (*Tursiops truncatus*), and the humpback whale (*Megaptera novaeangliae*) (Overstrom 1983; Connor and Peterson 1994; Johnson and Norris 1994). Agonistic displays of many unrelated species exhibit convergent properties that honestly inform rivals about the size and fighting capacity of the signaller (Parker 1974). Whether these cetacean agonistic display elements represent behavioural mimicry of sharks, shared hydrodynamic and morphological constraints, or some other form of convergence is not clear. But in the agonistic displays of both sharks and cetaceans, presentation of offensive weapons and the largest possible aspect come at the cost of decreased swimming ability.

Shark–human interactions

Human pursuit and proximity are sign stimuli known to elicit agonistic displays in sharks. However, intensity of agonistic responses by sharks is context dependent. Johnson and Nelson (1973) found the likelihood that a grey reef shark performs an agonistic display increased with speed and directness of diver approach as well as with degree of escape

route restriction. This pattern appears to hold true for most species of actively swimming (i.e. non-benthic) sharks (personal observation). Almost any object in the environment – bottom features, divers, other sharks, or possibly a boat – can restrict a shark’s escape route and may render it more likely to perform an agonistic display (personal observation; Figures 3m, 6, 7c). For example, while swimming near the bottom, individual sharks of most species appear agitated by any diver that maintains position a few metres above the animal’s back (Figure 6d); a situation in which diver proximity and pursuit, a suboptimal view of the diver, and restriction of escape routes by the bottom combine to increase the animal’s stress and the likelihood to perform an agonistic display (personal observation; C. Harvey-Clark, personal communication). A tightly packed group of scuba divers more readily provokes agonistic display in solitary sharks than does a single diver or dispersed group of divers (Figure 7a) and thus may be considered a supernormal stimulus (Bolhuis and Giraldeau 2005).

Use of bait is well known to induce sharks to approach divers more closely than they do without such provisioning (Nelson 1977; Stafford-Deitsch 2000; Figure 7b, compare Video clips 10, 11), although use of bait to stage “feedings” for diving tourists is highly controversial (Brylske 2000; Carwardine 2004). Single-species groups of sharks that have become acclimatised to being fed individually by taking bait impaled on the end of a feeding pole appear relaxed and—despite close proximity of divers and conspecifics—rarely, if ever, display agonistically (Figure 7b, Video clip 11). In contrast, shark agonistic displays may be elicited toward divers during mixed species feeding events, especially when food is thrown

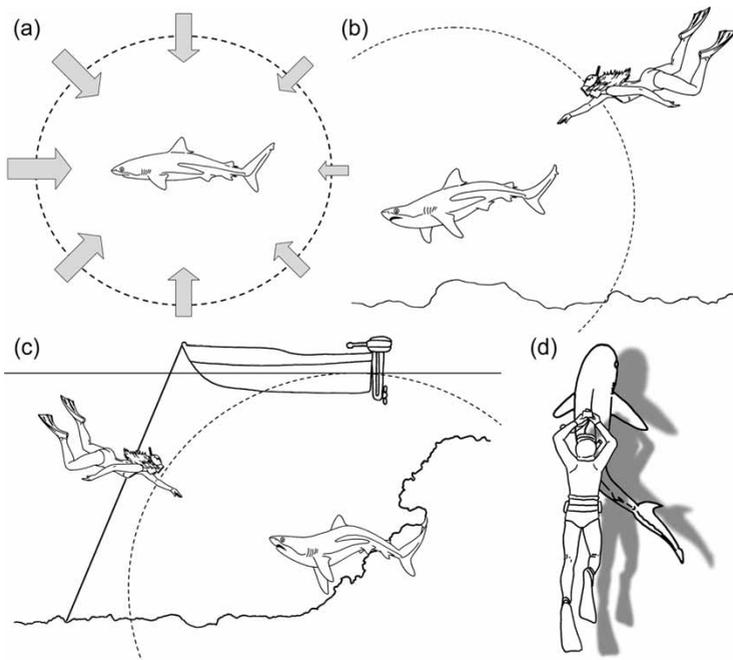


Figure 6. Shark-human interaction scenarios likely to elicit agonistic displays in sharks. (a) Diver approach angle and relative degree of shark agitation, represented by arrow thickness, (b) crowding a shark against the bottom, (c) crowding a shark against the bottom, a reef pinnacle, and a boat, (d) diver maintaining a 12 o'clock position above a shark's back as it swims over the bottom. Dashed circle = diver distance at which agonistic display is initiated.



Figure 7. Shark–diver interactions and degree of shark stress; (a) a tightly packed group of divers appears more stressful to many sharks, including this mildly agonistically displaying grey reef shark (*C. amblyrhynchos*), than a single diver or dispersed group. (b) During staged feeding events, single-species groups of sharks that have been conditioned to take bait from a feeding pole approach divers and conspecifics closely, yet appear relaxed. (c) In multi-species feeding events, especially those in which bait is thrown or scattered into the water, shark stress is often elevated; here a blacktip shark (*C. limbatus*, circled) constrained by the bottom and nearby bull sharks (*C. leucas*), performs an agonistic display toward the cameraman.

or scattered into the water (Figures 3p, 6c; Video clip 12). Under such conditions, proximity of the bottom and nearby sharks may restrict escape route of an agonistically displaying shark and increase risk of attack against a nearby diver. Interpreting the significance of these differences is hampered by general lack of data on the extent of learning from past inter- or intraspecific encounters among individual sharks, including the effects of previous agonistic wins and losses. However, as with any wildlife encounter, ability to anticipate and avoid shark–human encounter scenarios known to agitate sharks, such as those described here, can help reduce the inherent risks of such encounters.

Shark–diver interactions are inherently risky but the level of danger can be limited by a diver’s ability to recognise signs that a shark is becoming agitated and respond appropriately (personal observation). Under unbaited conditions, most sharks simply avoid divers. However, some individuals, particularly of relatively large and actively predatory species, appear curious about divers and may approach closely. It is probably safest for a diver to allow a shark to approach on its own terms; attempts to approach it will likely cause the animal to flee. A mildly agitated shark may accelerate away for a few body lengths and then resume a more relaxed cruising pace. As a shark becomes moderately agitated by diver encroachment, it often changes course frequently, using short, jerky movements. With increasing agitation, common elements of shark agonistic displays begin to appear. Most conspicuous of these are rapid, jerky movements and sustained, bilateral pectoral fin depression. The more agitated the shark, the more stiff and jerky its swimming movements and the more strongly its pectoral fins are depressed. These signs typically escalate in the regular – and thus predictable – patterns outlined here. Intensity of shark agitation increases with diver proximity, speed and directness of diver approach, and the number of sharks. However, in the vast majority of encounters, shark agonistic displays and signs of shark agitation reduce in frequency and intensity with diver withdrawal. Thus, to a certain extent, an experienced diver can mediate the intensity of shark encounters through his own actions. It is, however, absolutely vital that divers maintain visual contact with all sharks in the immediate vicinity throughout an encounter. Should a diver be unable to see all sharks in the vicinity at all times, prudence dictates leaving the water as quietly and efficiently as possible.

Based on results presented here, it seems likely that a shark performing an agonistic display is signalling that it is in a highly agitated state and on the verge of either attacking

or fleeing; if the receiver persists, the shark will attack rather than flee. Such ritualised threats appear to be mostly bluff (the shark usually flees without attacking), but prudence dictates that one should not depend on this. This comparative behavioural review identifies common elements in shark agonistic displays that could assist divers and other ocean users to recognise whether a shark is becoming agitated and may inform human responses to an agonistically displaying shark.

Critical approach distances and diver safety

Hediger (1964) noted that animals vary in inter-individual spacing. Extending this idea to humans, Hall (1966) found that humans use space differently depending upon their size, sex, status, and culture, establishing the field he termed “proxemics”. Individuals define and defend a “personal space” around themselves, the limits of which are dependent upon interpersonal relationships and context (Hall 1966). Personal space is modelled as a single, stable underlying characteristic that reflects a dynamic interplay of multiple factors (Hayduk 1994). Strube and Werner (1982) found that interpersonal distances and personal spaces expand reactively in response to a threat. This seems homologous to the apparent relationship between the intensity of perceived threats and the concomitant intensity of agonistic displays by sharks. The term “personal space” seems inappropriate to apply to animals, yet the phenomenon appears to be common to sharks, humans, and probably other social vertebrates as well. The new term “idiosphere” (from the Greek *idios*, meaning “own”) is hereby proposed for the volume immediately surrounding an individual animal (of any species) that it will defend if breached without appropriate signalling or permission.

Extrapolating from the lines of evidence outlined in this review, it appears that sharks, (1) regard an approaching human as a potential threat and, (2) use their superior swimming ability to set the limits of their idiosphere. Diameter of an individual shark’s idiosphere varies with species, sex, maturity stage, context, and possibly other factors. Based on these assumptions, the nested system of shark alert, flight, and defence distances diagrammed in Figure 8 is proposed to explain their behaviour toward divers. As a diver breaches the “alert distance” (2–10+ BL), the shark is likely to increase its speed and/or change course repeatedly; the more agitated the shark becomes, the greater its speed and the more frequent its course changes. If the diver breaches the “flight distance” perimeter, the shark is likely to accelerate away at 2–3 BL/s without displaying or attacking. Persistent breaches of this perimeter, however, may elicit an agonistic display, probably including the most frequently shared display elements identified in the present study. If the diver manages to breach the “attack distance”, the animal is likely to respond with a lightning fast slash with the upper jaw teeth followed by a rapid withdrawal at 3+ BL/s. In at least one case involving an agonistically displaying grey reef shark, the discharge of an underwater strobe incited the shark to break its display and attack the photographer and his buddy, resulting in serious injuries to both (Nelson 1981; P. Light, personal communication). Although the shark may not close its jaws or remove flesh, such an attack can inflict serious injuries and should be avoided or deflected if at all possible.

The best defence, when faced with a shark that appears to be agitated is to avoid exacerbating the situation. If a shark appears agitated (exhibits stiff, jerky movements and/or frequent direction changes) but has not yet begun to display, maintaining visual contact with the animal and withdrawing are likely to reduce signs of the animal’s agitation and stimulate it to withdraw from the area (personal observation). For divers faced with an

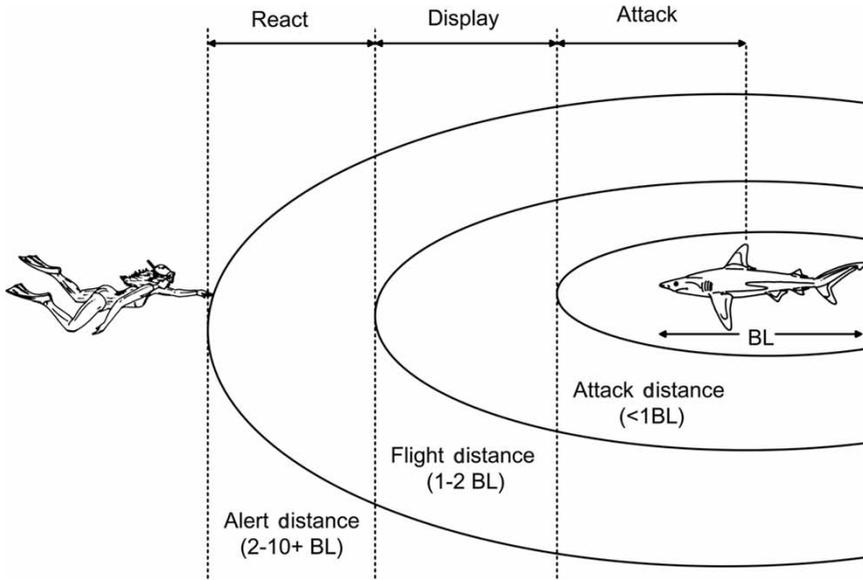


Figure 8. Hypothesised scheme of nested critical approach distances for a typical reef shark. BL = body length of the shark. See text for further explanation.

agonistically displaying shark, the outcomes of the present review and model suggest that the following safety recommendations may be of assistance:

- (1) Face the displaying shark and maintain eye contact
- (2) Do not touch, approach, or photograph a displaying shark
- (3) If carrying speared fish or collected marine animals, surrender them immediately
- (4) Back away from the displaying shark, using smooth purposeful movements; the shark will most likely seize the opportunity to withdraw
- (5) Remain on the bottom, with your back toward a reef, wreck, or – if nothing else is available – your dive buddy
- (6) Return to, or immediately below (if boat diving), your pre-planned exit point and exit the water unhurriedly but efficiently
- (7) During surfacing in open water and while at the surface, check water around and beneath in case the shark follows
- (8) If the shark follows, be ready to fend it off with any available object; avoid using your bare hands, if possible, as the shark's rough skin and teeth may cause injury.

The preceding recommendations are a best estimate based on the information reviewed here. Like all scientific models, they are subject to constant revision as new information comes to light and new experiments or observations lead to revision or rejection of previous hypotheses.

Future directions

Sound and video playback-style experiments are needed to test the functional significance of shark agonistic signals and sensory modalities involved, while long-term systematic studies of marked sharks are needed to make informed interpretations of the role of

experience in agonistic interactions. Controlled studies of agonistic behaviours of small sharks in captivity need to be verified under more natural conditions in the wild, perhaps using diver-acclimatised sharks to test how experience affects the outcome of agonistic interactions. Field experiments by suitably protected researchers on large, potentially dangerous, shark species are needed to test the model of nested critical approach distances and applicability of safety recommendations presented here.

It is clear that much remains to be learned about shark agonistic displays and also about their perception of and interactions with humans. Further study of agonistic behaviour in sharks is likely to pay dividends not only in a richer understanding of shark social dynamics but also in increased safety in shark–human interactions. With knowledge and care, sharks can be approached in their natural habitat and observed at close range in relative safety and with minimal observer impact. Such direct observations are likely to provide new insights into subtler aspects of shark social behaviour.

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References

- Alcock J. 1993. *Animal behaviour: An evolutionary approach*. 5th ed. Sunderland, MA: Sinauer.
- Alcock J. 2001. *The triumph of sociobiology*. Oxford: Oxford University Press.
- Allee DG, Dickenson JC. 1954. Dominance and subordination in the smooth dogfish, *Mustelus canis* (Mitchell). *Physiol. Zool.* 27:356–364.
- Baldrige HD. 1974a. Shark attack. New York: Berkley Medallion.
- Baldrige HD. 1974b. Shark attack: A program of data reduction and analysis. *Contri. Mote Marine Lab* 1:98.
- Baldrige HD. 1988. Shark aggression against man: beginnings of an understanding. *Calif. Fish Game* 74:208–217.

- Baldrige HD, Williams J. 1969. Shark attack: Feeding or fighting. *Mil. Med.* 134:130–133.
- Barash DP. 2003. *The survival game: How game theory explains the biology of cooperation and competition.* New York: Henry Holt.
- Barlow GW. 1974. Derivation of threat display in the gray reef shark. *Mar. Behav. Physiol.* 3:71–81.
- Barlow GW. 1977. Modal action patterns. In: Sebeok TA, editor. *How animals communicate.* Bloomington: Indiana University Press. pp 98–134.
- Bass AJ. 1978. Problems in studies of sharks in the southwest Indian Ocean. In: Hodgson ES, Mathewson RF, editors. *Sensory biology of sharks and rays.* Arlington VA: Office of Naval Research, Department of the Navy. pp 545–584.
- Bock WJ, von Wahlert G. 1998. Adaptation and the form-function complex. In: Allen C, Bekoff M, Lauder G, editors. *Nature's purposes: Analyses of function and design in biology.* Cambridge MA: MIT Press. pp 117–167.
- Bolhuis JJ, Giraldeau L-A. 2005. *The behavior of animals: Mechanisms, function, and evolution.* Oxford: Blackwell Publishing.
- Bone Q. 1988. Muscles and locomotion. In: Shuttleworth TJ, editor. *Physiology of elasmobranch fishes.* Berlin: Springer-Verlag. pp 99–141.
- Bradbury JW, Vehrencamp SL. 1998. *Principles of animal communication.* Sunderland, MA: Sinauer Associates Inc.
- Bres M. 1993. The behaviour of sharks. *Rev. Fish Biol. Fish.* 3:133–159.
- Brown JL. 1975. *The evolution of behaviour.* New York: WWW Norton and Co.
- Brunschweiler JM. 2006. Sharksucker-shark interaction in two carcharhinid species. *Mar. Ecol.* 27:89–94.
- Brylske A. 2000. Fish feeding, Part 1: The controversial shark dive. *Dive Train.* 10:28–40.
- Carew TJ. 2000. *Behavioral neurobiology.* Sunderland, MA: Sinauer.
- Carlson JK, Goldman KJ, Lowe CG. 2004. Metabolism, energetic demands, and endothermy. In: Carrier JC, Musick JA, Heithaus MP, editors. *Biology of sharks and their relatives.* Boca Raton, FL: CRC Press. pp 203–224.
- Carpenter CC. 1978. Ritualistic social displays in lizards. In: Greenberg N, MacLean PD, editors. *Behavior and neurology of lizards.* Washington DC: National Institute of Mental Health. pp 256–267.
- Carwardine M. 2004. *Shark.* Buffalo, NY: Firefly Books.
- Carwardine M, Hoyt E, Fordyce RE, Gill P. 1998. *Whales, dolphins & porpoises.* Sydney: Welson Owen.
- Church R. 1961. Shark attack. *Skin Diver Mag.* June:30–31.
- Cliff G. 1988. Raggedtooth shark. In: Venter AJ, Sachs P, Maxwell C, editors. *South Africa's second underwater handbook.* Rivonia, South Africa: Ashanti Publishing. pp 67–76.
- Colgan P. 1993. The motivational basis of fish behaviour. In: Pitcher TJ, editor. *Behaviour of teleost fishes.* . 2nd ed ed. London: Chapman and Hall. pp 31–55.
- Collier RS. 1993. Shark attacks off the California islands: Review and update. In: Hochberg FG, editor. *Third California Islands symposium: Recent advances in research on the California Islands.* Santa Barbara CA: Santa Barbara Museum of Natural History. pp 453–462.
- Collier RS. 2003. *Shark attacks of the twentieth century from the Pacific Coast of North America.* Chatsworth, CA: Scientia Publishing.
- Compagno JLV. 1984. *Sharks of the world: An annotated and illustrated catalogue of shark species known to date.* FAO Species Catalogue, Vol. 4, Pt. 2 (Carcharhiniformes). Rome: United Nations Development Program.
- Compagno LJV. 2001. *Sharks of the world: An annotated and illustrated catalogue of shark species known to date.* Volume 2. Bullhead, mackerel, and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes, No. 1, Vol. 2. Rome: FAO.
- Compagno LJV, Ebert DA, Smale MJ. 1989. *Guide to the sharks & rays of southern Africa.* Cape Town: Struik.
- Connor RC, Peterson DM. 1994. *The lives of whales and dolphins.* New York: Henry Holt and Co.
- Cuthill IC, Houston AI. 1997. Managing time and energy. In: Krebs JR, Davies NB, editors. *Behavioural ecology: An evolutionary approach.* . 4th ed ed. London: Blackwell Science. pp 97–120.
- Demski LS. 1990. Neuroendocrine mechanisms controlling the sexual development and behaviour of sharks and rays. *J. Aquaric. Aquat. Sci.* 5:53–67.
- Dewsbury DA. 1978. *Comparative animal behaviour.* New York: McGraw-Hill Book Co.
- Doak W. 1975. *Sharks and other ancestors: Patterns of survival in the South Seas.* Auckland: Hodder and Stoughton.
- Dugatkin LA, Reeve H, editors, 1998. *Game theory and animal behavior.* Oxford: Oxford University Press.
- Dusenbery DB. 1992. *Sensory ecology: How organisms acquire and respond to information.* New York: WH Freeman & Co.
- Eibl-Eibesfeldt I. 1966. *Land of a thousand atolls.* Cleveland, OH: World Publishing Co.

- Eibl-Eibesfeldt I, Hass H. 1959. Erfahrungen mit haien. *Z. Tierpsychol.* 16:733–746.
- Fellows DP, Murchison EA. 1967. A noninjurious attack by a small shark. *Pac. Sci.* 21:150–151.
- Fine ML, Winn HE, Olla BL. 1977. Communication in fishes. In: Sebeok TA, editor. *How animals communicate*. Bloomington: Indiana University Press. pp 472–518.
- Fish FE, Shannahan LD. 2000. The role of the pectoral fins in body trim of sharks. *J Fish. Biol.* 56:1062–1073.
- Froese, R, Pauly D, editors. 2006. FishBase. Available: www.fishbase.org via the INTERNET. Accessed May 2006.
- Gilbert PW. 1963. The visual apparatus of sharks. In: Gilbert PW, editor. *Sharks and survival*. Boston MS: D.C. Heath. pp 283–326.
- Giraldeau L-A, Caraco T. 2000. *Social foraging theory*. Princeton, NJ: Princeton University Press.
- Gruber SH. 1993. Confusing carcharhinids – the final chapter? *Bull. Am. Litt. Soc.* 22:16–23.
- Gruber SH, Cohen JL. 1978. Visual system of the elasmobranchs: State of the art 1960–1975. In: Hodgson ES, Mathewson RF, editors. *Sensory biology of sharks and rays*. Arlington VA: Office of Naval Research, Department of the Navy. pp 11–105.
- Guthrie DM, Muntz WRA. 1993. Role of vision in fish behaviour. In: Pitcher TJ, editor. *Behaviour of teleost fishes*. 2nd ed ed. London: Chapman and Hall. pp 89–128.
- Hall ET. 1966. *The hidden dimension*. Garden City, NY: Doubleday and Co.
- Hall M, Halliday T. 1998. *Behaviour and evolution*. Berlin: Springer-Verlag.
- Hammerschlag N, Fallows C. 2005. Galapagos sharks (*Carcharhinus galapagensis*) at the Basas da India atoll: First record from the Mozambique Channel and possible significance as a nursery area. *S. Afr. J. Sci.* 101:375–377.
- Hauser MD, Nelson DA. 1991. Intentional signaling in animal communication. *Trends Ecol. Evol.* 6:186–189.
- Hayduk LA. 1994. Personal space: Understanding the simplex model. *J. Nonverb. Behav.* 18:245–260.
- Hediger H. 1964. *Wild animals in captivity*. New York: Dover.
- Helfman GS, Collette BB, Facey DE. 1997. *The diversity of fishes*. London: Blackwell Science.
- Hinde RA. 1974. *Biological bases of human social behaviour*. New York: McGraw-Hill.
- Hinde RA. 1982. *Ethology: Its nature and relations with other sciences*. Oxford: Oxford University Press.
- Hobson ES. 1963. Feeding behaviour in three species of sharks. *Pac. Sci.* 17:171–194.
- Hobson ES. 1964. Sharks increasing visual field. *Underw. Natural.* 229.
- Hueter RE, Gilbert PW. 1991. The sensory world of sharks. In: Gruber SH, editor. *Discovering sharks*. Highlands NJ: American Littoral Society. pp 48–55.
- Hueter RE, Mann DA, Maruska KP, Sisneros JA, Demski LS. 2004. Sensory biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MP, editors. *Biology of sharks and their relatives*. Boca Raton FL: CRC Press. pp 325–368.
- Huntingford FA. 1976. The relationship between inter- and intra-specific aggression. *Anim. Behav.* 24: 485–497.
- Johnson CM, Norris KS. 1994. Social behavior. In: Norris KS, Würsig B, Wells RS, Würsig M, editors. *The Hawaiian spinner dolphin*. Berkeley CA: University of California Press. pp 243–286.
- Johnson RH. 1978. *Sharks of Polynesia*. Papeete: Les Editions du Pacifique.
- Johnson RH, Nelson DR. 1973. Agonistic display in the gray reef shark, *Carcharhinus menisorrah*, and its relationship to attacks on man. *Copeia* 1973:76–84.
- Johnson RH, Nelson DR. 1978. Copulation and possible olfaction-mediated pair formation in two species of carcharhinid sharks. *Copeia* 1978:539–542.
- Johnson RN. 1972. *Aggression in man and animals*. Philadelphia, PA: Saunders.
- Johnstone RA. 1997. The evolution of animal signals. In: Krebs JR, Davies NB, editors. *Behavioural ecology: An evolutionary approach*. 4th ed ed. London: Blackwell Science. pp 155–178.
- Jones L. 1991. Ten feet of death. In: Condon T, editor. *Great white sharks (Carcharodon carcharias), a perspective*. Underwater Special Edition. Vol. 17. pp 59–60.
- Kalmijn AJ. 1978. Electric and magnetic sensory world of sharks, skates, and rays. In: Hodgson ES, Mathewson RF, editors. *Sensory biology of sharks and rays*. Arlington VA: Office of Naval Research, Department of the Navy. pp 507–528.
- King JA. 1973. The ecology of aggressive behavior. In: Johnson RF, Frank PW, Michener D, editors. *Annual review of ecology and systematics*. Palo Alto CA: Annual Reviews. pp 117–138.
- Klimley AP. 1985. Schooling in *Sphyrna lewini*, a species with low risk of predation: A non-egalitarian state. *Z. Tierpsychol.* 70:297–319.
- Klimley AP, Pyle P, Anderson SD. 1996. Tail slap and breach: Agonistic displays among white sharks? In: Klimley AP, Ainley DG, editors. *Great white sharks: The biology of Carcharodon carcharias*. San Diego CA: Academic Press. pp 241–255.

- Krebs JR, Davies NB. 1993. 3rd ed. An introduction to behavioural ecology. Oxford: Blackwell Scientific Publications.
- Last PR, Stevens JD. 1994. Sharks and rays of Australia. Australia: CSIRO.
- Lehner PN. 1979. Handbook of ethological methods. New York: Garland STPM Press.
- Lorenz K. 1964. Ritualized fighting. In: Carthy JD, Ebling FJ, editors. The natural history of aggression. London: Academic Press. pp 39–50.
- Lorenz K. 1966. On aggression. London: Methuen.
- Manning A. 1979. 3rd ed. An introduction to animal behaviour. Cambridge: Cambridge University Press.
- Martin P, Bateson P. 1986. Measuring behaviour: An introductory guide. Cambridge: Cambridge University Press.
- Martin RA. 2003. Field guide to the great white shark. Vancouver Canada: ReefQuest Centre for Shark Research.
- Martin RA, Hammerschlag N, Collier RS, Fallows C. 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. J Mar. Biol. Ass. U.K. 85:1121–1135.
- Martin RA, Martin A. 2006. Sociable killers. Nat. Hist. 115:42–48.
- Maynard Smith J. 1982. Evolution and the theory of games. Cambridge, UK: Cambridge University Press.
- Maynard Smith J, Parker GA. 1976. The logic of asymmetric contests. Anim. Behav. 24:159–175.
- Maynard Smith J, Price GR. 1973. The logic of animal conflicts. Nature 246:15–18.
- McFarland D. 1987. The Oxford companion to animal behaviour. Oxford: Oxford University Press.
- McFarland W. 1991. Light in the sea: The optical world of elasmobranchs. J. Exper. Zool. Suppl. 5:3–5.
- McGregor PK. 2005. Communication. In: Bolhuis JJ, Giraldeau L-A, editors. The behavior of animals: Mechanisms, function and evolution. Malden MA: Blackwell Publishing. pp 226–250.
- McKibben JN, Nelson DR. 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. Bull. Mar. Sci. 38:89–110.
- McNair R. 1975. Sharks I have known. Skin Diver Mag. 24:52–57.
- Meltzoff S. 1988. Confusing Caribbean carcharinids. Underw. Natural. 17:14–20.
- Miller DJ, Collier RS. 1981. Shark attacks in California and Oregon, 1926–1979. Calif. Fish Game 67:76–104.
- Miller RJ. 1978. Agonistic behavior in fishes and terrestrial vertebrates. In: Reese ES, Lighter FJ, editors. Contrasts in behavior: Adaptations in the aquatic and terrestrial environments. New York, NY: Wiley-Interscience. pp 281–311.
- Moss SA. 1984. Sharks: An introduction for the amateur naturalist. Englewood Cliffs, NJ: Prentice-Hall.
- Myrberg AA. 1991. Distinctive markings of sharks: Ethological considerations of visual function. J. Exper. Zool. Suppl. 5:156–166.
- Myrburg AA, Gruber SH. 1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. Copeia 1974:358–374.
- Nelson DR. 1977. On the field study of shark behavior. Amer. Zool. 17:501–507.
- Nelson DR. 1981. Aggression in sharks: is the gray reef shark different? Oceanus 24:45–56.
- Nelson DR. 1983. Shark attack and repellency research: An overview. In: Zahuranec BJ, editor. Shark repellents from the sea: New perspectives. AAAS Sel. Symp. 83:11–74.
- Nelson DR. 1990. Telemetry studies of sharks: A review, with applications in resource management. NOAA Tech. Rep. NMFF 90:239–256.
- Nelson DR, Johnson RH. 1980. Behavior of reef sharks of Rangiroa, French Polynesia. Nat. Geo. Soc. Res. Rep. 12:479–499.
- Nelson DR, Johnson RR, McKibben JN, Pittenger GG. 1986. Agonistic attacks on divers and submersibles by gray reef sharks, *Carcharhinus amblyrhynchos*: antipredatory or competitive? Bull. Mar. Sci. 38:68–88.
- Overstrom N. 1983. Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). Zoo Biol. 2:93–103.
- Parker GA. 1974. Assessment strategy and the evolution of fighting behaviour. J. Theoret. Biol. 47:223–243.
- Parker GA. 2006. Behavioural ecology: Natural history as science. In: Lucas JR, Simmons LW, editors. Essays in animal behaviour celebrating 50 years of Animal Behaviour. Burlington MA: Elsevier Academic Press. pp 23–56.
- Reebs S. 2001. Fish behaviour in the aquarium and in the wild. Ithaca, NY: Cornell University Press.
- Reese ES. 1978. The study of space-related behavior in aquatic animals: special problems and selected examples. In: Reese ES, Lighter FJ, editors. Contrasts in behavior: Adaptations in the aquatic and terrestrial environments. New York, NY: Wiley-Interscience. pp 347–374.
- Reichert SE. 1982. Spider interaction strategies: Communication vs. coercion. In: Witt PW, Rovner JS, editors. Spider communication: Mechanisms and ecological significance. Princeton NJ: Princeton University Press. pp 281–315.

- Rief W-E. 1978. Wound healing in sharks: Form and arrangement of repair scales. *Zoomorphol.* 90:101–111.
- Ritter EK. 2002. Analysis of sharksucker, *Echineis naucates*, induced behavior patterns in the blacktip shark, *Carcharhinus limbatus*. *Envir. Biol. Fishes* 65:111–115.
- Ritter EK, Godknecht JM. 2000. Agonistic displays in the blacktip shark (*Carcharhinus limbatus*). *Copeia* 2000:282–284.
- Scharfer A. 2003. Site fidelity and behavior of sharks at a long-term shark feeding dive site [Internet]. U. Fl. J. Undergrad. Res., 5:1–10. Available from: http://www.clas.ufl.edu/jur/200312/paper_scharfer.html
- Scott JP. 1971. Theoretical issues concerning the origin and causes of fighting. In: Eleftheriou BE, Scott JP, editors. *The physiology of aggression and defeat*. New York: Plenum Press. pp 11–42.
- Scott JP, Fredericson E. 1951. The causes of fighting in mice and rats. *Physiol. Zool.* 24:273–309.
- Searcy WA, Nowicki S. 2000. Male-male competition and female choice in the evolution of vocal signalling. In: Espmark Y, Amundsen T, Rosenqvist G, editors. *Animal signals: Signalling and signal design in animal communication*. Trondheim: Tapir Academic Press. pp 301–315.
- Server L. 1989. *Sharks*. New York: The Image Bank. p 82.
- Sigmund K. 1993. *Games of life: Explorations in ecology evolution and behaviour*. Oxford: Oxford University Press.
- Simpson MJA. 1968. The display of the Siamese fighting fish, *Betta splendens*. *Anim. Behav. Monogr.* 1:1–73.
- Stafford-Deitsch J. 1987. *Shark: A photographer's story*. San Francisco: Sierra Club Books.
- Stafford-Deitsch J. 1999. *Red Sea sharks*. London: Trident Press.
- Stafford-Deitsch J. 2000. Identification, behaviour and natural history of sharks of Florida, the Bahamas, the Caribbean, the Gulf of Mexico. London: Trident Press.
- Stark W, Anderson A. 1978. *The blue reef*. New York: Knopf.
- Stoneman J. 1985. Requiem threats. *Disc.* 6:117.
- Strong WR. 1996. Repetitive aerial gaping: A thwart-induced behavior in white sharks. In: Klimley AP, Ainley DG, editors. *Great white sharks: The biology of Carcharodon carcharias*. San Diego CA: Academic Press. pp 207–215.
- Strube MJ, Werner C. 1982. Interpersonal distance and personal space: A conceptual and methodological note. *J. Nonverb. Behav.* 6:163–170.
- Thomas JW, Robinson FM, Marburger RG. 1965. Social behavior in a white-tailed deer herd containing hypogonadal males. *J. Mammal.* 56:314–327.
- Thomson KS. 1976. On the heterocercal tail in sharks. *Paleobiol.* 2:19–38.
- Thomson KS, Simanek DE. 1977. Body form and locomotion in sharks. *Am. Zool.* 17:343–354.
- Tinbergen N. 1952. "Derived" activities, their causation, biological significance and emancipation during evolution. *Q. Rev. Biol.* 27:1–32.
- Toates F, editor. 1998. *Control of behaviour*. Berlin: Springer-Verlag.
- Torricelli P, Lugli M, Bobbio L. 1983. The importance of male-male competition and sexually selected dimorphic traits for male reproductive success in site-attached fishes with paternal care: The case of the freshwater goby *Padogobius martensi*. In: Huntingford FA, Torricelli P, editors. *Behavioural ecology of fishes*. Chur Switzerland: Harwood Academic Publishers. pp 231–256.
- Vehrencamp SL. 2000. Handicap, index, and conventional signal elements of birdsong. In: Espmark Y, Amundsen T, Rosenqvist G, editors. *Animal signals: Signalling and signal design in animal communication*. Trondheim Norway: Tapir Academic Press. pp 277–300.
- Wilga CD, Lauder GV. 2000. Three-dimensional kinematics and wake structure of the pectoral fins during locomotion in leopard sharks *Triakis semifasciata*. *J. Exper. Biol.* 203:2261–2278.
- Wilga CAD, Lauder GV. 2004. Biomechanics of locomotion in sharks, rays, and chimeras. In: Carrier JC, Musick JA, Heithaus MP, editors. *Biology of sharks and their relatives*. Boca Raton, FL: CRC Press. pp 139–164.
- Wilson EO. 1975. *Sociobiology: The new synthesis*. Cambridge MA: Harvard University Press.
- Wingfield JC. 2006. Control of behavioural strategies for capricious environments. In: Lucas JR, Simmons LW, editors. *Essays in animal behaviour celebrating 50 years of Animal Behaviour*. Burlington MA: Elsevier Academic Press. pp 115–133.
- Wingfield JC, Jacobs JD, Soma K, Maney DL, Hunt K, Wisti-Peterson D, Meddle S, Ramenofsky M, Sullivan K. 1999. Testosterone, aggression, and communication: Ecological bases of endocrine phenomena. In: Hauser M, Konishi M, editors. *The design of animal communication*. Cambridge MA: MIT Press. pp 255–283.
- Wittenberger JF. 1981. *Animal social behavior*. Boston: Duxbury Press.

- Wyatt TD. 2003. Pheromones and animal behaviour. Cambridge MA: Cambridge University Press.
- Zahavi A. 1977. Reliability in communication systems and the evolution of altruism. In: Stonehouse B, Perrins C, editors. Evolutionary ecology. London: Macmillan. pp 253–259.
- Zahavi A. 1993. The fallacy of conventional signalling. *Philos. Trans. R. Soc. Lond., Biol. Sci.* 340:227–230.
- Zupanc GKH. 2004. Behavioral neurobiology: An integrative approach. Oxford: Oxford University Press.