



## The role of learning in shark behaviour

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### Abstract

The role of learning in behaviour is well known for many animal taxa, including teleost fishes, insects, birds and mammals. However, its importance to sharks in everyday behavioural processes has rarely been considered. Almost 50 years ago the first learning experiments on sharks were conducted; our first section discusses these studies and places them in a framework of associative and non-associative learning. These experiments showed that sharks were capable of different forms of learning, such as operant and classical conditioning and habituation. Sharks could learn associations as rapidly as other vertebrates and also remember training regimes for several months. However, much of this experimental evidence was based on small sample sizes and few shark orders, such as Carcharhiniformes and Orectobloformes, leaving large gaps in our knowledge of the general learning capabilities of other shark orders. We also examine recent research that has tested for, or inferred learning in behavioural processes. This section reveals that sharks, like teleost fishes use learning to improve prey search and capture to potentially navigate and orientate in their home range and recognize conspecifics, heterospecifics and mates. Learning is also discussed in relation to ecotourism and fisheries. Findings indicated that these activities may lead to conditioning of sharks and that considerable effort should go into investigating what impact this could have on the shark species involved. Finally, we discuss the importance of combining laboratory experiments with field studies, the use of new experimental techniques, the role of model species and research priorities for future work.

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## Introduction

Many animals live in fluctuating and complex environments that are constantly changing. In response to such environments many organisms have evolved different levels of phenotypic plasticity that allow for short- and long-term adaptive changes in morphology and behaviour. One such adaptation is learning, which is most commonly defined as a change in behaviour as a result of experience (Dill 1983). It excludes permanent changes to behaviour through maturity and changes in internal states, such as hunger and fear (Krause and Ruxton 2002).

Recent evidence has suggested that some of the learning abilities of teleost fishes are comparable to land vertebrates (Kieffer and Colgan 1992; Bshary *et al.* 2002; Brown and Laland 2003; Brown *et al.* 2006) and that the processes used are strikingly similar (Laland *et al.* 2003). Given the small size of many species and easy captive-breeding procedures, teleost fish now provide a popular vertebrate model system for studying many aspects of animal learning and cognition (Brown *et al.* 2006). However, and perhaps understandably, most research on fish learning has tended to focus on small freshwater species such as goldfish (*Carassius auratus*, Cyprinidae), guppies (*Poecilia reticulata*, Poeciliidae) and sticklebacks (Gasterosteidae) that are easy to manipulate and maintain in laboratories (Fernö *et al.* 2006). For marine fishes learning research has centred on commercially important species, such as salmon (Salmonidae) and cod (Gadidae). This is mainly because of the huge interest in fish farming and the need to devise rearing methods to enhance survival of captive-bred stocks after release into the wild (Brown and Laland 2003). Studies, on juvenile Atlantic cod (*Gadus morhua*, Gadidae) have identified that rearing them in enriched environments can promote behavioural flexibility (Braithwaite and Salvanes 2005; Salvanes *et al.* 2007). Whereas research on Pacific salmon (*Oncorhynchus* spp.,

Salmonidae) has provided important insights into what marine fishes might learn as they undergo migration (Dittman and Quinn 1996; Odling-Smee and Braithwaite 2003).

Sharks as a model animal cannot be considered a 'typical fish' (Sims 2003). They are part of a highly diverse group of marine vertebrates, known as the cartilaginous fishes (Chondrichthyes) that evolved independently of bony fishes (Osteichthyes) about 400 million years ago (Pough *et al.* 1999). Sharks range from planktivores to apex predators, exhibit diverse reproductive modes, have long life spans, display ontogenetic shifts in diet and habitat preference and have widespread variation in brain size and complexity (Wetherbee and Cortes 2004; Yopak *et al.* 2007; Lowry and Motta 2008; Pikitch *et al.* 2008). For these reasons, the aforementioned learning studies that focus on small teleosts are unlikely to be informative for sharks.

Our review will begin by introducing the different forms of learning, discussing terminology and early experimental evidence for learning in sharks. Studies will then be discussed in the context of free-ranging shark behaviour in the natural environment where learning is likely to play an important role, such as in foraging (search, capture and manipulation), travelling (orientation, navigation and migration) and social interactions (with mates, conspecifics/heterospecifics). In addition, learning will be discussed in relation to fisheries and the relatively new ecotourism practice of shark feeding by divers. Finally, we conclude the review by summarizing what is known about shark learning, identifying future research directions and proposing new techniques, methodology and model species.

## Learning terminology and early shark experiments

The general principles of learning can be described in two forms: (i) associative learning, which is the learning of an association or relationship between

two events; examples include: operant and classical conditioning, imprinting and observational learning (Lieberman 1990) and (ii) non-associative learning, which is when learning occurs as the result of the presentation of a single stimulus; examples include: habituation and sensitization (Lieberman 1990). These terms, developed by comparative psychologists have provided a useful conceptual framework for researchers working on learning in a variety of animal taxa including bees, pigeons, rats and teleost fish (Lieberman 1990; Brown *et al.* 2006). The following section integrates a description of these terms along with experimental evidence from early research on shark learning.

### Associative learning

Sharks' capacity to learn was first demonstrated experimentally by Eugenie Clark and colleagues in the late 1950s, using an operant conditioning regime (Clark 1959, 1963). In this experiment, two adult lemon sharks (*Negaprion brevirostris*, Carcharhinidae) were trained to bump an underwater target on hearing the sound of a submerged bell, in order to receive a food reward. Training was in accordance with positive reinforcement where the consequence of the correct voluntary behaviour (in this case bumping a target) produced a food reward. Sharks were trained in a 6-week period and retained a strong response even after a 10-week absence from exposure to the stimuli. The same experimental design was also conducted on five juvenile lemon and three bull sharks (*Carcharhinus leucas*, Carcharhinidae). The authors noted that learning rates were similar for conspecifics, but that there were interspecific differences, with lemon sharks learning quicker than bull sharks (Wright and Jackson 1964). For both of these experiments, individual learning rates should be considered with caution because sharks were not tested individually prompting possible facilitation of learning between subjects.

Further operant conditioning studies using both positive and negative reinforcement regimes went on to confirm these basic findings and to extend the results to include acoustic (Kritzer and Wood 1961; Nelson 1967) and visual discrimination learning (Tester and Kato 1966; Aronson *et al.* 1967). The latter study investigated the learning curves of three vertebrates (mouse, teleost and shark). The animals faced an identical discrimination test, where they had to choose the white from a pair of black and

white targets. A comparison of learning rates suggested that sharks are able to learn discriminative tasks as rapidly as other vertebrates (Aronson *et al.* 1967). During this period, some researchers broadened the discrimination experiments to integrate behavioural studies with brain structure and function. A study by Graeber *et al.* (1973) tested six juvenile nurse sharks (*Ginglymostoma cirratum*, Ginglymostomatidae), making large lesions bilaterally in the optic tectum of three individuals. These sharks were still able to perform the same visual discrimination within the normal criteria range indicating some type of recovery of the visual function. Additionally, the sharks were demonstrated to develop some of the stereotyped behavioural patterns seen in other vertebrates, such as side preference (Graeber and Ebbesson 1972).

These first experiments demonstrating the ability to learn through operant conditioning led to controlled studies of classical conditioning in sharks (Gruber and Schneiderman 1975). Classical conditioning occurs when two events overlap in time and space so that an originally neutral stimulus can be associated with an aversive or rewarding stimulus (Lieberman 1990). Gruber and Schneiderman (1975) reported the first authoritative account of classical conditioning in sharks. Training involved restraining the shark while exposing it to a conditioning stimulus (CS, light flash) that was paired with an unconditioned stimulus (US, electric shock), producing an eye-blink response. They tested 20 juvenile lemon sharks each exposed to 100 trials per day for seven consecutive days. They found that using this technique, classical conditioning of the nictitating membrane response occurred reliably in lemon sharks. The results also indicated comparable learning characteristics to mammals (Schneiderman and Gormezano 1964), with lemon sharks exhibiting gradual recovery when exposed to extinction sessions (where electric shock is removed and conditioned response becomes independent of the CS).

Imprinting is an important learning mechanism that occurs during the sensitive phase of an animal's life and is recognized as being important to salmon and coral reef fish larvae in their homing behaviour (Dittman and Quinn 1996; Gerlach *et al.* 2007) and birds in mate choice (Witte 2006). Very few studies discuss the importance of imprinting on shark behaviour however, those that do, implicate it in prey recognition and homing behaviour (Beulig 1982; Edren and Gruber 2005). In Beulig's study,

13 newborn juvenile lemon sharks were exposed to mechanically produced prey sounds. Results showed that sharks did not display the typical excited behaviours previously observed in this species (Banner 1972). Sharks were then exposed to wounded live fish and when re-exposed to the artificial sounds exhibited excited behaviour. The author attributed this change to sharks acquiring the necessary experience to recognize their prey. Unfortunately, the experimental protocol changed between experiments with sharks tested individually initially and then with conspecifics. Results are difficult to interpret because of the possible influence of social facilitation in the shark's responsiveness to sound. Interestingly, the fact that sharks performed better under social conditions, indicates that sociability might be important to this species.

Learning through observation of other animals is a well-documented phenomenon throughout the animal kingdom (Heyes and Galef 1996). It is often termed 'social learning' and refers to any incident in which individuals acquire new behaviour or information about their environment via observation of, or interaction with, other animals or their products (Brown and Laland 2003). It is common across a wide range of taxa (Heyes and Galef 1996) and has been shown to play an important role for teleost fishes in a number of different behavioural situations, such as navigation and orientation, foraging and mate choice (Brown and Laland 2003). Other than anecdotal observations and the aforementioned experiments that have tested the sharks' learning capabilities in groups, its occurrence or importance in shark behaviour remains empirically untested.

#### Non-associative learning

In the late 1960s and early 1970s field experiments investigating shark acoustic detection abilities were conducted using artificial low-frequency sounds (Myrberg *et al.* 1969, 1972). During preliminary playbacks of such sounds underwater, a simple form of learning known as habituation became apparent, defined as a decline in responsiveness to a neutral stimulus as a result of its repeated presentation (Lieberman 1990). Fewer sharks were observed to respond to the sound stimulus and their response intensity was seen to decrease within minutes or even seconds after their initial approach to the underwater speaker (Nelson and Johnson 1972). Furthermore, similar breakthroughs in the study of

neuroanatomy (Northcutt 1977) at the time-strengthened research opinion that behavioural modification through learning might play an important role in the lives of these top predators (Gruber and Myrberg 1977). A summary of these learning studies is given in Table 1.

#### Is there any evidence to suggest that sharks can use learning in natural situations?

##### Migration, navigation and orientation

Many behaviours used during reproduction, foraging, competition and predator avoidance require an animal to move from one location to another (Odling-Smee and Braithwaite 2003). These movements can range from long distance migrations (thousands of kilometres) made over several months, such as those made by salmon (Dittman and Quinn 1996), to short distances (few metres), used on a day-to-day basis to retrieve food, such as in honeybees (Apidae; Srinivasan *et al.* 1996). Navigation and orientation are two widely used terms, in this context; orientation refers to the moment-to-moment alignment of an animal's body, whereas navigation is the directed movement to a goal involving the neural processing of sensory inputs to determine a direction and perhaps distance (Capaldi *et al.* 1999; Gould 2004). They are both dependent on the formation, storage and retrieval of spatial memories, which permit repeated visits to fixed points in the environment. Clearly, having the capacity to learn provides flexibility, allowing animals to match their movement strategy to a variable environment on the basis of experience (Kieffer and Colgan 1992; Odling-Smee and Braithwaite 2003).

Sharks possess an excellent sensory system that provides them with visual, acoustical, chemical and electrical information about their physical environment (see Hueter *et al.* 2004, for review). These senses are important for location and orientation (Montgomery and Walker 2001) to a variety of clues, including inanimate electric fields (Kalmijn 1971; Kajiura and Holland 2002); low-frequency sounds (Nelson 1967; Myrberg 2001; Casper and Mann 2007), water movement (Maruska 2001; Peach 2001), visual stimuli (Gruber 1977; Hueter 1990), olfactory stimulants (Mathewson and Hodgson 1972; Kleerekoper *et al.* 1975) and geomagnetic fields (Klimley 1993; Meyer *et al.* 2005). In other animal taxa it is well-known that these

**Table 1** A summary of the studies that have investigated learning and used learning techniques to determine sensory thresholds in sharks.

Study goal	Types of learning	Common name	Scientific name	Family	Sample size	Sources
Ecotourism	Potential conditioning	White shark	<i>C. carcharias</i>	Lamnidae	4	Johnson and Kock (2006)
		White shark	<i>C. carcharias</i>	Lamnidae		Laroche <i>et al.</i> (2007)
Learning	Classical conditioning	Lemon shark	<i>N. brevirostris</i>	Carcharhinidae	20	Gruber and Schneiderman (1975)
		Small-spotted cat shark	<i>S. canicula</i>	Scyliorhinidae		Malyukova <i>et al.</i> (1983)
		Smooth dogfish	<i>M. canis</i>	Triakidae		Malyukova <i>et al.</i> (1983)
	Operant conditioning	Lemon shark	<i>N. brevirostris</i>	Carcharhinidae	2	Clark (1959, 1963)
		Nurse shark	<i>G. cirratum</i>	Ginglymostomatidae	3	Clark (1959, 1963)
		Lemon shark	<i>N. brevirostris</i>	Carcharhinidae	5	Wright and Jackson (1964)
		Bull shark	<i>C. leucas</i>	Carcharhinidae	3	Wright and Jackson (1964)
		Nurse shark	<i>G. cirratum</i>	Ginglymostomatidae	1	Aronson <i>et al.</i> (1967)
		Nurse shark	<i>G. cirratum</i>	Ginglymostomatidae	2	McManus <i>et al.</i> (1984)
Foraging efficiency	Trial and error	White-spotted bamboo shark	<i>C. plagiosum</i>	Hemiscylliidae	10	Ciaccio (2008)
	Skill retention	White-spotted bamboo shark	<i>C. plagiosum</i>	Hemiscylliidae	10	Ciaccio (2008)
Sensory Hearing	Classical conditioning	Bull shark	<i>C. leucas</i>	Carcharhinidae	1	Kritzler and Wood (1961)
		Nurse shark	<i>G. cirratum</i>	Ginglymostomatidae		Hamasaki and Bridges (1965)
	Habituation*	Lemon shark	<i>N. brevirostris</i>	Carcharhinidae	4	Nelson (1967)
		Horn shark	<i>H. francisci</i>	Heterodontidae		Kelly and Nelson (1975)
		Atlantic sharpnose shark	<i>R. porosus</i>	Carcharhinidae		Myrberg <i>et al.</i> (1969)
		Silky shark	<i>C. falciformis</i>	Carcharhinidae		Myrberg <i>et al.</i> (1969)
		Bonnethead shark	<i>S. tiburo</i>	Sphymidae		Myrberg <i>et al.</i> (1969)
		Grey reef shark	<i>C. amblyrhynchos</i>	Carcharhinidae		Nelson and Johnson (1972)
		Silvertip shark	<i>C. albimarginatus</i>	Carcharhinidae		Nelson and Johnson (1972)
		Lemon shark	<i>N. brevirostris</i>	Carcharhinidae		Nelson and Johnson (1972)
		Whitetip reef shark	<i>T. obesus</i>	Carcharhinidae		Nelson and Johnson (1972)
		Blacktip reef shark	<i>C. melanopterus</i>	Carcharhinidae		Nelson and Johnson (1972)
	Imprinting*	Lemon shark	<i>N. brevirostris</i>	Carcharhinidae	13	Beulig (1982)
Magnet	Classical conditioning	Sandbar shark	<i>C. plumbeus</i>	Carcharhinidae	6	Meyer <i>et al.</i> (2005)
		Scalloped hammerhead	<i>S. lewini</i>	Sphymidae	1	Meyer <i>et al.</i> (2005)
		Blacktip reef shark	<i>C. melanopterus</i>	Carcharhinidae	8	Tester and Kato (1966)
Visual	Classical conditioning	Grey reef shark	<i>C. amblyrhynchos</i>	Carcharhinidae	2	Tester and Kato (1966)
		Lemon shark	<i>N. brevirostris</i>	Carcharhinidae	5	Gruber (1967)
		Nurse shark	<i>G. cirratum</i>	Ginglymostomatidae	4	Graeber and Ebbesson (1972)
	Operant conditioning	Nurse shark	<i>G. cirratum</i>	Ginglymostomatidae	6	Graeber <i>et al.</i> (1973)
Electric	Operant conditioning	Nurse shark	<i>G. cirratum</i>	Ginglymostomatidae	2	Johnson <i>et al.</i> (1984)

\*Study where type of learning was discussed.

Blank cells in sample size indicate undetermined.



sensory clues provide information that can be learnt, stored and reused at a later date to navigate and orientate (Capaldi *et al.* 1999; Bingman and Cheng 2005; Braithwaite and de Perera 2006). However, the role that learning plays in refining and using these sensory clues to navigate and orientate in sharks remains unclear. There is evidence to suggest that sharks have impressive spatial capabilities (Montgomery and Walker 2001). The vast information available on shark movement and space utilization (Nelson 1977; Simpfendorfer and Heupel 2004) recognizes that sharks can track both abiotic (Hopkins and Cech 2003) and biotic (Heithaus *et al.* 2002) changes with some considerable accuracy. For example, planktivorous basking sharks (*Cetorhinus maximus*, Cetorhinidae) track changes in prey distribution, actively selecting areas with high prey abundance over others (Sims *et al.* 2006b). It was suggested that learned responses to previously encountered prey distributions may explain the high foraging performance of basking sharks (Sims *et al.* 2006b, 2008).

Arguably the most famous example of a fish using learning to navigate long distances is the salmon. They have been demonstrated to imprint on olfactory clues to guide them back from the ocean to their spawning grounds (Dittman and Quinn 1996). This type of behaviour is known as 'homing'. A study completed in the waters of Bimini, Bahamas, on 32 juvenile lemon sharks confirmed that these sharks were capable of homing when displaced up to 16 km from their observed home ranges. All but one of the sharks returned to the Bimini Islands and most returned to their specific, spatially limited home ranges (Edren and Gruber 2005). Furthermore, Port Jackson horn sharks (*Heterodontus portusjacksoni*, Heterodontidae) use particular resting sites in Sydney Harbour, Australia, with observational studies showing that when displaced 3 km away from these sites, the same sharks were located in the same resting locations only two days later (O'Gower 1995). It is very difficult to determine the mechanisms that these sharks used to return home without speculating too much, but the documentation of this type of behaviour in elasmobranchs is exciting and warrants further investigation. Interestingly, Klimley (1993), working on scalloped hammerheads (*Sphyrna lewini*, Sphyrnidae), proposed that sharks use a geomagnetic navigational mechanism, following features of underwater magnetic topography such as anomalies associated with ridges or valleys to return to

day-time seamounts. Whether these magnetic 'habitat signatures' are learnt boundaries that elicit active changes in swimming direction, remains unknown.

Some teleost fish can also use learnt spatial maps to navigate and orientate with. This was first identified through field-based experiments completed on the gobiid fish (*Bathygobius soporator*, Gobiidae; Aronson 1971). Fish that were given prior experience of artificially constructed tide pools over varying tide cycles were able to successfully escape a simulated attack, by jumping from one pool to another. Since then, animal researchers have investigated spatial learning by using controlled laboratory experiments (Capaldi *et al.* 1999; Odling-Smee and Braithwaite 2003). These involve manipulating fish sensory systems or spatial cues, or laboratory-based spatial tasks where fish are trained to learn particular associations (Odling-Smee and Braithwaite 2003). Goldfish (*C. auratus*, Cyprinidae) have been shown to locate a food reward by using landmarks as indirect reference points and also use visual cues to locate a goal (Warburton 1990). Other species like the long-tail knifefish (*Sternopygus macrurus*, Sternopygidae) can use their electrical sense to recognize specific spatial electrode configurations and extract a feature, e.g. a vertical connectivity, present in many novel configurations (Graff *et al.* 2004). Loggerhead turtles (*Caretta caretta*, Cheloniidae) and Caribbean Spiny lobsters (*Panulirus argus*, Palinuridae) can apparently learn the magnetic topography of the area where they settle, or regularly range over, and develop a magnetic map to facilitate navigation to and from that area (Lohmann and Lohmann 2006; Lohmann *et al.* 2007).

Recent experimental work on fresh water stingrays (*Potamotrygon motoro*, Potamotrygonidae) has confirmed that elasmobranchs are also able to construct a cognitive map of their environment. A cognitive map can be defined as a map-like, world-centred representation of the objective space that provides a stable framework, allowing the subject to reach the goal independently of its own actual position (Rodriguez *et al.* 2006). Like goldfish, stingrays remembered specific feeding locations even from different starting positions and new routes (Rodriguez *et al.* 1994; Schluessel and Bleckmann 2005). When trials were conducted without visual stimuli, the performance of the rays was reduced significantly, indicating that this sense plays a primary role for this species. In addition, the

rays performed the same spatial task just as quickly as the goldfish (Rodriguez *et al.* 1994) and slider turtles (*Pseudemys scripta*, Emydidae; Lopez *et al.* 2000). The authors concluded that elasmobranchs exhibit similar orientation mechanisms and spatial memory functions to other vertebrates (Schluessel and Bleckmann 2005). Similar types of experiments will prove useful to investigate whether sharks like rays are able to navigate and orientate using such mechanisms, although there are limitations to these experiments in that they do not always reveal the circumstances under which the mechanisms identified are used in nature (Lohmann *et al.* 2008). Therefore, future research should look to also incorporate field-based studies to provide information about when and where such navigational abilities are used.

Recent advances in telemetry techniques have enabled the movements of some free-ranging shark species to be recorded in their natural environments (Sims *et al.* 2008). Large-scale migrations for a number of shark species are now widely documented (Bonfil *et al.* 2005; Heithaus *et al.* 2007; Weng *et al.* 2007). Genetic research and mark-recapture studies have also confirmed that many shark species are philopatric, returning to give birth in the same location for multiple years (Feldheim *et al.* 2004; Hueter *et al.* 2005). With the improvement of telemetry and environmental monitoring techniques, sharks can now provide a useful model for investigating how animals navigate in the open ocean. More specifically how do sharks navigate between continents? How do sharks track prey populations? And is there a learnt component to these foraging strategies or migratory behaviour?

### Foraging

The acquisition of food is essential to an animal's survival. It requires both accuracy and timing to detect, capture and consume a prey item successfully. Prey populations are subject to much variability changing year-by-year, seasonally, day-by-day and even moment-to-moment (Brown and Chivers 2006). Prey themselves are capable of learnt anti-predatory behaviour such as avoiding risky habitats (Brown *et al.* 2001), detecting predators through chemical and olfactory clues (Chivers and Smith 1998) as well as performing evasive manoeuvres (Huntingford *et al.* 1994). It is equally likely that learning is an important means by which predators can counteract the behavioural plasticity of their

prey, fine tuning their foraging tactics and capture. This may be a crucial weapon in the predator-prey arms race (Kelley and Magurran 2003).

Sharks are a species-rich taxon occupying a diversity of ecological niches (Wilga *et al.* 2007). They are carnivorous and employ numerous tactics such as stalk, ambush, engulf or chase to feed on a variety of organisms from plankton to whales (see Wetherbee and Cortes 2004; Wilga *et al.* 2007, for reviews). The vast majority of sharks have a generalist diet preying on a range of organisms from both pelagic and benthic environments (Wilga *et al.* 2007). For example, Smoothhound (*Mustelus canis*, Triakidae) forage on crustaceans, molluscs and fish using an array of capture techniques ranging from suction and biting to ram feeding. Some sharks, however, are specialists by their behaviour in selecting specific prey types and through their specialized biting or crushing behaviours (Wilga *et al.* 2007). Bonnethead sharks (*Sphyrna tiburo*, Sphyrnidae) feed almost exclusively on swimming crabs (Calinectidae; Bethea *et al.* 2007) and horn sharks (*Heterodontus francisci*, Heterodontidae) on molluscs (Summers *et al.* 2004) suggesting that in addition to a genetic component some specialization may have arisen through learned behaviour resulting in more efficient capture, manipulation and consumption of prey.

It is also well established that many shark species have an ontogenetic shift in diet preference. There are examples of sharks broadening their diet (Lowe *et al.* 1996) as well as increasing their dietary specialization (Tricas and McCosker 1984; Bethea *et al.* 2007; Taylor and Bennett 2008) through ontogeny. In addition, intraspecific dietary preferences vary both temporally and spatially (Lucifora *et al.* 2005; Ellis and Musick 2007). To better understand these ontogenetic dietary shifts recent studies have focused on shark prey capture performance (Lowry and Motta 2008). In leopard and white-spotted bamboo sharks (*Chiloscyllium plagiosum*, Hemiscylliidae) developmental changes in suction pressure were tracked through ontogeny. Performance improvements were primarily accounted for by growth, with size-independent behavioural changes contributing little to overall performance variability (Lowry and Motta 2008). This finding is also consistent with other organisms; such as banded water snakes (*Nerodia fasciata*, Colubridae; Vincent *et al.* 2007), Anole lizards (*Anolis equestris* and *Anolis garmani*, Iguanidae),

turtles (*Chelydra serpentina*, Chelydridae; Herrel and O'Reilly 2006) and teleost fish (*Rutilus rutilus*, Cyprinidae; Hjelm *et al.* 2003). However, the studies do highlight the fact that although little variability was found as a result of behaviour in captivity, natural situations are likely to enhance this owing to more diverse prey being available and the nature of dynamic encounters.

A number of authors have suggested that ontogenetic dietary changes in sharks could be facilitated by an improvement in predator hunting ability of white sharks (*Carcharodon carcharias*, Lamnidae), Tricas and McCosker (1984); tiger sharks (*Galeocerdo cuvier*, Carcharhinae), Lowe *et al.* (1996); leopard sharks, Lowry *et al.* (2007) and lemon sharks, Newman (2003). A recent study quantified the effects of maturation and experience on the predatory efficiency of white-spotted bamboo sharks (Ciaccio 2008). Comparisons of sharks were made before and after 20 days of foraging experience, at varying ages and naivety. Predator efficiency was defined as the time taken to capture and consume prey. Two types of live prey were used during experiments, sand worm (*Nereis virens*, Nereidae) and ghost shrimp (*Palaeomonetes* sp., Palaeomonidae) to simulate non-elusive and elusive prey. For both younger and older sharks, predatory efficiency improved after 20 days of foraging on either live worms or shrimp (Ciaccio 2008). The author concluded that maturation and experience probably act in unison to improve the predatory abilities of this shark. Maturation may allow sharks to utilize more elusive or harder-to-eat prey, whereas experience improves foraging efficiency, with sharks improving their ability to find and manipulate prey once located (Ciaccio 2008). The same study also investigated the retention of predatory skills, testing sharks after an 18-day absence from live prey. Sharks were found to be just as efficient showing no decrease in time to capture and consume prey. Many of the aforementioned learning experiments undertaken in the 1950s and 1970s also found that sharks could retain their response to operant conditioning regimes, from periods of 2–10 weeks (Clark 1963; Graeber and Ebbesson 1972). Other fish show this ability to retain predatory skills. However, the time taken to lose such an ability can vary (three-spine stickleback, *Gasterosteus aculeatus*, Gasterosteidae, 2 days; Mackney and Hughes 1995; Silver perch, *Bidyanus bidyanus*, Terapontidae, up to 5 weeks; Warburton and Thomson 2006). The improvement of pred-

tory abilities with experience has been demonstrated in other animals, such as teleost fish (Warburton 2006), garter snakes (*Thamnophis sirtalis*, Colubridae; Krause and Burghardt 2001), squid (*Loligo opalescens*, Loliginidae; Chen *et al.* 1996) and birds (Marchetti and Price 1989).

Searching for and locating prey is an essential part of most predators' daily routine. Prey populations commonly undergo rapid changes in distribution and abundance making them unpredictable and difficult to track. In addition, natural food sources vary considerably in productivity and in the likelihood of renewal following depletion (Hughes and Blight 2000).

To remain successful in such a variable environment predators must therefore acquire information continually and adapt their behaviour accordingly. Recent work on basking sharks investigated whether large-scale movements reflect preferences for areas of high-zooplankton biomass (Sims *et al.* 2006b). The relative performance of basking shark movements were compared to random walks simulated through a dynamic zooplankton (copepod) biomass landscape. Results demonstrated that sharks did structure movement patterns to utilize the richest prey areas available in the preferred habitats. It was theorized that this high performance might be explained by learnt responses to previously encountered prey distribution (Sims *et al.* 2006b). Indeed, the encounter rate of the one juvenile basking shark tracked was no better than the average achieved by randomly moving model sharks, whereas adult and sub-adult shark encounter rates outperformed approximately 90% of the model sharks. The authors hypothesized that this could reflect ontogenetic differences in habitat selection, such that juveniles learn about the underlying structure of prey distributions as they gain foraging experience. This result, however, should be viewed with caution owing to the limitation of testing only one juvenile shark. Ontogenetic differences in habitat selection have also been identified for narwhals (*Monodon monoceros*, Monodontidae) and southern elephant seals (*Mirounga leonina*, Phocidae), where juvenile movement patterns were significantly different to older individuals (Laidre *et al.* 2004; Field *et al.* 2005); again, experience was identified as a potentially important contributing factor.

Furthermore, space utilization studies on 39 juvenile lemon sharks, aged 0–4 years, have demonstrated that sharks in two distinct nursery



areas (South Bimini and the North Sound, Bimini, Bahamas) had significantly different-sized home ranges (Franks 2007). Sharks in both nurseries are required to balance energy costs with energy intake. For sharks in the North Sound larger home ranges may help to improve energy return owing to encountering more available prey, but by definition this will increase the area that they need to cover and so sharks will incur greater energetic costs as a result of increased movement. However, if prey abundance and its location are more predictable in the South Bimini nursery, it is possible for those sharks to be able to use smaller home ranges so as to obtain their necessary daily food intake. Therefore, it is possible that sharks in both nurseries were able to decide or perhaps learn about their local environment, developing a foraging strategy that best fits the area covered. Indeed, for predators foraging in highly changeable prey fields a memory of past locations where prey was previously abundant may be maladaptive, since to adapt rapidly to change, a shorter memory window is desirable for finding new prey locations (Mackney and Hughes 1995). However, it is also possible that the differences observed between the behaviour of lemon sharks in the Bimini nurseries could also be attributed to other factors such as differences in predation risk, shape and bathymetry of the nursery areas.

It is clear from the literature that there is a large amount of information available on shark foraging behaviour, including feeding mechanisms, dietary composition and in recent year's habitat selection (see previous section). Sharks provide an excellent model for fine-scale monitoring of developmental changes in feeding morphology (Lowry and Motta 2008) and free-ranging predatory foraging behaviour (Sims 2003). Using this extensive knowledge, base sharks could also become a very useful model for studying the interaction between developmental and experiential changes and how these contribute to ontogenetic changes in foraging performance.

### Social interactions

#### *Conspecifics/heterospecifics*

There is much evidence to suggest that sharks are capable of various forms of social recognition. Sharks are known to group in size-, sex- and species-specific groups (Klimley and Nelson 1981; Economakis and Lobel 1998; Sims 2003; Heupel and Simpfendorfer 2005; Guttridge *et al.* 2009). Some studies have identified that within these

groups dominance hierarchies exist whereby sharks will display subordinate behaviour to individuals of a larger size or different sex (Myrberg and Gruber 1974; Klimley and Nelson 1981). Furthermore, a recent review on agonistic interactions within and between different shark species identified that there are many common behavioural elements to these displays that are observed in a variety of families (Martin 2007). These types of displays appear to be predominantly motivated by defence of self (Martin 2007). However, schooling scalloped hammerheads use a display known as 'corkscrewing' in order to retain or displace other individuals from central positions within a school (Klimley and Nelson 1981). Whether these displays are innate or learnt is unknown but intraspecific differences between populations of grey reef shark (*Carcharhinus amblyrhynchos*, Carcharhinidae) in the intensity and frequency of such displays (Martin 2007) indicates that learning may play a role in the development of such behaviours. The aforementioned studies on dominance hierarchies also noted that these were prevalent between species providing evidence of heterospecific discrimination and recognition in sharks. Myrberg (1991) proposed that distinctive fin markings in many carcharhiniform sharks may serve as species recognition badges and/or accentuate both interspecific and conspecific social signals.

Individual recognition in other taxa appears to enhance group living by formalizing social relationships improving anti-predatory behaviour, reducing competition/aggression and facilitating social learning (Griffiths and Ward 2006). In teleosts, recognition abilities have been identified through the use of controlled laboratory experiments such as two-choice tests, or by looking at associative patterns of nearest neighbours (Dugatkin and Wilson 1993). Recently, a series of captive choice experiments conducted on juvenile lemon and nurse sharks identified that active mechanisms can play a role in the formation and composition of shark groups (Guttridge *et al.* 2009). Juvenile lemon sharks aged 0–3 years were attracted to associate with conspecifics over empty compartments and in addition sharks aged 2–3 years showed a preference to associate with size-matched individuals vs. those aged 0–1 years. Results from these trials highlight additional complexities in group-joining decisions and emphasize the need for further studies to determine whether sharks can recognize individuals and if/how they use social information. Recently, free-ranging teleost fish populations were assessed

using network analysis providing evidence for preferred partnerships in the wild (Croft *et al.* 2005). The application of this type of analysis with recent technological advances in acoustic and radio telemetry could provide an avenue for assessing grouping behaviours and social learning in wild sharks.

#### *Mates*

Elasmobranch reproductive behavior has been implied from freshly caught specimens, laboratory studies of reproductive structures and from observations of sharks in captivity (Gordon 1993; Pratt and Carrier 2001; Powter and Gladstone 2008). However, recent advances in diving and video/photography have enabled researchers to obtain direct observations of free-swimming wild animals (Whitney *et al.* 2004). This has allowed for the description and quantification of courtship behaviours, such as those described in Pratt and Carrier (2001) and Whitney *et al.* (2004). These studies identified behaviours that suggested that females of some shark species might choose to mate or avoid mating with particular males. Females of both nurse and white-tip reef sharks (*Triaenodon obesus*, Carcharhinidae) performed 'acceptance' behaviours such as arching towards the male and cupping their pelvic fins upwards. In contrast, females also performed 'avoidance' type behaviours, such as arching, pivoting and rolling away (Pratt and Carrier 2001). The female nurse sharks were also noted to retreat to extremely shallow waters <40 cm, when pursued by lighter, perhaps younger, weaker or inexperienced males, whereas in the presence of larger males this behaviour was not observed. More quantitative information on the attributes of participants of such behaviour are required to assess whether females are making specific choices with whom they mate with and if male sharks also display selective behaviour towards females they mate with.

It is also unknown how males detect or recognize that females are receptive to mating. Behavioural observations of a pair of black-tip sharks (*Carcharhinus melanopterus*, Carcharhinidae) described how the male was closely following a female with his nostrils almost in contact with her cloaca (Johnson and Nelson 1978). A neuroendocrine study also revealed that regions of the brain were sensitive to sex steroids (Demski 1990). These studies implicate that chemical signals may play an important role in mate recognition for sharks. Research on round

stingrays (*Urolophus halleri*, Urolophidae) identified that these elasmobranchs use their electrosense to detect and locate conspecifics during the mating season (Tricas *et al.* 1995). Male stingrays were shown to use their electrosense to detect and locate buried females, whereas females used their sense to locate other females to refuge with them (Tricas *et al.* 1995; Sisneros and Tricas 2002). Sharks are known to use their electrosense in prey detection (Kalmijn 1971) but its involvement in conspecific or mate detection is unknown.

Sexual selection is widespread in other vertebrates (Krebs and Davies 1993) and recent evidence has suggested that social environment and learning are important factors in forming mate preferences (Dugatkin 1996). For other animals such as fishes four different forms of learning have been described: sexual imprinting, learning after reaching maturity, eavesdropping and mate-choice copying (Witte 2006). The finding that some shark species are able to avoid or accept mating advances from specific males provides evidence that mate recognition may play an important role in the mating system of these animals. However, whether experience affects these mate choice decisions remains completely unexplored, but owing to its abundance in other taxa, future studies should look to incorporate the role of learning.

#### **Human effects on shark learning**

In the modern era there are now many opportunities for humans to interact with sharks and other animals both on a commercial scale, such as fisheries (FAO 2006) and on a recreational scale, such as in tourism (Kuenzi and McNeely 2008).

#### *Ecotourism*

Marine tourism is one of the fastest growing market sectors in the tourism industry (Orams 2000). In particular, wildlife ecotourism alters the behaviour of target species by using food incentives to attract animals to areas that are then frequented by tourists (Orams 2002). These types of situations provide novel stimuli for animals to interact with and react to. Repeated exposure to these stimuli presents the opportunity to learn, leading to problematic behavioural changes, such as animals becoming dependent on tourists for food or damaging effects on wild interactions between predators and prey in their ecosystem (Orams 2002).

Elusive 'showcase' predators such as sharks, which are difficult to observe in their natural habitat (Bres 1993), have become the prime target for these types of ecotourism practices. A number of species, e.g. bull, tiger, white and Caribbean reef sharks (*Carcharhinus perezi*, Carcharhinidae) are attracted in this way providing a visual spectacle to observing tourists. However, the impact that this feeding has on their behavioural patterns and the repeated exposure to humans with food has led to concern over the damaging affects of such ecotourism techniques. Recent evidence in this area has come from studies conducted on white sharks in South Africa (Johnson and Kock 2006; Laroche *et al.* 2007). A combination of acoustic tracking and visual observations during ecotours were used to quantify the effect of ecotourism practices on local movement and associative behaviour of white sharks. Animals at both study sites were attracted to the boat through the use of 'chum', and then lured closer to tourist vessels by using additional fish pieces; occasionally, these were consumed by sharks and were recorded as positive reinforcement for the sharks. Interestingly, the studies showed differing results. Laroche *et al.* (2007) in South Africa found a trend of decreasing response with time, animals receiving more rewards showing no greater inclination to remain near the boat. Along the same coast, Johnson and Kock (2006) found that the 'speed of arrival' to the chumming boat of four individual white sharks from a particular bay was significantly reduced with increasing experience. These four individuals, however, were unique in that they gained more rewards than other sharks and in doing so fulfilled the requirements for conditioning by gaining predictable rewards at regular intervals. Both of these studies consider that white sharks are potentially affected by conditioning during ecotours; nevertheless, the extent to which they are conditioned depends on the regularity and number of food rewards that they receive. The low sample sizes of sharks exposed to conditioning prevented a more detailed investigation into the effects of conditioning on movement and site fidelity. However, a separate study undertaken in Australia determined that chumming alone increased the acoustic detection rate on data loggers for a relatively short period in close range of the chumming sites (Bruce *et al.* 2005). Artificial feeds rely on a reliable population of individual sharks willing to interact/feed on a regular basis. For white sharks, it is clear from the

forementioned studies that in general conditions are rarely met for sharks to develop a learned response, indicating that moderate levels of tourism activity may not have a broad impact on white shark behaviour across a wide range of space and time scales (Laroche *et al.* 2007).

In practices where rewards are made readily available and a learning criterion can be reached, greater risks for altering behaviour of target animals are incurred. A number of recent studies on another elasmobranch, the southern stingray (*Dasyatis americana*, Dasyatidae) in Grand Cayman have determined that the rays experience damaging physiological and behavioural changes (Cocoran 2006; Semeniuk and Rothley 2008). Rays were observed to have a lower body condition when compared to stingrays from a non-tourist-impacted site (Semeniuk and Rothley 2008), attributed to increased conspecific bites, ectodermal parasites and aggressive interference competition. An extensive habitat utilization study demonstrated that southern stingrays utilizing the tourist-feeding sites displayed strong site fidelity and reduced space use compared to those in the undisturbed sites (Cocoran 2006). This indicates that rays were learning to associate specific locations with food rewards and altering their behavioural strategies so as to gain further benefits. The authors recognized that the feeding sites could become an 'ecological trap' and have cascading effects on the surrounding marine ecosystem (Cocoran 2006; Semeniuk and Rothley 2008).

The detrimental effects associated with artificial feeding are also very well documented in other taxa, such as cetaceans (Bejder and Samuels 2003), primates (*Papio cynocephalus*, Cercopithecidae; Altmann and Muruthi 1988), teleost fish (*Chromis chromis*, Pomacentridae; Milazzo *et al.* 2006) and reptiles (*Varanus komodoensis*, Varanidae; Walpole 2001). These studies have often led to bans on feeding wild animals (Smith *et al.* 2008) and have highlighted further damaging effects such as population and social structure changes (Kamal *et al.* 1997). They also emphasize that habituation to humans and/or learning to associate food with specific sites, contributed significantly to behavioural changes in the target species.

#### Fisheries

In recent years, the role of learning in fisheries has been identified as an important factor that needs to be incorporated into ecosystem-based management

(Fernö *et al.* 2006). It is now widely accepted that fishing techniques need to be selective and environmentally friendly to reduce by-catch of non-target species and maintain fish stocks (Gilman *et al.* 2008). To achieve this, an understanding of animal behaviour towards fishing stimuli is required. As already discussed in this review, sharks have the capability of learning about their environment and adjusting their behaviour accordingly, so it is probable therefore that sharks, like other animals (Fertl and Leatherwood 1997; Fernö *et al.* 2006), also use previous experience when interacting with commercial and recreational fisheries. A substantial number of sharks survive contact with fishing gear (Gilman *et al.* 2008) and many long-line fishermen have reported stolen baits or half-eaten target species (Rosa and Secchi 2007) creating the potential for learning. This could lead to either negative or positive interaction with fishing gear. Sharks may learn through classical conditioning to associate a sound from a trawl or later contact with fishing gear. Operant conditioning may also take place when sharks attack baited hooks or are trapped in a net for some time, creating the potential for active avoidance. Cod (*G. morhua*, Gadidae) tested in captivity learnt to treat baited hooks more carefully even after only one aversion experiment (Fernö and Huse 1983) and catch rates of rainbow trout (*Oncorhynchus mykiss*, Salmonidae) in five small lakes, British Columbia, quickly dropped within 7–10 days (Askey *et al.* 2006). In contrast, there are examples of other fishes such as, white-spotted char (*Salvelinus leucomaenis*, Salmonidae), which are more likely to be captured having been previously hooked (Tsuboi and Morita 2004). It is also possible for sharks to receive positive reinforcement; a shark could steal a bait or target species and in doing so receive a reward for interacting with the long-line. This may lead to repeated visits to other sections of the line for more free food. Some other marine organisms have also been known to steal baits and or target species from long-lines including haddock (*Melanogrammus aeglefinus*, Gadidae; Fernö *et al.* 2006), bottlenose dolphins (*Tursiops truncatus*, Delphinidae; Hernandez-Milian *et al.* 2008) and killer whales (*Orcinus orca*, Delphinidae; Rosa and Secchi 2007).

The use of nets has long been established as a successful method for capturing a variety of marine organisms (FAO 2006). These nets are also used as a preventative measure to restrict movement of animals to certain areas. For example, the shark

nets in Durban, South Africa are set to reduce the number of large sharks that utilize popular tourist beach waters (Dudley *et al.* 2005). The nets are effective in capturing a wide array of marine organisms (Dudley *et al.* 2005), but are fixed in place and so provide an obstacle that can be actively avoided. Learned net avoidance has been observed in teleost fish (Pyanov 1993) and cetaceans (Read 2008). Manire and Gruber (1993), during a population census of juvenile lemon sharks in Bimini, also found that sharks became progressively difficult to capture in gillnets with repeated capture attempts. This study identified that learning to avoid capture has the potential to bias estimates of population size, such as catch per unit effort (CPUE). To combat this bias, long-term sampling of the lemon shark population at Bimini now takes place only once annually.

Sharks are a diverse subclass of vertebrates with different movement strategies. Some species display site fidelity (Sundström *et al.* 2001; Sims *et al.* 2006a) whereas others make long distance migrations (Bonfil *et al.* 2005). The extent to which these movement patterns of sharks are influenced by other individuals is unknown, although observations of long-term aggregations of 'refuging' site-attached cat sharks (*Scyliorhinus canicula*, Scyliorhinidae) implies a social component to daily movement patterns (Sims 2003; Sims *et al.* 2006a). The transfer of information via social transmission is well-known in cetaceans and teleosts (Brown and Laland 2003; Whitehead *et al.* 2004), and although these exchanges can allow rapid adaptation within generations it has been suggested that information that is passed on between generations is more susceptible to anthropogenic effects. Whether sharks are capable of social learning remains unknown, but evidence that the loss of socially transmitted information may damage other marine organism stocks has led scientists to view it as an important factor when making decisions regarding management and conservation (Fernö *et al.* 2006).

## Discussion and future directions

Learning in sharks was first investigated formally in the 1960s and 1970s with numerous accounts demonstrating the ability of these animals to learn through operant and classical conditioning techniques (see Table 1). Other studies went on to describe simple forms of learning such as habituation, with some suggesting the importance of imprinting in



neonatal sharks (Beulig 1982). However, since these early basic demonstrations, conditioning techniques have been primarily used as a tool to investigate sensory thresholds (see Table 1). In these, sharks were trained to associate a conditioned stimulus, such as a sound or light, with an unconditioned stimulus, such as an electric shock or food reward. Researchers varied the conditioned stimulus using different sound frequencies or differing light levels to determine whether sharks could still detect the stimulus. These studies, although providing much needed information on the capabilities of shark sensory systems, generally failed to generate additional knowledge on the learning processes and mechanisms used by sharks. This is in contrast to other vertebrates such as teleost fishes, where research has progressed to a level where it has been possible to see real parallels in some learning and memory systems with other vertebrate groups (Rodriguez *et al.* 2006).

Working with such large, elusive marine predators has made captive experimentation very difficult with certain species (Bres 1993) forcing many researchers to have low sample sizes. For these reasons, many learning studies have primarily conducted experiments on smaller bodied species within the Carcharhiniform and Orectobiform orders, leaving substantial gaps in our general knowledge of learning among shark species. Recent extensive studies on brain organization and cerebella foliation have revealed that sharks exhibit widespread variation in brain size and morphology (Yopak *et al.* 2007). The authors indicate that these differences are a consequence of phylogenetic grouping as well as locomotory behaviour, habitat and lifestyle. They also noted that shark species that use complex reef habitats, such as white-tip reef sharks, tiger sharks and great hammerheads (*Sphyrna mokarran*, Carcharhinidae) had the largest relative brain and telencephalon sizes. For teleost fish there is significant evidence concerning the presence of a telencephalon-dependent spatial memory system (Broglia *et al.* 2003). In addition, the cerebellum region of the brain plays an essential role in classical conditioning (Yoshida *et al.* 2004; Rodriguez *et al.* 2005). For sharks, this new extensive structural knowledge (Yopak *et al.* 2007; Yopak and Montgomery 2008) coupled with the use of magnet resonance imaging (MRI), in even more recent studies (Yopak and Frank 2008), should make it possible to obtain more quantitative data on specific brain areas. Combining such detailed

information on structure with learning experiments will help to elucidate the functions of these brain areas and also help to determine whether behavioural processes can help to explain structural and size differences between shark species. Two interesting questions in this context are the following: How do shark learning capabilities fit in with teleost fish and other vertebrates? Do similar brain areas serve the same learning function?

Future studies should also identify species from a range of families that are abundant, small bodied and able to reproduce in captivity, such as Port Jackson horn shark, black-tip reef, bonnethead and numerous cat sharks. Breeding sharks in captivity will allow researchers to control the environment that experimental animals grow up in, manipulating the physical and social stimuli that test sharks are exposed to. Neonate white-spotted bamboo sharks were recently used to identify the role of experience in foraging efficiency (Ciaccio 2008). Further studies could investigate whether early life experience or development affect social recognition and/or associative patterns (Salvanes *et al.* 2007). These types of controlled experiments, however, should be conducted in parallel with field studies to ensure that experiments in captivity are relevant and applicable to wild animals. The aforementioned shark species exhibit site fidelity and relatively short-range movement patterns making them ideal model species for these types of combined studies.

Advances in data loggers, acoustic and satellite tags can also help with long-term monitoring of sharks. Recently developed multichannel loggers that incorporate tri-axial accelerometry have the potential to investigate animal movement, behaviour, energy expenditure (from movement costs estimated by laboratory-based respirometry validations) and the physical characteristics of an animal's environment (Wilson *et al.* 2007). Combining such techniques to investigate shark homing behaviour, e.g. could help to identify the mechanism behind such remarkable behaviour determining if learning is an important component.

It is also important that future experiments are designed using standard experimental protocols to ensure that results can be compared/contrasted to other taxa. For example, when testing partner preference and recognition abilities in teleosts, designs such as two-choice test, nearest neighbour and flow tanks could prove useful. Additionally modifying these may provide information on the mechanisms that sharks use to identify individuals.



For navigation and orientation studies, the standard plus maze design could be used to analyse spatial cognition in sharks; e.g. this technique was utilized successfully for another elasmobranch species, the freshwater stingray (Schluessel and Bleckmann 2005). Furthermore, researchers should look to develop more on-site laboratories, utilizing aquaria and small *in-situ* pens to conduct experiments, such as those used to test social preferences of juvenile lemon sharks in Bimini, Bahamas. These provide more natural housing conditions for the sharks facilitating the observation of natural behaviours (Guttridge *et al.* 2009). Linking wild studies of sharks with captive controlled experiments is important so that learning can be placed in the context of natural behaviour, ensuring that patterns, processes and mechanisms identified in the lab are useful when explaining wild behaviour.

The fisheries and ecotourism section of this review identified that humans can influence and alter the behavioural patterns of sharks. Investigating how sharks interact with fishing equipment on a finer scale is required to provide basic information about the behavioural processes that lead to capture or avoidance. This leads to a number of important questions. Does experience affect future behavioural decisions, leading to sharks revisiting specific areas and avoiding others? Or can sharks learn to avoid trawls/long-lines or steal baits? Are some shark species more susceptible to capture than others, if so why? Even simple hook design, leader wire type or bait presentation, size or species can have a significant impact on the number of non-target species caught through long-lining (Ward *et al.* 2008). In addition, if sharks are capable of learning to avoid baits or nets owing to an operant conditioning response, from a negative experience with fishing gear, then developing effective repellents could become an important means by which fisherman might reduce/avoid incidental shark by-catch (Gilman *et al.* 2008). Recent research on magnets and electropositive metals have provided some promising results (Stoner and Kaimmer 2008; Brill *et al.* 2009) in this study area.

Furthermore, studies on stingray artificial feeds (Cocoran 2006; Semeniuk and Rothley 2008) revealed some very concerning damaging effects both behaviourally and physiologically to tourist-fed animals compared to non-tourist fed individuals. There are numerous shark-feeding ecotourism sites throughout the world (Cawardine 2004) that utilize very similar 'free food' techniques

allowing sharks to obtain many rewards, leading to learning criteria being met very quickly. How these feeds effect shark physiology, population structure, group behaviour, movement and the ecosystem of these sharks is currently unknown at a wide range of spatio-temporal scales utilized by these highly mobile predators. Moreover, increased human–shark interactions allow the sharks, in such feeds, to lose their innate natural fear of humans, perhaps associating them with food rewards that ultimately enhance the potential for dangerous agonistic behaviours towards divers (Martin 2007). These concerns should be addressed through close monitoring of shark populations that are targeted for tourist feeds.

There is a real need for the basic principles of shark learning to be revisited and tested using modern day experimental techniques. At this stage, few studies have related brain structure and morphology to learning processes in sharks and there still remain many other unanswered questions. Principal among such questions, include: are there any intraspecific or interspecific differences in learning? Do sharks imprint on cues in their early life history and use these to identify prey and predators or return to their birth place? Are sharks capable of forming a cognitive map, do they use learnt information to navigate? How long can sharks learn an association for? Where do shark learning capabilities fit in with other vertebrates?

Shark scientists should look to teleost fish research for inspiration on experimental ideas and design (Brown *et al.* 2006). Fish are no longer regarded as pea-brained machines with 3-s memories; instead, they are now known to exhibit a rich array of sophisticated behaviours with impressive learning capabilities (Laland *et al.* 2003). Sharks are often referred to in the public domain as 'killing machines' or 'swimming noses'. To detach these damaging stigmas further studies are required, developing our knowledge of the role of learning in this ancient class of vertebrates.

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