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Natural History Note

White Sharks Exploit the Sun during Predatory Approaches

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abstract: There is no conclusive evidence of any nonhuman animal using the sun as part of its predation strategy. Here, we show that the world's largest predatory fish— the white shark (*Carcharodon carcharias*)— exploits the sun when approaching baits by positioning the sun directly behind them. On sunny days, sharks reversed their direction of approach along an east-west axis from morning to afternoon but had uniformly distributed approach directions during overcast conditions. These results show that white sharks have sufficient behavioral flexibility to exploit fluctuating environmental features when predating. This sun-tracking predation strategy has a number of potential functional roles, including improvement of prey detection, avoidance of retinal overstimulation, and predator concealment.

Keywords: *Carcharodon carcharias*, behavioral flexibility, concealment, hiding strategy, predation strategy, prey detection.

Introduction

Predation is one of the key forces driving animal evolution, with predator-prey interactions being fundamental to the survivorship of both participants (Darwin 1871; Dawkins and Krebs 1979; Endler 1991). Although most studies have historically treated predators as abstract sources of risk to which prey respond, the fundamental role of predators and their malleable behavioral response in predator-prey dynamics has only been recognized recently (Lima 2002). Nevertheless, the behavior and movements of predators affects antipredator responses and the scale at which they occur and should be accounted for when investigating predator-prey relationships (Lima 2002; Heithaus and Vaudo 2012).

Many species of sharks are considered apex predators within the ecosystem in which they live and fill a diverse range of predatory niches in marine and some freshwater ecosystems (Cortés 1999; Heithaus et al. 2010). The predator-prey relationship between sharks and lower trophic levels has previously been used as a successful model to predict ecological consequences of marine predator declines (Heithaus et al. 2008) and to develop a predictive framework for predatory risk effects (Heithaus et al. 2009). Sharks are therefore a useful model species to investigate predation strategies during predator-prey interactions. Here, we examine a strategy used by the white shark (*Carcharodon carcharias*) to facilitate food capture. This species has complex movement and foraging behaviors that vary between prey types and habitat (Bruce et al. 2006; Sims et al. 2012). Most previous studies on the predatory behavior of white sharks have focused on interactions with pinnipeds (Klimley et al. 1996; Martin et al. 2005), environmental factors influencing predation frequencies (Klimley et al. 1992; Anderson et al. 1996; Pyle et al. 1996; Hammerschlag et al. 2006), and how pinniped-shark interactions affect the relative spatiotemporal distribution of white sharks (Klimley et al. 2001; Laroche et al. 2008; Domeier et al. 2012; Fallows et al. 2012; Kock et al. 2013). Comparatively little is known about the predation or approach strategy of white sharks because of the logistic difficulties and relatively rare opportunity to observe natural predatory events. A conceptual model based on optics and physical laws recently suggested that white sharks ambush from depth and around dawn and dusk to take advantage of backlighting and scotopic conditions and to hide from their prey (Martin and Hammerschlag 2012). However, there currently are limited empirical and no experimental studies that have examined in detail the predation strategies or approach behavior of white sharks.

Here, we examined whether white sharks direct their approach to baits in relation to a key environmental variable— the sun— and suggest the functional role of this ap-

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proach strategy. To enable us to obtain larger sample sizes than accidental observations of natural predation events, the approach behavior of white sharks toward bait was used as a proxy to test the hypothesis that white sharks can exploit the sun when approaching an object of interest.

Methods

We investigated the approach behavior of white sharks to tuna bait during 30 days between July and November 2011 at the North and South Neptune Island Groups (357149 ′S, 1367049 ′E), South Australia, near the approach to Spencer Gulf, about 30 km from the Australian mainland. We sampled during both clear and overcast days. Overcast days eliminate any directional or glare effects from the sun.

White sharks were attracted to the vessel using an odor plume (berley), which was established by continuously disbursing a mix of unrefined fish oil and minced southern bluefin tuna (Thunnus maccoyii) flesh and blood into the water at the stern of an anchored vessel. Sections of southern bluefin tuna (~6 kg) were used as bait and attached to a float secured by a 15-m line. Tuna forms part of the white shark's natural diet (Cliff et al. 1989) and so was selected to elicit a feeding motivation similar to that for natural prey. The tuna section was retracted as soon as a shark attempted to bite the bait, making it difficult for the shark to gain the bait, and it created, from the shark's perspective, a situation analogous to a failed attack on a fleeing prey. This was reflected by the observed speed of approach, which was faster than when sharks approach carrion (Dudley et al. 2000; Dicken 2008; C. Huveneers, personal observation). Although the behavior observed does not necessarily represent that of a hunting white shark, it allows experimental investigation of the behavior of unrestrained wild sharks. The bait was allowed to drift from the stern of the vessel to attract white sharks. Only one line with one bait was used per approach. The bait and line were deployed from about 0700 to 1800 hours, with the bait being refreshed approximately every 2 h. For each approach, the following parameters were recorded: shark sex, size, and identification marks; direction of approach; type of approach; and the sun direction (table 1).

We used only initial predatory approaches to the bait to investigate approach direction in relation to the sun. According to optimal foraging theory, sharks would be more likely to employ a strategy that optimizes chances of success during predatory approaches than during an investigatory approach (Dill 1983; Helfman and Winkleman 1991; for definitions of each type of approach, see table 1). Additionally, secondary or subsequent approaches— where the shark made repeated attempts at the bait in a single interaction— were more likely a response of the shark position in relation to the bait following the first approach rather than an indication of any approach strategy.

During each predatory interaction, we measured the direction of both the sun (if present) and the sharks' approach to the bait relative to the boat and then adjusted for the boat orientation. Approaches under overcast conditions— when sun glare was not present— were analyzed separately to examine whether environmental factors other than sun direction were responsible for our results. We categorized all approaches and sun directions into twelve 307 segments. Recording exact approach direction or using bins smaller than 307 segments would have implied a higher level of precision than achievable in this study. As sharks swam toward the bait, the directionality of approach could

Table 1: Descriptions of the parameters recorded for each shark approach

Parameter recorded	Description
Shark sex	Sex of sharks was recorded on the basis of the presence or absence of claspers and could be determined from the surface or underwater while diving.
Shark size	Experienced observers on the boat estimated shark length by comparing shark lengths to known dimensions, such as vessel or diving cage width.
Shark identification	Shark identity was recorded for each individual shark, using natural markings and coloration (Domeier and Nasby-Lucas 2007). Three physical features were used for identification: trailing edge of the first dorsal fin (Anderson et al. 2011; Chapple et al. 2011), pigmentation of the lower caudal fin (Domeier and Nasby-Lucas 2007), and external markings or scars (e.g., fin damage, major scars, mutilations).
Direction of approach	The direction from which the sharks approached the bait. Quantified using 307 segments in relation to the boat, where 07 is positioned directly in front of the transom deck (from which baits were deployed) and 1807 is directly behind (i.e., the bow of the vessel).
Type of approach	Classified as either predatory or investigative. Predatory approaches were defined as the shark actively pursuing the bait; attempting to take the bait by snapping, lunging, or partially breaching; following the bait as it was retracted; or changing its swimming course direction toward the exact location of the bait. Investigative approaches were defined as approaches where the shark swam past, under, or around the bait without changing course toward the bait location or pursuing the bait.
Direction of the sun	Quantified similarly to direction of approach by using 307 segments in relation to the boat.

slightly change, such that the body angle measured when sharks were 5 m from the bait was not exactly the same as when sharks were 1 m from the bait. For each approach, the 307 segment was recorded on the basis of the average body angle of the shark from when sharks where first sighted (up to a maximum of 5 m from the bait) until it attempted to consume the bait. We tested whether sharks were approaching from the same direction as the sun (i.e., with the sun behind them) more often than would be expected by chance, using the modified Rayleigh test for circular distribution, also known as the V test (Rayleigh 1919; Greenwood and Durand 1955).

We examined shark approach direction in the morning (0700–1000 hours) and in the afternoon (1500–1800 hours) with respect to compass direction. V tests were used to test whether sharks were more likely to approach from the east in the morning and from the west in the afternoon compared with a uniform distribution. For this analysis, sharks were considered to approach from the same direction as the sun if they were approaching from 307–907 in the morning or 2707–3307 in the afternoon (07 p north). The 607 angle allowed for the progression of the sun within the 3-h observation period (Johnsen 2012).

We conducted within-subject analyses of the predatory behavior of sharks to test whether the results across multiple sharks were also observed at an individual level. The use of within-subject binomial tests is a standard way of examining the behavioral strategies of individual humans and animals in the field of comparative cognition, despite the issue of independence (e.g., Tomasello et al. 1997; Kaminski et al. 2004; Silva et al. 2005; Seed et al. 2009; Taylor et al. 2009). For this analysis, we selected sharks (n p 7) that interacted regularly with the bait, with regular interaction defined as a minimum of five predatory approaches per day for 2 days, with approaches occurring over a time period of at least 2 h. We used this strict definition because sun direction could have covaried with odor trails created by wind or tide direction for short periods on certain days. By examining only the sharks that approached the bait over a minimum of 2 h on two different days, we reduced the possibility that our results could be due to such covariation, because wind or tide direction were unlikely to constantly change in the same way as the sun throughout the study period. Although wind direction can predictably change throughout the day, as air temperature increases over land masses producing onshore winds, the study site was 30 km from the closest sizable land mass and was not affected by onshore winds. To ensure that our results were not solely due to the behavior of these persistent sharks, we also performed a V test excluding them.

The potential influence of environmental variables on white shark approach direction was tested using a generalized linear mixed model (GLMM). The error structure of GLMM corrects for nonindependence of sampling units due to repeated measures of the same individual and shared temporal structure. Our GLMM had sun direction, wind direction and strength, swell height, and water depth as fixed factors and individual sharks as a random effect. Before applying the model, collinearity between variables was tested using a stepwise function to iteratively remove collinear variables by calculating the variance inflation factor of variables against each other. Variables with a variance inflation factor 15 were not included in the GLMM. Modeling was undertaken using the glmmPQL function of the MASS R package. The most appropriate statistical family and error distribution (gamma distribution with inverse link) and the validity of the model were determined through an examination of the distribution of the response variable, a visual inspection of the residuals for the saturated models, and an ANOVA test between the fitted and residual values of the model.

The uniformity of approach direction across the twelve 307 segments was also tested during overcast days to determine whether directionality of approaches still occurred when light was diffused by clouds by using the Rayleigh test for uniformity, and this was compared with approach direction during sunny days through the Watson-Williams two-sample test (Mardia and Jupp 2000). The influence of other behavioral drivers (e.g., boat direction, wind, surface berley) was assessed by testing directionality of approaches in relation to boat and wind directions against a uniform approach direction using the V test.

In addition, circular variance (S^2; Zar 2010) of approach direction was compared between sunny and overcast days. Circular variance was calculated for each shark that interacted regularly with the bait to measure the dispersion of the data and assess whether approaches originated from the exact direction of the sun (small variance) or across the 1807 segment with the sun behind the sharks (large variance).

The measure of success rate also enabled us to assess whether the sun-hiding strategy resulted in higher probabilities of successful predation. The success rate of each approach was recorded in this study, but differences in the experience of the various bait handlers used in the study and the lack of complete recording of who the bait handler was on each approach prevented any analysis from being meaningful. Some handlers were highly experienced at preventing the sharks from gaining the bait, others were not. Thus, the chance of sharks gaining the bait fluctuated inconsistently over time. The bait was, however, presented the same way by each bait handler.

Results

A total of 958 approaches by 44 different white sharks were recorded. Out of those, 579 approaches by 37 sharks were categorized as predatory approaches, with 400 approaches (36 sharks) being initial predatory approaches. Of these, 63 approaches were by 11 sharks during overcast conditions, and 337 approaches were by 34 sharks during sunny conditions (data deposited in the Flinders University of South Australia Repository, http://hdl.handle.net/2328.1/1125, and in the zip file, available online).

Preliminary analysis combining all initial predatory approaches ($n = 337$) showed that approach direction was not uniformly distributed ($u = 0.116$, $P = .001$), with sharks primarily approaching the bait from the direction of the 30° segment containing the sun (20.0%; fig. 1A; video 1). If sharks were exploiting the sun, we would expect them to approach from the east in the morning and the west in the evening. Out of the 337 recorded approaches, only 20 approaches were recorded between 0700 and 1000 hours. Eight of those were from 30°–90° (40.0%), leading to the overall approach direction during the morning to be significantly more oriented than expected by chance ($u = 0.476$, $P = .001$). Fifty-seven approaches were recorded between 1500 and 1800 hours. Fifteen approaches were from 270°–330° (26.3%), which also led to approach direction during the afternoon being significantly more likely to come from the direction of the sun ($u = 0.224$, $P = .008$; table 2). These results suggested that sharks were more likely to approach the bait from the east in the morning and from the west in the afternoon than expected by chance.

Analysis of the behavior of the seven individual sharks that interacted frequently with the bait showed that four of the seven sharks approached with the sun behind them more than would be expected by chance (table A1; tables A1, A2 available online). Thus, the significant effect identified across all the sharks in our study was also seen in the behavioral strategies of individual sharks. Our main conclusion was not solely due to the behavior of these four sharks; the analysis of the full data set excluding these sharks still showed that approaches from the direction of the sun were marginally more frequent than expected by chance ($n = 190$ approaches, $u = 0.103$, $P = .049$).

All variables included in the GLMM had a variance inflation factor < 2 and were therefore included in the model. The only environmental variable that significantly affected the approach direction of white sharks was the sun direction (GLMM: $t_{298} = -3.35$, $P < .0001$; table A2), with wind direction and strength, swell height, and depth not having a significant effect on the direction of approach of white sharks (table A2). In addition, the approach direction of white sharks was also dependent on the individual shark (random effect: $t_{298} = 5.44$, $P < .0001$; table A2), supporting findings from the within-subject analysis that not all white sharks exploit the sun in similar ways.

In contrast to sunny days, approaches during overcast days were uniformly distributed ($n = 63$ approaches, $z = 0.027$, $P = .954$) and were significantly different from the mean approach directions during sunny conditions (Watson-Williams test: $F = 13.06$, $P < .0001$). Approach directions were also homogeneously distributed in relation to the boat on both sunny and cloudy days (sunny: $n = 337$, $z = 0.075$, $P = .153$; cloudy: $n = 63$, $z = 0.047$, $P = .871$) and was not more frequent from the direction of the surface berley than expected by chance ($n = 400$ approaches, $u = 0.041$, $P = .876$). Thus, odor trails due to berley or position of the boat cannot explain our results.

Overall, circular variance of approaches during sunny days (0.81) was smaller than during overcast days (0.987). For all sharks that interacted regularly with the bait, circular variance of the data was less than the variance estimated if approaches were random across the 180° segment around the sun. Overall, this decrease of circular variance was more pronounced for sharks approaching from the sun significantly more than expected by chance (table A2). The lower circular variances from the data support our findings that sharks did not just approach the bait with the sun behind them or to their side but specifically targeted the exact direction of the sun.

Discussion

Our results show that white sharks approached with the sun directly behind them more often than expected by chance and appeared to reverse their direction of approach along an east-west axis from morning to afternoon. Further analyses showed that this behavior was not observed on overcast days, nor did it correlate with other potential behavioral drivers, such as the boat or wind direction, which could affect the dispersal of surface berley. The lack of correlation with or significant effect from other environmental variables—coupled with directionality disappearing on overcast days—demonstrates that our results are likely due to shark's sensitivity to the direction of the sun and not to confounding variables. Given the low number of approaches observed in the morning and afternoon, further sampling of shark approaches at these times would be useful to confirm the hypothesis that individual sharks reverse their direction of approach across the day.

The approach strategy of using the sun was not observed in all sharks and suggests interindividual variation. This variation likely results from differences in feeding histories or other individual histories, motivations, conditions, or behavioral syndromes. This does not negate the findings of this study but instead reinforces the increasing recognition that individuals foraging in the same area can exhibit consistent differences in foraging patterns (individual specialization; Bolnick et al. 2003). Even within individuals, sharks can vary strategies with prey type (Heithaus and Vaudo

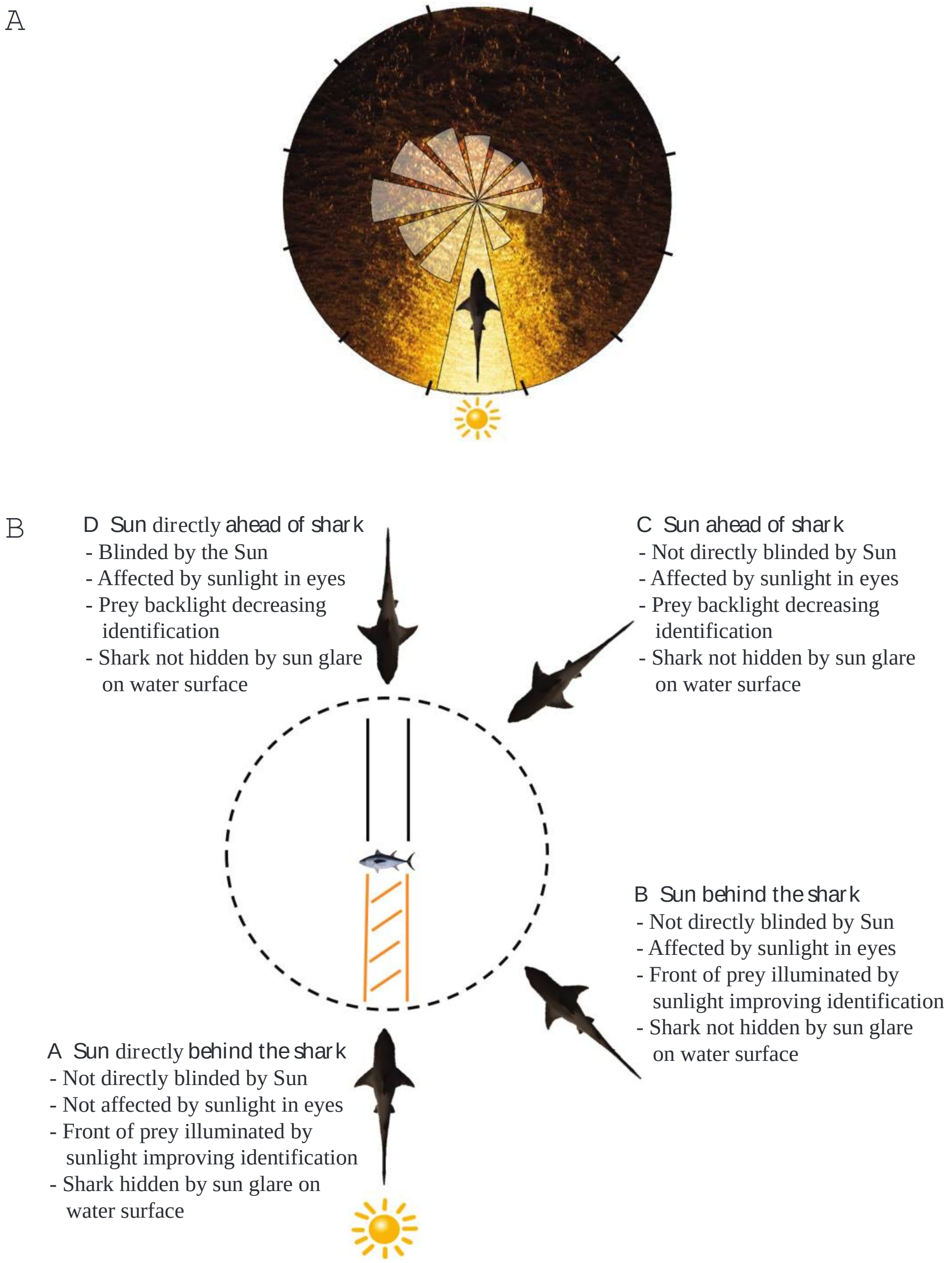

Figure 1: A, Percentage of shark predatory approach direction in relation to the position of the sun. Segments represent the twelve 30° segments, with the bottom segment representing approaches with the sun behind the shark, as illustrated by the shark, sun, and sun glare. The largest proportion of approaches by white sharks (20% of the 337 approaches) were from the same direction as the sun (i.e., with the sun directly behind the shark). This was significantly different from the expected random approach ($P < .001$). B, Illustration of the hypothesized functional roles of sharks orienting themselves in relation to the sun (view from above).

Video 1: Still photograph from a video (video 1, available online) showing examples of white sharks (Carcharodon carcharias) approaching a bait to illustrate the difference in visibility due to the sun glare on the water surface. The first approach illustrates a shark approaching from a different direction from the sun and shows that the shark is visible. The second approach illustrates a shark approaching from the direction of the sun and shows that the shark cannot be seen until it already has the bait.

2012). For example, whale sharks change their feeding technique— from active surface feeding to vertical feeding or passive feeding— with decreasing zooplankton densities (Nelson and Eckert 2007). White sharks attack sea lions with greater force than elephant seals because of differences in escape abilities and probability of getting wounded (Klimley et al. 1996). Differences in foraging strategies and tactics can play an important role in population, community, and ecosystem dynamics and deserve increased attention (Heithaus and Vaudo 2012).

Our findings represent the first empirical evidence of a nonhuman animal exploiting the sun as part of its predation strategy. Past studies have successfully shown that the behavior of prey species can be mediated by light intensity (Fernández-Juricic and Tran 2007; Braña et al. 2010) and sun direction (Carr and Lima 2014), with those studies often relating these behavioral changes to the trade-off between feeding and predator avoidance. The few studies that suggested that predators exploit the sun during predation provide poor or ambiguous evidence. For example, the Mauritius kestrel (Falco punctatus) might use sun-orientated hunting behavior (Temple 1987); however, the tracking of the sun by that species appears to be driven by the heliotrophic behavior of its prey, geckos of the genus Phelsuma. Peregrine falcons (Falco perigrinus) have also been found to approach prey from the east in the morning (Tucker et al. 2000). This study was then used by Carr and Lima (2014) to suggest that prey species predominantly faced south in response to the behavioral tactics of predators attacking out of the sun. However, because no observations of predation were made in the afternoon, the behavior described by Tucker et al. (2000) may be affected by other environmental variables.

There are several non–mutually exclusive hypotheses that could explain the functional role for sharks to use the sun (fig. 1B). White sharks may approach with the sun directly behind them to increase the detectability and visual identification of the pursued bait. This can occur in three ways. First, visual detection and identification of the intended prey is improved when the sun is behind the approaching shark because the sun directly illuminates the side of the prey facing the shark (fig. 1B, positions A and B). In contrast, when the sun is in front of the shark, the prey side facing the shark is in shadow, hampering prey identification (fig. 1B, positions C and D).

Second, if the sun is behind the shark, the contrast between the prey and the visual background is further increased because of the darker visual background. The visual background consists of the light coming from the water behind the prey (sidewelling light), which is at its minimum when the sun is behind the shark because this spacelight is a result of water backscattering. Consequently, by having the sun behind them, sharks will see the prey most strongly illuminated with the least intense visual background, maximizing the prey-background contrast. This also occurs when the prey is within Snell's window and the sky rather than when the sidewelling spacelight is the

Table 2: Summary of approach direction in the morning (0700–1000 hours) and afternoon (1500–1800 hours)

Compass direction	No. approaches (%) 0700–1000 hours	No. approaches (%) 1500–1800 hours	P 0700–1000 hours	P 1500–1800 hours
3307–307	1 (5)	5 (9)	.97	.97
307–907	**8 (40)**	6 (10)	**.011**	.93
907–1507	**7 (35)**	11 (19)	**.037**	.35
1507–2107	0 (0)	11 (19)	1	.35
2107–2707	1 (5)	10 (17)	.97	.48
2707–3307	3 (15)	**15 (26)**	.67	**.043**
Total	20	57		

Note: Results in bold indicate that approach direction was significantly more frequent than expected by chance.

visual background. The use of Snell's window to increase prey detectability during white shark predatory behavior has previously been conceptually demonstrated but was not statistically tested (Martin and Hammerschlag 2012).

Third, the observed approach strategy can also be explained by white sharks avoiding the sun inside Snell's window either anywhere in their field of view or close to the line of sight toward the prey, which would affect their visual ability to track the bait. When the sun strikes their retina, it results in an excess of sunlight in the eye chamber, which reduces retinal image contrast and visual resolution. Such an effect has been referred to as disability glare (Koch 1989; Martin and Katzir 2001) and has been proposed to explain why prey can take longer to detect predators in sunlit compared with shaded areas (Fernández-Juricic et al. 2012). Moreover, if the sun is close to or behind the prey, then the sun directly interferes with the prey image. Considering that most elasmobranchs have a monocular visual field of ~1707 (McComb et al. 2009), sharks would need to position the sun within an ~207 segment directly behind them to align the blind area toward the sun and avoid having the sun striking their retinas during an approach (fig. 1B, position A). This is close to the 307 range of angles that we observed. The ability to detect and identify prey would be maximized when the sun is directly behind the shark (position A) and would fall off as the angle between the shark and the sun approaches 907. This is supported by the significantly reduced variance of attack angles compared with the variance if approaches were homogeneous across the 1807 segment with the sun behind the sharks. It is possible that sharks can tolerate the sun striking their retina and still attack successfully, as long as the sun is not within a few degrees of the prey direction. This would predict a much larger range of attack directions than simply keeping the sun off the retina. However, without knowing the critical angle of image interference, and considering that sharks are constantly making minor angle changes, it is impossible to predict what the attack angle variance should be. In any case, it is likely that both visual contrast and avoiding sun on the retina are affecting the sharks' behavior simultaneously.

Concealment is another explanation for our results. Sharks occasionally attack prey when the prey's head is above water (e.g., pinnipeds or birds). White sharks might approach such prey with the sun directly behind them (fig. 1B, position A) to exploit the surface sun glare and decrease their detectability to a targeted prey above the water surface (video 1). Although seabirds are not considered frequent prey of white sharks, birds have been found in their stomachs (Bass et al. 1975; Malcolm et al. 2001). They are also responsible for the majority of the injured and dead African penguins recovered from St. Croix and Bird Islands, South Africa (Randall et al. 1988), with evidence of attempted predation on seabirds observed at Dyer Island, South Africa (Johnson et al. 2006), and the Neptune Islands, South Australia (C. Huveneers, personal observation). Obviously, penguins and seals could have been attacked while underwater. Nevertheless, the initial attack could occur when a prey's head is above the water surface. In this case, on a sunny day, the prey will see a large patch of sun glare from the water surface in the direction of the sun, hiding an approaching shark (video 1). This would work only if the sun was behind the shark, allowing its movement to be concealed by the glare corridor. (fig. 1B, position A). This approach direction was the one used most often by sharks on sunny days (fig. 1A).

To date, white sharks have been shown to predate around dawn and dusk (Fallows et al. 2012) and to ambush from depth (Martin and Hammerschlag 2012). Sun hiding could also improve the success rate of attacks and may be a further reason why white sharks show increased predation activity and success around dawn and dusk, when directionality of sun light and effects of sun glare are strongest (Hammerschlag et al. 2006). Future studies should account for sun angle, distance, and depth for each type of prey (e.g., fishes, pinnipeds, seabirds) during experimental and natural predatory events to attempt to disentangle and estimate the relative contributions of the multiple explanations for white sharks to expressly approach with the sun directly behind them.

In our study, a section of tuna was used to elicit predatory behavior in white sharks, since it would have been logistically difficult to collect as many observations of the initial approach direction during natural predations. Consequently, we cannot infer that white sharks use this predatory strategy when hunting a live prey. Nevertheless, it shows the ability of some white sharks to track the position of the sun and then use this cue to coordinate the direction of their approach toward an object of interest, which is likely to be a nontrivial cognitive task. Not only was the sun's position constantly shifting but also the relative position of the bait was continually changing as a result of currents, wind, and the actions of the bait handler. Thus, even if sharks simply positioned themselves with both eyes receiving the same amount of light to place themselves with the sun directly behind them, they would need to simultaneously monitor light levels and bait position to exploit the sun. White sharks, therefore, have sufficient behavioral flexibility to modify their behavior in real time in response to two fluctuating environmental cues. This behavior may well be underpinned by perceptual-motor feedback (Taylor et al. 2010, 2012). Future work will focus on describing the interindividual variation in white shark predation strategies and the cognitive mechanisms that underpin them.

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