

Effects of lunar phase on predator-prey interactions between white shark (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*)

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Abstract Predator-prey relationships can be influenced by environmental conditions, including changes in moon phase and associated lunar illumination. Two primary hypotheses have been proposed underlying the effects of moonlight on predator-prey interactions: the *predation risk hypothesis* and *visual acuity hypothesis*. However, few studies have tested these hypotheses during twilight hours or involved large mobile aquatic species. In the present study, we evaluated these hypotheses using data collected over 16 years on predator-prey interactions between white shark (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at sunrise. Data from 1476 natural predation events demonstrated shark attack frequency and seal capture success was significantly higher at sunrise during periods of low (0–10 %) versus high (90–100 %) lunar illumination, which is consistent with the *visual acuity hypothesis*. We propose that during full moon periods, white sharks at night are at a visual and tactical advantage over seals which are

silhouetted at the surface in the moonlight and thus easier to isolate in darkness, while sharks remain camouflaged hunting from below through deep water. However, at sunrise, we hypothesize this advantage shifts to seals as the added lunar illumination, combined with emerging sunlight, may decrease shark stealth and increase the ability of seals to detect and avoid sharks. These findings suggest that lunar effects on predator-prey dynamics can be context specific, likely moderated by visual acuity of predators and prey which may change according to the photoperiod.

Keywords Predator-prey interactions · Sharks · Seals · Moon · Lunar phase · Predation risk

Introduction

Predators can impact ecosystem structure and function via prey consumption and/or through ‘risk effects’, which include alteration in prey behavior or physiology in response to the risk of predation (Lima and Dill 1990; Creel and Christianson 2008; Ripple et al. 2014). Thus, studying predator-prey interactions and the factors that may affect these relationships is important, especially given population declines of many predators globally (Estes et al. 2011). Predation can be influenced by the effects of environmental conditions on the sensory capabilities of both predators and prey (Ellis 1986; Lim and Dill 1990; Martin and Hammerschlag 2012). For example, predatory gastropods (whelks *Busycon* spp.) exhibit higher foraging success on hard clams when bottom

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roughness increases turbulent mixing of prey chemicals or disrupts prey abilities to detect and respond to predator odors (Ferner et al. 2009).

One environmental factor that can have an effect on predator-prey relationships is moon phase and the associated changes in lunar illumination due to the moon's orbit (Mougeot and Bretagnolle 2000; Penteriani et al. 2011; Prugh and Golden 2014). The effects of lunar illumination on predation dynamics is believed to be most pronounced for visual species, because the amount of available moonlight may influence a predator's capability to visually detect and capture a prey and likewise, a prey's capability to visually detect and evade a predator (Kotler et al. 2002; Creel et al. 2008; Mukherjee et al. 2009). Two primary hypotheses have been proposed underlying the effects of moonlight on predator-prey interactions: the *predation risk hypothesis* and *visual acuity hypothesis* as outlined and modified from Prugh and Golden (2014). The *predation risk hypothesis* predicts that increases in moonlight will enhance predation due to increases in the ability of visual predators to detect and capture prey. Whereas, the *visual acuity hypothesis predicts* that increases in moonlight will suppress predation due to increases in the ability of visual prey to detect and avoid predators. More recently, it has been proposed that habitat cover will modulate predation efficiency with increasing moonlight (i.e. *habitat-mediated predation risk*). Studies have reported mixed results for these hypotheses (e.g. Clarke 1983; Kotler et al. 2010; Penteriani et al. 2011; Penteriani et al. 2013). Moreover, the majority have involved rodents in mesocosm or laboratory experiments (Daly et al. 1992; Upham and Hafner 2013; Busch and Burroni 2015). In contrast, there have been a lack of comparable studies involving mobile predators and prey in natural aquatic systems, likely due the inherent logistical and technological challenges of working with large species in these systems. Studies evaluating the effects of moonlight on predator-prey relationships have also predominantly focused on nocturnal periods (Mougeot and Bretagnolle 2000; Penteriani et al. 2011; Prugh and Golden 2014). However, few investigation of this kind have occurred during twilight hours (i.e., sunrise and sunset), although changes in lunar illumination during these low-light periods may also impact the detection capability of predators and prey.

White sharks (*Carcharodon carcharias*) are visual apex predators that frequently feed on visual prey, such

as seals, across their global range (e.g., Klimley et al. 2001; Domeier et al. 2012; Kock et al. 2013; Jewell et al. 2013; Towner et al. 2016). Seal Island in False Bay, South Africa, provides a unique opportunity to study predator-prey interactions between white sharks and Cape fur seals (*Arctocephalus pusillus pusillus*). During winter months, white sharks patrol the waters around Seal Island, which are inhabited by over 60,000 Cape fur seals, to actively hunt seals when they enter and exit the water to and from foraging (Martin et al. 2005, 2009; Fallows et al. 2012). Predatory attacks average 6.7 per day, with up to 42 predations recorded on a single day (Hammerschlag et al. 2006). Frequency and success rate of white shark attacks on seals is highest within two hours of sunrise and during low light levels when sharks are at a visual advantage over seals (Hammerschlag et al. 2006). White sharks have also been suggested to be capable of exploiting changes in sun direction and intensity to enhance predation through increasing their concealment and improving prey detection (Huvenceers et al. 2015). Therefore, it is plausible that changes in moon phase and associated moonlight could influence shark predation frequency and success at dawn. In the present study, we evaluated the *predation risk hypothesis* and *visual acuity hypothesis* at twilight in response to moon phase by comparing the frequency and success rate of white shark attacks on Cape fur seals within an hour of sunrise during periods of low (0–10 %) versus high (90–100 %) lunar illumination.

Methods

Predations by white sharks on cape fur seals were studied between 1998 and 2013 at Seal Island in False Bay, South Africa, following the methodology of Martin et al. (2005, 2009); Hammerschlag et al. (2006) and Fallows et al. (2012), which is provided in the following descriptions of the study site and predation event detection.

Study site

Seal Island is an elongated rocky islet centred at latitude 34.1374°S, longitude 18.5825°E, with its south terminus facing the 25 km-wide mouth of False Bay. The underwater topography around the waters of Seal Island features a sharp drop-off along most of the western side of the islet, where the water depth reaches 20 m within 50 m of shore, and a broad, shallow shelf along the north

east side, where the water does not reach comparable depths until 400 m or more from shore. Seal Island is inhabited by over 60,000 Cape fur seals. The seals typically leave the island in coordinated groups of 5–20 to feed in False Bay or up to 12–30+ km offshore, outside of the Bay, returning to the island at irregular intervals as solitary individuals or often in groups of 2–3 and occasionally larger. The primary entry/exit point for the seals, termed the ‘Launch Pad’, is an identifiable spot seaward of a small rock outcrop located off the south end of the island. Seals mostly travel to and from the Island via porpoising at the surface where they are attacked by sharks hunting below.

Predation events

Observations were made at Seal Island during every month by one or two boats. At least part of the research team averaged some 200 days per year on the water, although the majority of observation occurred during winter months (May–September), when most predatory activity occurs (Hammerschlag et al. 2006). The research vessel arrived and began observations at Seal Island at about 0700 h (~1.5 h before sunrise), sea conditions permitting.

As described in Fallows et al. (2012), predatory events were detected at the surface by one or more of the following: (1) white shark breach with a seal in its mouth or a seal leaping away from its mouth; (2) a sudden change in the travel behavior of seals, switching from directional porpoising to zigzag evasive maneuvers with a shark in pursuit; (3) a splash accompanied by a blood stain, oil slick, a distinctive odor, and by any of the following indicators such as a floating seal head or entrails floating on the surface or trailing from the gill openings of a white shark in the immediate vicinity and/or highly localized plunge-diving black-backed kelp gulls (*Larus dominicanis vetula*) picking up and feeding on seal entrails. Any subsurface kills could be detected by the appearance of a blood stain at the surface and floating seal entrails. Observed predatory events were recorded and classified as unsuccessful, in which the seal escaped, or successful, in which the seal was consumed.

Attacks by white sharks occur at the surface on seals porpoising to and from the Island. Attacks are concentrated on the southern side of the Island, close to shore (within 2 km). Thus, by positioning at the south end of Seal Island where the majority of predatory activity

occurs, a single vessel can survey at least 270° uninterrupted to a distance of at least 3.5 km.

Seal movements

To obtain a sample of seal availability and movement around the Island, the time and number of seal groups leaving from and returning to Seal Island per day was recorded in the 2003 field season over 21 days.

Moon data & light levels

Lunar data was extracted from the US Naval Office’s Astronomical Applications Department (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). These data were the percent of the moon illuminated at midnight in the southern hemisphere in the time zone of South Africa (i.e. Universal Time – 2 h). To evaluate potential relationships between shark predation and lunar illumination, we considered “full moon” periods as those days where 90–100 % of the moon was illuminated. We considered “new moon” periods as those days where 0–10 % of the moon was illuminated.

Data analyses

While observations were made year-round, we focused our analyses on data collected during the winter months when white sharks aggregate at Seal Island to actively hunt juvenile Cape fur seals. To standardize data analyses and avoid the confounding effects of illumination from full sunlight on potential relationships between predations and moon illumination, we restricted our analysis to predation data collected at dawn, between 07:00 h and 09:30 h (approximately ± 1 h of sunrise). We considered a 120–150 min observational period between 07:00 h and 09:30 h per day as a sample.

Predation data were not normally distributed, even after transformation, and thus were not suitable for parametric statistical comparisons. Thus, we statistically compared frequency of all predation events and successful kills during new moon (0–10 % illumination) versus full moons (90–100 % illumination) using three metrics. First, we used Kruskal-Wallis tests to compare the number of predations per sample as well as the number of kills per sample during full versus new moon periods. Second, we similarly used Kruskal-Wallis tests to

compare the number of predations observed per hour as well as the number of kills per hour for each sample during full versus new moons. Third, we used chi-squared analyses to compare the percent of samples in which a predation event and/or a kill occurred during new versus full moons.

Seal movement data collected between July 1 and August 10 were normally distributed and thus suitable for parametric statistics. Therefore, we used ANOVA to compare the mean number of seal groups moving about Seal Island during new versus full moons.

Results

Between 1998 and 2013, 219 sampling events occurred between 07:00 h and 09:30 h under full moon ($N = 116$ samples) versus new moon ($N = 103$ samples). These samples accounted for a total of 1476 predations, 650 predations (262 kills) occurring during full moons and 826 predation events (404 kills) during new moons. This corresponded with a mean \pm SE of 5.6 ± 0.6 predations per sample during full moon versus 8.0 ± 0.7 predations per sample during new moons (Fig. 1). Similarly, mean \pm SE kills per sampling period was 2.3 ± 0.3 during full moons and 3.9 ± 0.4 per sample period during new moons (Fig. 1). Total predations per sample was significantly higher during new versus full moon periods (Kruskal-Wallis, $P < 0.01$) as was total kills per sample (Kruskal-Wallis, $P < 0.0002$, Table 1; Fig. 1a). Predations per hour was significantly higher on new versus full moons (Kruskal-Wallis, $P = 0.002$) as was kills per hour (Kruskal-Wallis, $P = 0.01$; Table 1, Fig. 1b). The percent of sampling periods in which a predation event occurred did not significantly differ (Chi-square, $P = 0.95$) during new moons (predations occurred in 90 % of samples) versus full moons (predations occurred 91 % of samples). Similarly, the percent of sampling periods in which a kill occurred did not significantly differ (Chi-Square, $P = 0.11$) during new moons (kills occurred in 84 % of samples) versus full moons (kills occurred in 76 % of samples).

Sampling of seal groups moving to and from Seal Island revealed no significant differences (ANOVA, $P = 0.65$) in the number of seal groups moving about the Island during new moon (57 seal groups) and full moons (62 seal groups) between 07:00 h and 09:30 h.

Discussion

Data collected over 16 years on 1476 natural predation events between white sharks and Cape fur seals demonstrated that during winter months, the probability of at least one white shark attack and successful kill on a seal was equal within approximately an hour of sunrise on a full versus new moon. However, both shark attack frequency and seal capture success was significantly higher during new moon (0–10 % lunar illumination) compared to full moon (90–100 % lunar illumination) periods. Data collected on seal movements about the Island suggest these results are not driven primarily by differences in the availability of seals. Our findings are consistent with the *visual acuity hypothesis* that predicts moonlight will increase the ability of visual prey to detect and avoid predators (based on Prugh and Golden 2014). Below we discuss how differences in lunar illumination may effect a white shark's ability to detect, isolate and ambush seals as well as a seal's ability to detect and evade an attacking shark.

Light intensity influences the visual range of predator and prey, directly affecting their foraging decisions (Lima and Dill 1990). The visual capabilities of white sharks remain unknown, but histological examination of the white shark retina has revealed a rod-to-cone ratio of 4:1 and retinal specializations consistent with scotopic vision (Gruber and Cohen 1985). In terms of a seal's visual capability, they should be able to visually identify a white shark at distances of about 4.8 m under sunlit conditions and approximately 2.6 m under crepuscular condition when at the surface looking down below (Martin and Hammerschlag 2012). Thus a white shark's ability to ambush seals undetected is hindered during higher light conditions. Indeed, Hammerschlag et al. (2006) found that at Seal Island, white shark daily frequency of attack and seal capture success rate was highest (55 %) during low light levels ($<200 \mu\text{E}$), but declined significantly during high light conditions ($>300 \mu\text{E}$). White sharks appear to have the behavioral flexibility and cognitive ability to detect changes in ambient light levels and modify their feeding behavior in real time in response to environmental clues (Huveneers et al. 2015). White sharks at Seal Island appear to cease daily hunting activity when their seal capture success rate drops to about 40 % during high light levels, likely to conserve time and energy during these unproductive conditions (Martin et al. 2005). During periods of full moons, ambient light levels

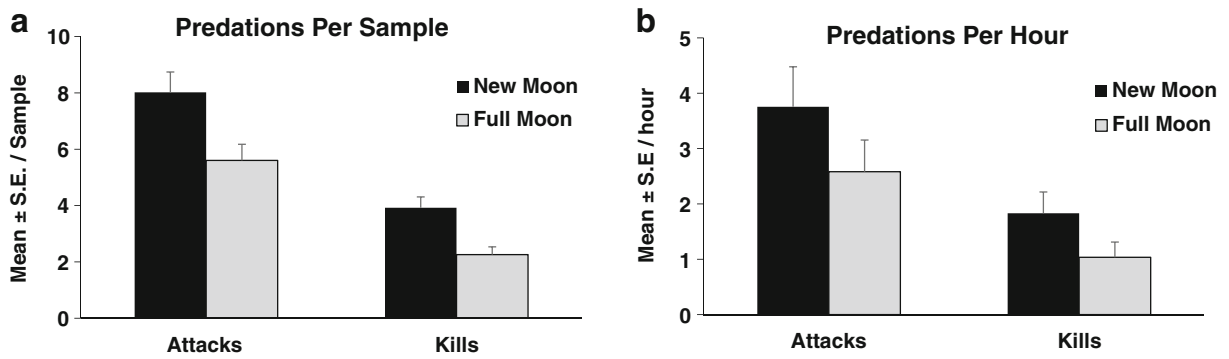


Fig. 1 Mean ± standard error (S.E.) of total predation events and kills observed per sample **a** and per hour **b** during new (0–10 % lunar illumination) and full moon (90–100 % lunar illumination) periods

around Seal Island are higher (>300 μE) within an hour of sunrise than compared to ambient light levels at the same time (<200 μE) during new moon periods (Hammerschlag et al. 2006). Accordingly, we hypothesize that the decrease in white shark attack frequency and success during full moons at sunrise is a result of the increased lunar illumination in addition to sunlight that effectively reduces a white shark’s stealth and ambush ability, enabling seals to better visually detect and potentially avoid an attacking shark (Fig. 2). Consequently, sharks may reduce hunting activity as well as incur lower predatory success as reflected in the data.

Hammerschlag et al. (2006) proposed that during the night, a full moon may silhouette a cape fur seal’s location against the surface, rendering the seal more visible to a hunting white shark and thus vulnerable to predation from a shark concealed through dark water below. Moreover, the added lunar illumination may allow a shark to more efficiently isolate a single seal target from a group at night which would otherwise likely be more

difficult for a shark during a new moon. Trillmich and Mohren (1981) found that Galapagos fur seals (*Acrotocephalus galapagensis*) reduced at sea excursions during full moons, potentially as an anti-predatory strategy to avoid being silhouetted at the water surface in the moonlight, thereby reducing vulnerability to shark predation. Here, we also hypothesize that the lower white shark attack frequency and prey capture success observed during our sampling could also be due, at least in part, by an increase in nocturnal shark hunting prior to sunrise enabled by lunar illumination from a full moon (consistent with the *predation risk hypothesis*). Thus by sunrise, sharks may already be satiated or finished their peak predation activity. Such a result is consistent with white sharks hunting Cape fur seals at a rookery in Mossel Bay, South Africa, in which shark predation peaks in the early night believed to be the result of light pollution from the city providing sharks with a visual advantage to detect seals silhouetted at the surface, while sharks remain camouflaged from below through dark water (E. Gennari, pers. Comm.).

Table 1 Summary statistics for total predation events and successful kills per sample and per hour during new moon and full moon periods

Lunar phase	Variable	Mean	Std error	N	Lower quartile	Median	Upper quartile
New	Predations / sample	8.0	0.7	103	2.0	7.0	12.0
	Kills / sample	3.9	0.4	103	1.0	2.0	6.0
	Predations /hr	3.8	0.3	103	1.0	3.0	5.6
	Kills / hr	1.8	0.2	103	0.5	1.0	2.8
Full	Predations / sample	5.6	0.6	116	2.0	4.0	8.0
	Kills / sample	2.3	0.3	116	1.0	1.0	3.0
	Predations / hr	2.6	0.3	116	0.9	1.8	3.7
	Kills / hr	1.0	0.1	116	0.4	0.5	1.4

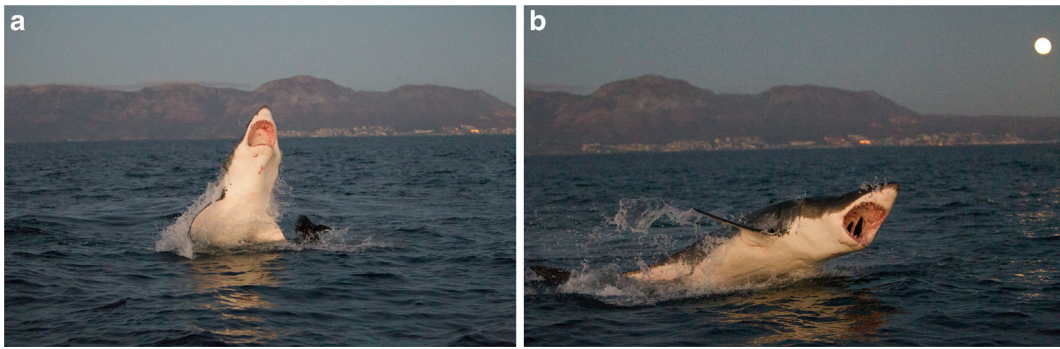


Fig. 2 Photo sequence of an unsuccessful predation attempt by a white shark on a Cape fur seal at sunrise during a full moon. In **a**, the seal was able to avoid the advancing white shark, potentially

due to added lunar illumination (moon in top right corner of **b**) that enabled the seal to visually detect the approaching shark from below

Nocturnal trips to our study site have revealed that seal departures from the Island at night are far greater than during any other time of day. This is consistent with acoustic tracking data of Cape fur seals at Seal Island that has revealed increased seal movement about the Island at night (Laroche et al. 2008). We suspect that this is due to reduced predation risk to seals moving under the cover of darkness. Indeed, Cape fur seals at the study site undertake nocturnal movements about Seal Island during the winter months when white sharks are actively hunting at the Island (i.e. high risk season); but in contrast, seals do not exhibit any diel patterns in movements during summer months when sharks are not actively hunting seals (i.e. low risk season) (De Vos et al. 2015). Given that white sharks likely have the ability to detect and approach seals in complete darkness using sound, vibration or smell (Fay et al. 1974; Maruska 2001; Casper and Mann 2007; Gardiner and Atema 2007, 2014), we hypothesize that it is difficult for sharks to isolate a single seal target from within a large group in complete darkness which is why predation risk to seals is reduced at night and consequently why seals primarily move about the Island at night. Indeed, when we have towed a single seal decoy at night under dark conditions, where there are no apparent visual cues for the sharks but still mechanical signals through sound and vibration, we have documented attacks on the decoy. In contrast, preliminary observation at night have revealed relatively fewer attacks on groups of seals moving about the Island as compared to during the day, despite the high availability of seals at night.

A limitation of our study is that we did not assess nocturnal predator-prey relationships at Seal Island and

the potential influences of changes in lunar illumination on such interactions at night. Thus, further research is needed at Seal Island at night during full and new moon conditions to test our hypotheses. In July and August 2015, we conducted a preliminary study of this kind that included tows of seal decoys, use of imaging sonar, acoustic tracking of white sharks and observations for natural predation events using low light cameras during new and full moons. These preliminary data provided some initial support for our hypotheses, but additional research of this kind is needed to investigate further.

In summary, here we found that attack frequency and success of white shark predation on Cape fur seals within an hour of sunrise was reduced during periods of full moon compared to new moon in a manner consistent with the *visual acuity hypothesis*. We propose that this is due to changes in lunar illumination that affect the detection capabilities of sharks and seals and their associated sensory modalities which can differ by photoperiod. Specifically, during full moon periods, we hypothesize that white sharks at night are at a visual advantage over seals which are silhouetted at the surface in the moon light and easier to isolate as targets within groups, while sharks remain camouflaged hunting below through deep murky water. However, at sunrise, we propose this advantage shifts to seals as the added lunar illumination, combined with sunlight, may decrease shark stealth and increase the ability of seals to detect and avoid sharks. Taken together, our findings build on previous research revealing that lunar illumination can effect a predator's capability to visually isolate and capture prey, and in turn, a prey's capability to detect and evade a predator; and further, that such

lunar effects on predator-prey dynamics can be context specific, moderated by visual acuity and habitat characteristics (Prugh and Golden 2014).

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References

Busch M, Burroni NE (2015) Foraging activity of commensal *Mus musculus* in semi-captivity conditions. Effect of predator odours, previous experience and moonlight. *Pest Manag Sci* 71(12):1599–1604. doi:10.1002/ps.3962

Casper BM, Mann DA (2007) Dipole hearing measurements in elasmobranch fishes. *J Exp Biol* 210(1):75–81. doi:10.1242/jeb.02617

Clarke JA (1983) Moonlight’s influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behav Ecol Sociobiol* 13(3):205–209. doi:10.1007/BF00299924

Creel S and Christianson D (2008) Relationships between direct predation and risk effects. *Trends Ecol Evol* 23(4): 194. doi: 10.1016/j.tree.2007.12.004

Creel S, Winnie JA, Christianson D. Jr., Liley S (2008) Time and space in general models of antipredator response: tests with wolves and elk. *Anim Behav* 76: 1139e1146. doi:10.1016/j.anbehav.2008.07.006

Daly M, Behrends PR, Wilson MI, Jacobs LF (1992) Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim Behav* 44(1):1–9. doi:10.1016/S0003-3472(05)80748-1

De Vos A, Justin O’Riain M, Meyer MA, Kotze PGH, Kock AA (2015) Behavior of Cape fur seals (*Arctocephalus pusillus pusillus*) in relation to temporal variation in predation risk by white sharks (*Carcharodon carcharias*) around a seal rookery in False Bay, South Africa. *Mar Mam Sci* 31(3):1118–1131. doi:10.1111/mms.12208

Domeier ML, Nasby-Lucas N, Lam CH (2012) Fine-scale habitat use by white sharks at Guadalupe Island, Mexico. Page 121–132 In: Domeier ML. editor. Global perspectives on the biology and life history of the white shark. Boca Raton, FL CRC Press, pp. 121–132

Ellis DV (1986) Animal behaviour and its applications. Lewis Publishers, Inc., Chelsea, p. 329

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JB, Marquis RJ (2011) Trophic downgrading of planet earth. *Science* 333(6040): 301–306.

Fallows C, Martin RA, Hammerschlag N (2012) Comparisons between white shark-pinniped interactions at Seal Island (South Africa) with other sites in California. In: Domeier ML. editor. Global Perspectives on the Biology and Life History of the White Sharks Boca Raton, Florida CRC Press p. 105–117.

Fay RR, Kendall JJ, Popper AN, Tester AL (1974) Vibration detection by the macula neglecta of sharks. *Comp Biochem Physiol (A)* 47(4):1235–1240. doi:10.1016/0300-9629(74)90097-8

Ferner MC, Smee DL, Weissburg MJ (2009) Habitat complexity alters lethal and non-lethal olfactory interactions between predators and prey. *Mar Ecol Prog Ser* 374:13–22

Gardiner JM, Atema J (2007) Sharks need the lateral line to locate odor sources: rheotaxis and eddy chemotaxis. *J Exp Biol* 210(11):1925–1934. doi:10.1242/jeb.000075

Gardiner JM and Atema J (2014) Flow sensing in sharks: lateral line contributions to navigation and prey capture. In: Bleckmann H, Joachim M, Coombs SL. editors. Flow sensing in air and water Berlin Heidelberg, Springer. p. 127–146.

Gruber SH, Cohen JL (1985) Visual system of the white shark, *Carcharodon carcharias*, with emphasis on retinal structure. *Memoirs Southern California. Acad Sci* 9:61–72

Hammerschlag N, Martin RA, Fallows C (2006) Effects of environmental conditions on predator–prey interactions between white sharks (*Carcharodon carcharias*) and cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environ Biol Fish* 76(2–4):341–350. doi:10.1007/s10641-006-9038-z

Huveneers C, Holman D, Robbins R, Fox A, Endler JA, Taylor AH (2015) White sharks exploit the sun during predatory approaches. *Am Nat* 185(4):562–570. doi:10.1086/680010

Jewell OJD, Johnson RL, Gennari E, Bester MN (2013) Fine scale movements and activity areas of white sharks (*Carcharodon carcharias*) in Mossel Bay, South Africa. *Environ Biol Fish* 96:881. doi:10.1007/s10641-012-0084-4

Klimley AP, Le Boeuf BJ, Cantara KM, Richert JE, Davis SF, Van Sommeran S, Kelly JT (2001) The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar Biol* 138:617–636. doi:10.1007/s002270000489

Kock A, O’Riain MJ, Mauff KM, Meyer M, Kotze D, Griffiths C (2013) Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS One* 8:e55048. doi:10.1371/journal.pone.0055048

Kotler BP, Brown JS, Dall SRX, Gresser S, Ganey D, Bouskila A (2002) Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evol Ecol Res* 4: 495e518.

Kotler BP, Brown J, Mukherjee S, Berger-Tal O, Bouskila, A (2010) Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proc R Soc Lond [Biol]* 277(1687): 1469–1474. doi:10.1098/rspb.2009.2036

Laroche RK, Kock AA, Dill LM, Oosthuizen WH (2008) Running the gauntlet: a predator–prey game between sharks and two

- age classes of seals. *Anim Behav* 76(6):1901–1917. doi:[10.1016/j.anbehav.2008.06.025](https://doi.org/10.1016/j.anbehav.2008.06.025)
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68(4):619–640. doi:[10.1139/z90-092](https://doi.org/10.1139/z90-092)
- Martin RA, Hammerschlag N (2012) Marine predator–prey contests: ambush and speed versus vigilance and agility. *Mar Biol Res* 8(1):90–94. doi:[10.1080/17451000.2011.614255](https://doi.org/10.1080/17451000.2011.614255)
- Martin RA, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J Mar Biol Assoc UK* 85(05):1121–1135. doi:[10.1017/S002531540501218X](https://doi.org/10.1017/S002531540501218X)
- Martin RA, Rossmo DK, Hammerschlag N (2009) Hunting patterns and geographic profiling of white shark predation. *J Zool* 279(2):111–118. doi:[10.1111/j.1469-7998.2009.00586.x](https://doi.org/10.1111/j.1469-7998.2009.00586.x)
- Maruska KP (2001) Morphology of the mechanosensory lateral line system in elasmobranch fishes: ecological and behavioral considerations. In: Tricas TC and Gruber SH. editors. *The behavior and sensory biology of elasmobranch fishes: an anthology in memory of Donald Richard Nelson* Netherlands. Springer. p. 47–75.
- Mougeot F, Bretagnolle V (2000) Predation risk and moonlight avoidance in nocturnal seabirds. *J Avian Biol* 31(3):376–386. doi:[10.1034/j.1600-048X.2000.310314.x](https://doi.org/10.1034/j.1600-048X.2000.310314.x)
- Mukherjee S, Zelcer M, Kotler BP (2009) Patch use in time and space for a meso-predator in a risky world. *Oecologia*, 159:661e668. doi:[10.1007/s00442-008-1243-3](https://doi.org/10.1007/s00442-008-1243-3)
- Penteriani V, Kuparinen A, del Mar Delgado M, Lourenço R, Campioni L (2011) Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. *Anim Behav* 82(2):413–420. doi:[10.1016/j.anbehav.2011.05.027](https://doi.org/10.1016/j.anbehav.2011.05.027)
- Penteriani V, Kuparinen A, del Mar Delgado M, Palomares F, López-Bao JV, Fedriani JM, Calzada J, Moreno S, Villafuerte R, Campioni L, Lourenço R (2013) Responses of a top and a meso predator and their prey to moon phases. *Oecologia* 173(3):753–766. doi:[10.1007/s00442-013-2651-6](https://doi.org/10.1007/s00442-013-2651-6)
- Prugh LR, Golden CD (2014) Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J Anim Ecol* 83(2):504–514. doi:[10.1111/1365-2656.12148](https://doi.org/10.1111/1365-2656.12148)
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ (2014) Status and ecological effects of the world's largest carnivores. *Science* 343(6167): 1241484. doi:[10.1126/science.1241484](https://doi.org/10.1126/science.1241484)
- Towner AV, Leos-Barajas V, Langrock R, Schick RS, Smale MJ, Kaschke T, Jewell OJ, Papastamatiou YP (2016) Sex-specific and individual preferences for hunting strategies in white sharks. *Funct Ecol*. doi:[10.1111/1365-2435.12613](https://doi.org/10.1111/1365-2435.12613)
- Trillmich F, Mohren W (1981) Effects of the lunar cycle on the Galapagos fur seal, *Arctocephalus galapagoensis*. *Oecologia* 48(1):85–92. doi:[10.1007/BF00346992](https://doi.org/10.1007/BF00346992)
- Upham NS, Hafner JC (2013) Do nocturnal rodents in the Great Basin desert avoid moonlight? *J Mammal* 94(1):59–72. doi:[10.1644/12-MAMM-A-076.1](https://doi.org/10.1644/12-MAMM-A-076.1)