Behavior of Cape fur seals (Arctocephalus pusillus pusillus) in response to spatial variation in white shark (Carcharodon carcharias) predation risk

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Abstract

Foraging and predation risk are often separated at rookeries of marine central place foragers, thus offering an opportunity to gain insight into how predator-avoidance shapes the behavior of prey. Here we compare the behavior of Cape fur seals (Arctocephalus pusillus pusillus) at two island rookeries with and without white shark (Carcharodon carcharias) predations, and assess seal behavior in relation to marked spatiotemporal variation in risk at the high-risk site (Seal Island, South Africa). Our results show that seal behavior at the two sites is comparatively similar in summer, when predation risk is low at both sites, but not in winter. Compared to seals at the "low-risk" site, seals at Seal Island avoided deep-water habitat around the island at high risk times and restricted their use of this habitat in favor of safe, shallow waters when engaging in social and thermoregulatory behaviors. Seals increased their frequency of jostling, porpoising, and diving when moving through the danger zone and seals in groups were safer than single individuals. Overall, our results suggest that seal behavior around the high-risk site is strongly affected by predation risk, and show this rookery to be an excellent predator-prey system at which to evaluate long-standing ecological hypotheses.

Key words: predation, Cape fur seals, white sharks, risk avoidance, predator-prey system, Seal Island, False Bay, grouping, antipredation behavior.

Prey animals in both terrestrial and marine environments have been shown to adjust their spatial and temporal patterns of behavior in accordance with predation risk (Lima and Bednekoff 1999, Caro 2005, Heithaus et al. 2009). Animals may adjust their use of habitat, restrict their activity to places of greater relative safety, adjust their temporal activity budgets, or alter their behavior in more dangerous patches by, for example, grouping or increasing vigilance (see Caro 2005 for a review). Thus many herbivores avoid waterholes frequented by lions (Panthera leo)

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(Valeix et al. 2009), nymph tadpoles (*Rana pipiens*) use leaf-litter as structural refuges in response to predation pressure from dragonfly nymphs (*Anax junius*) (Hossie et al. 2010), little blue herons (*Florida carolina*) switch their foraging behavior to safer times when under intense predation pressure from the common black-hawk (*Buteogallus anthracinus*) (Caldwell 1986), and Australian fur seals (*A. pusillus doriferus*) avoid detection by sharks by diving towards the sea floor at high speed and then hugging the substrate as they swim (Arnould and Hindell 2001). Changes in prey behavior and spatial distribution are particularly pronounced around scarce and patchily distributed resources or habitats that force the aggregation of prey individuals and subsequently attract predators (Flaxman and Lou 2009, Valeix et al. 2009).

Marine central place foragers (e.g., animals that forage away from their central place of breeding or roosting, like pinnipeds and penguins) form dense aggregations on islands, which often attract apex marine predators, such as sharks (Wirsing and Heithaus 2007, Laroche et al. 2008), leopard seals (*Hydrurga leptonyx*) (Hall-Aspland and Rogers 2004, Ainley et al. 2005) and killer whales (*Orcinus orca*) (Hoelzel 1991). Marine central place foragers offer an opportunity to reduce the confounding effects of reproduction and foraging on their behavior in open water, as they typically forage far from their breeding rookeries, restricting breeding and social behaviors to generally predator-free terrestrial island patches (e.g., Rand 1956, 1959; David et al. 1986). The behavior of prey at rookeries attended by large predators may thus be affected primarily by predation risk, although decisions on when to leave and return to the islands will still be affected by foraging needs at sea and the attendance of young on the island.

Seal Island in False Bay, South Africa, is a Cape fur seal (*Arctocephalus p. pusillus*) rookery that experiences high levels of predation by white sharks (*Carcharodon carcharias*) in the waters around the island (Martin et al. 2005, Laroche et al. 2008, Kock et al. 2013). In addition to spatial separation of foraging and predation, a number of other features make this an ideal predator/prey system in which to study antipredator behavior. Firstly, shark attacks on fur seals are frequent and, because sharks typically breach on surface-swimming fur seals from depth, are highly visible (Martin 2005, Laroche et al. 2008, Martin and Hammerschlag 2012). Secondly, predation events are spatiotemporally concentrated, with most attacks happening in the first 2 h after sunrise, and within 400 m of the southern and western sides of the island (Martin 2005, Laroche et al. 2008, Kock 2014). Together these features allow for robust estimates of predation patterns and ultimately the fitness costs of different antipredator behaviors by the prey.

Although shark attack patterns and gradients of risk around Seal Island have received considerable attention and have been well defined, few studies have detailed the behavioral response of seals (Martin et al. 2005). Antipredator tactics of seals have been explored (Laroche et al. 2008, De Vos and O’Riain 2010, 2013) but have largely excluded sublethal impacts of such predation on spatiotemporal movement patterns and both social and thermoregulatory behaviors in different predation risk scenarios.

The goal of this study was to investigate if and how Cape fur seals adjust their behavior in response to marked spatial and temporal changes in predation risk by white sharks at island rookeries. To achieve this we compared the behavior of seals at Seal Island where there is high predation, with seals at Egg Island where predation is reportedly rare or absent. We then exploited the marked spatial and temporal difference in white shark presence and predation at Seal Island to determine how seals may adjust their behavior to reduce both spatial and temporal overlap with this apex predator. If seals do indeed adjust their behavior to spatiotemporal variation in white...
shark predation risk, one would expect to observe differences in seal behavior between high and low risk sites and times. These differences are likely to manifest, as they do in other predator-prey systems, in habitat use, grouping patterns and other ways in which seals move towards their foraging areas and back to the island. Specifically we investigated whether (1) there were differences in the spatial zones from where seals left and returned at different sites and times; (2) seals used the shallow “safe” zone around Seal Island as a refuge area, as inferred from differences in deep and shallow water use at different sites and times; (3) seals benefitted from grouping under predation risk and whether they appeared to use grouping as an antipredatory strategy; and (4) seals adjusted their behavior when traveling on the surface through the danger zone at Seal Island.

**Methods**

**Study Sites**

We collected behavioral data on seals at both Seal Island, in False Bay on the south coast of South Africa, where there are high levels of shark presence and shark/seal interaction (Kock et al. 2013) in winter and at Egg Island, off Paternoster Rocks on South Africa’s west coast, where no seal/shark interactions have been documented (Fig. 1).

**Seal Island (South Coast)**

Seal Island is a granite outcrop about 2 ha in area and the only breeding locality of Cape fur seals in False Bay. Seal Island is the second largest breeding colony in South Africa.
Africa in terms of pup production, and the largest colony (between 12,000 and 18,000 pups) that is based on an island (Kirkman et al. 2007). The habitat around the island is fairly homogenous with no kelp cover. The underwater topography features a sharp drop off to the northwest, west, and south of the island, whereas a more shallow drop off is evident to the east and northeast. To the south of the island is an area dubbed the “launch pad,” a shallow outcrop where seals typically aggregate before leaving the island.

_Egg Island near St. Helena Bay (West Coast)_.

Egg Island is also a granite outcrop, although much smaller in size than Seal Island. Egg Island represents the second largest island-breeding colony in South Africa (between 1,000 and 3,000 pups; Kirkman et al. 2007). The habitat around the island is more complex than Seal Island with extensive kelp beds surrounding the island.

**Observational Sampling**

All observational sampling (ad libitum data collection, instantaneous scans, focal follows) was carried out from a 5.5 m semirigid, inflatable boat stationed at four different positions (north, south, east, and west) around the two study islands. Daylight hours were divided into four time blocks: after sunrise (0700–0829), morning (0830–1059), mid-day (1100–1459), and afternoon (1500–1759). We recorded the movement of seals through deep water habitat, which we classified as water more than 10 m in depth, and more than 10 m from the most exposed part of the islands at low tide. We further divided the deep water habitat at Seal Island into two zones based on predation patterns from previous studies (Martin et al. 2005, Laroche et al. 2008, Kock 2014): a “danger zone” within 1.5 km of the island and a “safe zone” more than 1.5 km away from the island.

All counts of seal presence were made using instantaneous scans, taken at 20 min intervals with the observer recording all seals within their field of vision in a 30 s period. We assumed that our error in estimating seal numbers in this habitat would be similar across sites and seasons, but acknowledge that we cannot reliably estimate diving seals in the absence of underwater observations. As a measure of habitat use, we calculated the average proportion of individuals per scan present in each zone and compared this across sites and seasons, testing observed patterns against a null hypothesis of no mean difference.

Although we conducted observational sampling around all sectors of Egg Island we excluded these data from further analyses as we recorded no predation in any sector throughout the study and could thus not relate seal sector use to spatial variation in predation risk. We did, however, retain comparisons of relative seal presence and behavior in “deep open water” habitat between the two study sites, as well as the behavior and group size of returning and leaving seals in different seasons. The latter allowed a general comparison of seal behavior around an island rookery with and without predation risk.

**Ad Libitum Data Collection in the Deep Water Habitat**

All seal behavior and surface predation events in the deep water habitat were recorded ad libitum between scans. A surface predation event was defined as any
successful or unsuccessful attempt by a white shark to capture a Cape fur seal. Attacks were detected using the following cues: (1) a shark leaps out of the water (breach); (2) blood or fatty deposits on the water; and (3) birds (usually kelp gulls, *Larus dominicanus*, or subantarctic skua, *Stercorarius parasiticus*) circling and diving into the water to pick up the remains of an attacked seal, or aggregating around visually conspicuous splashing (Laroche *et al.* 2008). Attacks were classified as “successful” or “unsuccessful” depending on whether the shark bit the seal or there was evidence of blood/fatty deposits in the water.

*Ad libitum* data were collected in both summer and winter, at both islands, and both inside and outside the danger zone at Seal Island in winter, for a total of 595 field hours. Seal behavior was broadly classified as either returning (swimming towards the island from a distance of at least 400 m) or leaving (swimming away from the island at least 10 m from the lowest exposed areas of the island at low tide). In all cases, the number of seals in a group and the size class of all seals was estimated. Size classes were assigned as pups (class one, 0–4 mo of age), young-of-the-year juveniles (class two, 5–11 mo of age), subadults (class three, 1–3 yr of age), adult cows (class four), and bulls (class five) (Rand 1956, 1967). Groups were classified as small (1–4 individuals), medium (5–9 individuals), large (10–14 individuals), and extra-large (>14 individuals).

**Focal Animal Sampling Within and Beyond the Danger Zone at Seal Island**

Random subsamples of seals detected in deep water habitat during *ad libitum* sampling were followed by boat and the behavior of a focal seal in the group was recorded for 30 s. Behavior categories included jostling, surface swimming, diving, and rafting/milling or playing, as described in Table 1. These data were only collected at Seal Island as no clear danger zone was apparent at Egg Island.

Ecotourism operations have been active around Seal Island for more than 15 yr, and seals are habituated to the presence of boats. Previous observers have not noted any disturbance of seal groups when following them (Laroche *et al.* 2008) and we were confident that the presence of a research craft did not influence the behavior of followed seals. We followed 50 seal groups as they returned to or departed from the island in summer (*n* = 16) and winter (*n* = 34), maintaining a distance of 20 m from the nearest member of the group to minimize disturbance.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
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<tbody>
<tr>
<td>Jostling</td>
<td>Changing positions within a group of seals by porpoising over or swimming under a neighbouring individual or individuals.</td>
</tr>
<tr>
<td>Surface swimming</td>
<td>Swimming in a directional manner towards or away from the island, without changing position relative to conspecifics (to distinguish it from jostling).</td>
</tr>
<tr>
<td>Diving</td>
<td>Submerging with a strong downward directionality without reappearing within an observer’s scan period.</td>
</tr>
<tr>
<td>Evasive maneuvering</td>
<td>Swimming in a fast zigzag pattern at the surface, combined with high porpoising and sharp turns.</td>
</tr>
<tr>
<td>Rafting/Milling/Playing</td>
<td>When engaged in any activity that lacks directionality and vigilance and that is associated with thermoregulatory and social behaviors.</td>
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We recorded the same variables (e.g., leaving vs. returning) as detailed in the *ad libitum* section, in addition to GPS data at 100 m intervals while following seals for a maximum distance of 2,000 m. As most attacks occur within 1,000 m of the shallow area where seals gather to the south of the island (calibrated as 0 m during our follows), we considered seals between 1,500 m and 2,000 m distance from the island as representative of activity outside the danger zone. We measured the speed (determined from boat speed) at which a group was traveling using the speed of the boat (km/h), which was calculated every 100 m, but averaged within two broad spatial categories (inside the danger zone and outside the danger zone) to correct for erratic increases and decreases in boat speed. We measured distance as calculated from spatial coordinates logged with a Garmin 320 GPS (winter 2005), and a hand-held Garmin e-trex (2006, 2007).

**Prey Selection Index**

To assess the relative risk associated with different group sizes, age classes, or behaviors we used Jacob’s prey selection index ($D$) (Jacobs 1974). This index takes into account prey availability as well as predator abundance, and is thus a better measure of risk than absolute number of attacks alone. $D$ can be calculated using the formula:

$$D = \frac{(r - P)}{[(r + P) - 2rP]}$$

where $r$ = proportion of prey in the predator’s diet (i.e., the frequency of predation on a prey category), $P$ = proportion of prey in the environment (i.e., seal counts). We calculated the index based on group numbers present in the habitat, and not individuals.

**Statistical Analyses**

All statistical analyses were conducted using the statistical package Stat Soft. We performed exploratory descriptive statistics prior to running all statistical tests to test relevant assumptions of normality of distributions and homogeneity of variances. Where appropriate we transformed data to meet assumptions of normality and homogeneity of variances using arcsine transformations (we prioritized homogenizing variances over normalizing data as heterogeneity of variances are particularly difficult to deal with statistically). If data were normal or could be transformed to normality, parametric statistics were used following (Quinn and Keough 2002). In all other cases we used the robust rank-based, nonparametric equivalents following Wilcox (2005). All statistical tests are two-tailed. Parametric means are given with standard errors of the mean and rank-based values of locations with average absolute deviation from the median (Wilcox 2005).

To analyze two-sample data sets we employed Student $t$-tests or the nonparametric Mann-Whitney $U$ when data sets were independent or paired $t$-tests and nonparametric Wilcoxon paired tests when data points were paired. In instances where a single categorical variable predicted a continuous response variable we employed single factor ANOVAS or either nonparametric Kruskal-Wallis or Friedman’s ANOVA (if variables were dependent) to test the null hypothesis of no differences between the means and medians, and post hoc Tukey and rank-based Tukey tests to infer resolution from these results. Where we were unable to homogenize variances
through transformation, we performed the Brunner-Dette-Mank rank-based ANOVA and calculated standard errors based on the recommended bootstrapping techniques (Wilcox 2005).

For parametric data with a continuous response variable and several categorical predictor variables, we employed 3- and 2-factor fixed factorial ANOVA to test null hypotheses of no differences in means between and amongst factors. To test covariation between two linear continuous variables, with bivariate normal distributions, we used Pearson’s product-moment correlation coefficient to test the null hypothesis that $\beta_1 = 0$.

To analyze behavioral frequencies we employed single and multilevel chi-squared statistics (all sample sizes were such that more than 20% of the variables contained more than five data points). To analyze group size distributions, we employed Kolmogorov-Smirnoff distribution fitting to test the goodness of fit of group size distributions to normality, and Kolmogorov-Smirnoff 2-sample test for differences between them. To control for the large variation in sample sizes and seasons, we randomly subsampled within the spatial data set, and compared variables recorded inside the danger zone with those recorded outside of the danger zone and compared variables between sites and seasons, and between age-classes among sites and seasons.

Results

Patterns of Predation: Site, Age Class, Sector, Danger Zone and Group Size

We recorded 123 predation events at Seal Island for which we could discern the age class of the attacked individual, the behavior of the seal, and the size of the group it was in prior to being attacked. No predation was recorded at Egg Island. Predation at Seal Island was skewed towards the southern and western spatial sectors and were most frequent in the observation period immediately following sunrise. Juveniles were attacked ($\chi^2 = 10.89$, df = 1, $n = 122$, $P < 0.001$) more frequently (70.21%) than subadults (15.93%) or adults (18.7%). There was, however, little difference in the strength of the prey selection index (Table 2) between age classes ($D = 0.088$, $-0.269, 0.098$ for juveniles, subadults, and adults, respectively).

Despite the frequency of attacks being higher to the south and west of Seal Island, these areas were actually safer, when controlling for prey availability (Fig. 2). A Friedman’s ANOVA revealed a significant (Kendall coefficient $= 15.221$, $n = 95$, $P < 0.01$) difference in the prey selection index values between different spatial sectors, but a post hoc sign test revealed that only the northern sector was significantly more dangerous than the southern ($z = 9.06$, $P < 0.001$) and western ($z = 2.262$, $P < 0.05$) sectors.

Table 2. Frequency of attacks on different age classes and the corresponding prey selection index (Jacob’s prey selection index, $D$).

<table>
<thead>
<tr>
<th>Age class</th>
<th>Frequency of attacks</th>
<th>$D$</th>
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<tbody>
<tr>
<td>Juveniles</td>
<td>86</td>
<td>-0.088</td>
</tr>
<tr>
<td>Subadults</td>
<td>20</td>
<td>-0.269</td>
</tr>
<tr>
<td>Adults</td>
<td>17</td>
<td>0.098</td>
</tr>
</tbody>
</table>
Prey selection indices (Fig. 3) also varied significantly for different group sizes (Kruskal-Wallis rank-based ANOVA, $H = 70.817, P < 0.001$) and were higher (multiple comparison of mean ranks, $P < 0.001$ in all cases) for single (mean $D = 0.432 \pm 0.056$ SE) and paired seals (mean $D = 0.397 \pm 0.097$ than all larger group sizes. Similarly, selection indices were significantly ($P < 0.01$) higher for group sizes of three (mean $D = 0.042 \pm 0.114$) and four (mean $D = 0.075 \pm 0.016$) than group sizes of 5 (mean $D = 0.00 \pm 0.1676$), 6–9 (mean $D = -0.32 \pm 0.193$), 10–14 (mean $D = -0.25 \pm 0.194$), and $\geq 15$ (mean $D = -0.17 \pm 0.084$). There was no significant difference in preference for any of the group size categories $>5$.

Figure 2. Mean prey selection (measured as Jacob's prey selection index $\pm$ SE at the 95% confidence interval) in different spatial sectors.

Figure 3. Mean prey selection index for different group sizes of seals at Seal Island. Error bars represent standard error at the 95% confidence interval.
Spatiotemporal Patterns of Seal Movement: Site, Sector, Danger Zone and Group Size

There was significant variation in the proportion of seals observed in the deep water habitat between seasons and sites (Fig. 4, ANOVA, $F = 42.238, P < 0.001$). The average proportion of seals present in the deep water habitat was significantly lower at Seal Island in winter (mean = 0.063 ± 0.020, $n = 58$) compared to summer (mean = 0.76 ± 0.073, $n = 58$) and both seasons at Egg Island (0.650 ± 0.071, $n = 58$ in summer; 0.948 ± 0.036, $n = 62$ in winter). There was no difference in deep water use between summer at Seal Island and either season at Egg Island.

Marked variation was evident in the spatial sector that seals used when leaving from (Fig. 5a, Kruskal-Wallis, $H = 2,418.383, P < 0.001$) and returning to (H = 2331.933, $P < 0.001$) Seal Island (Fig. 5a). Seals were more likely to depart from the island through the southern sector (mean = 1.06 ± 0.019 groups/h) than from any other sector (multiple comparison of mean ranks, $z = 9.714$ (E), 18.054 (W), 15.865 (N), $P < 0.001$). There was no difference in the number of seals leaving from the western (mean = 0.127 ± 0.010 groups/h), northern (mean = 0.158 ± 0.017 groups/h), or eastern sectors (mean = 0.19 ± 0.023 groups/h) of the island.

There were significantly ($\chi^2 = 228.9378$, df = 3, $P < 0.001$) fewer seals observed leaving the island ($n = 84$ groups) than returning ($n = 398$ groups), despite the fact that the latter constituted mostly single seals, seals in pairs, and small groups, and that these were less likely to be detected in the field by observers. We found that single individuals and individuals in pairs were significantly ($\chi^2 = 204.556$, df = 1, $P < 0.001$) more likely to be observed in the danger zone between 0700 and 1000 than any other group size. These single/paired seals were also significantly ($\chi^2 = 139.874$, df = 3, $P < 0.001$) more likely to be juveniles ($n = 188$) than they were to be subadults or adults ($n = 15$). We also found that small groups were significantly ($\chi^2 = 131.157$, df = 3, $P < 0.001$) more frequently observed than medium groups, large groups or extra-large groups, and that juveniles and juveniles accompanied by one adult ($n = 85$) constituted a significantly ($\chi^2 = 40.238$, df = 1, $P < 0.001$)
greater proportion of these groups than any other combination of size classes (\( n = 20 \)). Medium, large, and extra-large groups consisted mostly of a mix of age classes, rather than a single size class.

There was significant variation in the median size of groups between study sites, seasons and whether seals were leaving or returning to the island (Fig. 6, Kruskal-Wallis nonparametric ANOVA, \( H = 690.416, P < 0.001 \)). The median size of leaving groups was significantly larger (multiple comparison of mean ranks, \( P < 0.001 \) for all comparisons) at Seal Island than at Egg Island, both in summer (median ± absolute average deviation from median = 2 ± 1.617, Egg Island, \( n = 86 \); 8 ± 1.359, Seal Island, \( n = 163 \)) and winter (3 ± 0.823, Egg Island, \( n = 142 \); 10 ± 0.478, Seal Island, randomly subsampled \( n = 152 \) from 282). The median size of leaving groups was also significantly (\( P < 0.01 \)) larger than returning groups at Seal Island, but not at Egg Island. There were no significant differences in median sizes of returning groups at either island or in either season.

![Figure 5. Mean number of groups observed leaving (white bars) and returning (gray bars) per hour in different spatial sectors off Seal Island. Error bars represent standard errors at the 95% confidence interval.](image)

![Figure 6. Median size of returning and leaving seal groups in winter and summer at the two different study sites (Seal and Egg Islands). Error bars represent average absolute deviation from the median.](image)
Seal Behavior Within and Outside the Danger Zone in Both Winter and Summer at Seal Island

Seals within the danger zone between 0700 and 1000 consisted mostly (52.1% of all seals observed) of seals returning alone or in pairs, and small groups (27.6%). Juveniles comprised 74.9% of all single seals, and 86% of all small groups consisted of three juveniles accompanied by one adult seal. Medium, large, and extra-large groups comprised only 8.3%, 6% and 7.2% of all observed seals.

Seals did not swim at different speeds inside vs. outside the danger zone within a season, nor when they were returning to or leaving the island. However, there was significant variation in swimming speed within the danger zone (one-way ANOVA, \( F = 20.77, P < 0.001 \)) across seasons and depending on the direction of movement. A post hoc Tukey test revealed that seal swimming speed was faster in winter (mean = 9.840 ± 2.052 km/h, \( n = 17 \)) than in summer (mean = 6.838 ± 2.507 km/h; \( P < 0.001 \)) and seals leaving the island in winter swam faster than seals leaving and returning in summer and faster than seals at Egg Island in both seasons (winter: 6.65 ± 0.828 km/h, \( n = 8; P < 0.001 \); summer: mean = 4.643 ± 1.801 km/h, \( n = 9; P < 0.001 \)).

**Jostling**

There was significant seasonal and spatial variation in the time leaving seals spent jostling, but no difference for returning seals (Fig. 7a). In winter, leaving seals spent more time jostling (Wilcoxon signed-rank test, \( z = 2.599; P < 0.01 \)) inside the danger zone (mean = 7.08 ± 0.740 min) than outside (mean = 0.800 ± 0.610 min). There were no significant differences in the time spent jostling inside compared to

![Figure 7](image-url)
outside the danger zone in summer \((n = 10)\). Seals also spent significantly more time jostling in winter than summer (Kruskal-Wallis, \(H = 30.586, P < 0.001\)) within the danger zone, but there were no significant seasonal differences outside the danger zone.

**Surface-porpoising**

Returning seals spent more time porpoising than leaving seals (Kruskal-Wallis \(H = 27.090, P < 0.001\), Fig. 7b) and less time porpoising inside the danger zone (mean = 2.796 ± 1.315 min, \(n = 8\)) relative to outside (Wilcoxon signed-rank test, \(z = 1.95, P = 0.05\)) in winter. There was no significant difference in the frequency with which this behavior was performed between these habitats in summer (mean = 4.315 ± 0.701 min).

**Milling/rafting**

Leaving seals spent significantly (Kruskal-Wallis \(H = 18.950, P < 0.001\), multiple comparison of mean ranks, \(P < 0.05\) Fig. 7c) less time milling, rafting, and playing inside the danger zone during winter (mean = 0.127 ± 0.249 min, \(n = 26\)) than in summer (mean = 1.267 ± 0.790 min, \(n = 10\)). There was no significant difference in time spent rafting and milling inside the danger zone compared to outside of it in summer, and no significant difference in the mean minutes rafting/milling outside the danger zone in winter compared to summer, or inside the danger zone compared to outside the danger zone in winter. Returning seals showed a similar pattern to leaving seals, with the time spent rafting/milling only being significantly different (Kruskal-Walls, \(H = 18.950, P < 0.001\)) in winter inside the danger zone (mean = 0.074 ± 0.145 min, \(n = 9\)) compared to summer in the same spatial area (mean = 1.251 ± 0.798 min, \(n = 8\)). There was no difference in time spent rafting/milling in either summer or winter outside the danger zone, or between the two deep water zones in summer.

**Diving**

Seals spent more time diving (Wilcoxon signed-rank test, \(z = 2.07, 2.52, P < 0.05, n = 8\), Fig. 7d) when inside the danger zone (mean = 7.5 ± 1.691 min) compared to outside (mean = 0.833 ± 0.0809 min) in both winter (mean = 7.5 ± 1.691 min inside, mean = 0.833 ± 0.0809 min outside danger zone, \(n = 8\), Fig. 7d.) and summer (mean = 1.905 ± 1.493 min inside, mean = 0.190 ± 0.373 min outside, \(n = 7\)). Returning seals spent more time diving (Kruskal-Wallis, \(H = 17.820, P < 0.001\)) than leaving seals inside the danger zone, but not outside of it.

An analysis of shark prey selection, which controls for the proportion of seals engaged in each behavior at Seal Island in winter (Table 3), revealed that seals engaged in surface-swimming \((n = 76, 38\) attacks), milling/rafting/playing \((n = 58, 10\) attacks) were selected by sharks \((D = 0.73\) and 0.65, respectively), whilst jostling and diving seals were avoided \((D = -1, n = 138\) and 60, 0 attacks). Seals engaged in evasive maneuvering were selected by sharks, but less so than surface swimming or milling/rafting/playing individuals \((D = 0.154)\).
Overall our results show differences in seal behavior in relation to spatiotemporal variation in predation risk from white sharks. While there were no differences between sites and seasons in the spatial zones where seals left from and returned to, there was marked spatiotemporal variation in their use of shallow and deep areas around the island, grouping patterns and behavior when traversing through the danger zone.

**Did Seals Adjust Their Use of Sector Around the Island When Commuting to and from the Rookery?**

The result that seals did not appear to adjust their behavior to traverse areas with lower predator densities is not particularly surprising. Animals under pronounced risk of predation are expected to modify spatiotemporal patch use to decrease probabilities of encounter, attack, capture, and the time spent vulnerable to predation (Lima and Dill 1990; Lima 1998, 2002; Sih 1998; Sih *et al.* 2000; Heithaus and Dill 2002; Khan and Ghaleb 2003). Spatial adjustment, however, may not benefit prey if both prey and predators are mobile, as predators can simply adjust their behavior to match the areas of highest prey density.

Laroche *et al.* (2008) suggested that the low number of seals moving through areas with fewer predators results from a trade-off with grouping. There is a single safe, gathering point in the water to the south of the island that seals appear to use to form groups before departing from the island. Laroche *et al.* (2008) argue that in using any other spatial area adjacent to the island for departure, seals would forfeit the opportunity to aggregate in safety. While we are not discounting this explanation for seal movement patterns entirely, single returning seals also showed a preference for the southern and western sides of the island in this study, and we show that a trade-off with grouping does not need to be invoked to explain activity patterns, even for departing seals. Furthermore, owing to dilution, predation risk (as per our calculated prey selection index) was actually lower on the south and western sides of the island relative to the eastern and northern sides.

In contrast to our findings Jewell *et al.* (2014) showed that fur seals at Geyser Rock shifted their use of spatial sectors around the rookery in response to variation in white shark presence. During winter when shark presence is highest fur seals reduced their use of sectors characterized by deep open water and increased their use of sectors with abundant refugia (*e.g.*, kelp forests). It would be of interest to see whether artificial spatial refuges (*e.g.*, a kelp forest, artificial rocky outcrop with a shallow patch) placed in the deep water within the danger zone at Seal Island would attract fur seals (*sensu* Table 3. Jacob’s prey selection index ($D$) ranging from −1 (avoidance) to 1 (selection) by sharks for the different behaviors engaged in by seals at Seal Island in winter.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>$D$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jostling</td>
<td>−1</td>
</tr>
<tr>
<td>Milling, rafting, playing</td>
<td>0.651</td>
</tr>
<tr>
<td>Diving</td>
<td>−1</td>
</tr>
<tr>
<td>Surface-swimming</td>
<td>0.730</td>
</tr>
<tr>
<td>Evasive maneuvering</td>
<td>0.154</td>
</tr>
</tbody>
</table>

DISCUSSION

Overall our results show differences in seal behavior in relation to spatiotemporal variation in predation risk from white sharks. While there were no differences between sites and seasons in the spatial zones where seals left from and returned to, there was marked spatiotemporal variation in their use of shallow and deep areas around the island, grouping patterns and behavior when traversing through the danger zone.
Jewell et al. (2014) and hence result in a change in space use to reduce encounters with predators (for examples of such experiments see Hochman and Kotler 2006, Stankowich and Coss 2006, Morgan and Fernández-Juricic 2007).

**Do Fur Seals Minimize the Time Spent in Deep Open Water Habitat When Predators Are Present?**

There was a near-absence of nondirectional behavior (e.g., rafting, milling, and playing) recorded at Seal Island during winter (Fig. 4, Table 1) relative to summer and both winter and summer at Egg Island. Rafting, milling and play behaviors were largely restricted to the shallow, safe waters around Seal Island during the high predation winter months, but were performed in the deep water habitat during the low predation summer months and in both seasons at Egg Island. Thus fur seals avoid spending time in the deep open water habitat at times when predation risk is high and restrict the performance of social and thermoregulatory behaviors at such times to the apron of shallow, safe water around the Island. A similar result was obtained for adult fur seals in “shark alley” at Geyser Rock, Gaansbaai which avoided resting and playing in the deep open water habitat during winter when white shark presence was high (Jewell et al. 2014).

**Do Fur Seals Benefit from Grouping under Predation Risk?**

Our results showed a pronounced difference in group size distribution of fur seals leaving Seal Island in winter compared to summer and both seasons (Fig. 6), and a large discrepancy in the behavior, group size and age class composition of leaving and returning fur seals (Fig. 4, 5, 7) at Seal Island in winter. The observed differences in the group size and behavior of leaving and returning fur seals may be explained in part by life history and foraging patterns. Fur seals feed far from Seal Island on trips lasting several days and thus lactating females have to intersperse foraging trips with attendance bouts. In the Cape fur seal, foraging trips and attendance bouts are approximately 2–5 days in duration (David et al. 1986, Gamel et al. 2005). Departing fur seals gather at the launch pad to the south of the island and typically leave in medium (median = 8 ± 1.359) groups. However, once at sea, fur seals appear to forage alone (Rand 1967, David et al. 1986), perhaps to reduce competition for limited food resources (Yodzis 1998, 2000). As a consequence of foraging alone and without a safe gathering point when returning to Seal Island, most returning fur seals traverse the danger zone either in small groups or alone. Our results, like those of Martin et al. (2005) suggest that sharks target lone juveniles as they return from the foraging grounds.

**Do Seals Adjust Their Behavior When Traversing the Danger Zone in Winter?**

Fur seals leaving Seal Island have two antipredator options: they can either join a group and traverse the danger zone at the surface, or travel alone whilst diving and hugging the substrate to avoid detection. There is probably a trade-off between these strategies (Laroche et al. 2008) as diving fur seals are slower and less energetically efficient than surface swimming fur seals, while surface fur seals in groups are more visible to sharks hunting in the mid-water zone. Additionally, fur seals, more so than larger elephant seals, are constrained by their smaller lung capacities as to the length of time they are able to dive underwater (Burns et al. 2004, 2005). Even if a fur seal
should choose to conceal itself at depth it will still have to surface at intervals for small periods, during which it will be at risk to predators. The small proportion of leaving fur seals that dive relative to returning fur seals suggests that traversing the danger zone in a surface swimming group is a more beneficial defense than diving and that fur seals only perform the latter when they return as it is not possible to safely form large groups.

Another clear behavioral difference between leaving and returning fur seals was the extensive use of jostling by leaving fur seals. Jostling is characterized by fur seals constantly changing positions relative to one another when traveling in a group. Jostling was observed to be more common in leaving groups inside compared to outside the danger zone, as well as more common in winter than in summer. It is possible that jostling both confuses potential predators and/or reflects movement rules (e.g., moving towards their nearest neighbors or nearest neighbors’ neighbors) by individual fur seals within a group to reduce their domain of danger (De Vos and O’Riain 2013) and hence predation risk (De Vos and O’Riain 2010). One of the aims of this study was to establish whether predation risk alone could explain the formation of groups at Seal Island. We argued that if predation was driving group formation then by removing the predation risk fur seals should no longer group up. The presence of groups at Egg Island in the absence of any detectable white shark predation risk suggests that predation risk is not the sole driver of group formation in Cape fur seals. It should be noted that we did not have good information on subsurface white shark predations for either island. Nor did we have information about non-white shark predators e.g., broad nose sevengill sharks (*Notorynchus cepedianus*) which are known to consume fur seals in this region. Hence we cannot conclude that fur seals forming groups at Egg Island does not confer some antipredator advantages.

There is, however, some evidence that predation risk may influence the size and structure of fur seal groups leaving Seal Island. There is a virtual absence of fur seals leaving by themselves, or in small groups during winter at Seal Island, but not during summer. Group sizes seem to be limited to <20 individuals in winter and had a normal distribution, while this was not the case in summer.

While we attempted to control for as many variables as possible in this study there are some notable limitations which we share with previous studies that should be considered when interpreting the overall findings. Firstly, the logistical difficulties and dangers of working on a small boat in the dark precluded the collection of data at night when fur seal movement through the danger zone is suggested to peak (Laroche et al. 2008). Secondly, because we were not working with individually recognizable animals our data are affected by pseudoreplication. Lastly, we could not account for any subsurface fur seal movement and thus underestimated the importance of this behavior in avoiding detection by sharks and below water predation events.

Overall, our results provide support for previous studies that have revealed that fur seal behavior at island rookeries off the South African coast is affected by predation risk. By comparing the behavior of fur seals at an island with and without white shark predations in addition to the same island with marked spatiotemporal variation in predation we have presented strong evidence that fur seals adjust their behavior in response to white shark predation risk through adjustment in habitat use, grouping and swimming behavior through the danger zone. The ecological homogeneity of the danger zone, the potential to separate proximate causes of grouping, and an already quantified “landscape of fear” together with improved technology for observing and recording marine vertebrates make Seal Island an excellent system for future predator-prey studies.
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