



Running the gauntlet: a predator–prey game between sharks and two age classes of seals

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We present both an empirical study and a behavioural game model exploring a predator–prey game between white sharks, *Carcharodon carcharias*, and Cape fur seals, *Arctocephalus pusillus pusillus*, around a small island colony in South Africa. Behavioural tactics used by adult seals appear to account for the variance in risk from sharks, while shark tactics seem more influenced by the behaviour of pup seals, probably because pup seals engage in riskier behaviours. A dynamic game model of the interaction predicts that, if pups and adult seals account for risk in a similar manner, then tactic selection used by sharks and seals should be more evenly distributed across all possible options. Instead, a second model in which pups were constrained to choose the riskiest option produced evolutionarily stable strategy (ESS) solutions for both species that more closely approximated the tactics recorded, suggesting that behavioural variation within subgroups of a population should be accounted for when modelling predator–prey interactions. These results also suggest that pups may act as initiators in a behaviourally mediated indirect interaction with adult seals, mediated by the behaviour of their common shark predator; this would represent the first record of an intergenerational two-species indirect interaction.

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Prey species often trade off some benefit to reduce predation risk from predators (reviewed in Lima & Dill 1990). However, predators can also alter their behaviour in response to that of their prey. Thus, the optimal course of action for either species probably depends on the other's behaviour (Hugie & Dill 1994; Sih 1998; Brown et al.

1999), meaning that predator–prey interactions should often be viewed as behavioural games.

The importance of considering behavioural games when modelling predator–prey interactions has been shown repeatedly (Brown 1992, unpublished data; Hugie & Dill 1994; Bouskila et al. 1998; Sih 1998). Most models have considered uniform prey groups interacting with uniform predator groups, typically leading to pairs of ideal free distributions (IFD; Fretwell & Lucas 1970; Sih 1998) based on equal tactical payoffs for all individuals of both species. However, natural populations are rarely uniform; in reality, each group of players in a game may be composed of subgroups with different behavioural patterns.

We present both an empirical study and a behavioural game model of a system that was initially expected to fit the mould of a traditional predator–prey game, but where the prey population the Cape fur seal, *Arctocephalus pusillus pusillus*, consists of distinct subgroups with differing

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vulnerabilities to predation by white shark, *Carcharodon carcharias*, in South Africa. The empirical study, presented first, served to determine the range of tactics used by predator and prey; the model, presented subsequently, attempts to provide an evolutionary framework for the data collected by contrasting a traditional predator–prey game with one that considers behavioural differences between the various subgroups.

EMPIRICAL RESEARCH

White sharks are important pinniped predators whose primary hunting strategy involves patrolling waters near a seal colony and attacking seals moving to or from it (Klimley et al. 2001; Kock 2002). In South Africa, all colonies frequented by white sharks are breeding colonies, where the seal population ranges in age from young-of-the-year pups to breeding age adults. All age classes travel from the colony to feed in open water (although the extent to which pups feed is unknown) and return to it to rest and, in the case of mothers and pups, to nurse (David 1987). Thus, the prey population available for sharks to attack comprises several age classes.

When present near a seal colony, sharks are probably exclusively hunting seals. However, white sharks are generalist predators, and at smaller sizes are predominantly piscivorous (Estrada et al. 2006), so they regularly move between seal colonies and other potential hunting or resting grounds (A. A. Kock, unpublished data). Consequently, their hunting strategy includes not only a spatial component, in terms of where to hunt and what depth to swim, but also a temporal component in terms of when to be present at a colony.

Seals usually depart their colonies for periods from several days to several weeks (Gentry & Kooyman 1986) and appear to be relatively safe from white shark predation when about 1000 m from the colony, or in the shallow waters immediately adjacent to the colony where they can be observed rafting (large groups of seals ‘playing’ in the water, possibly for thermoregulatory reasons; David 1987). However, seals are at high risk when travelling in between, because sharks concentrate within several hundred metres of shore (Klimley et al. 2001). Thus, seals probably select movement tactics to minimize this risk, as opposed to based on foraging opportunities or other time or energetic considerations mitigated by their long trips. Like the sharks, the seals’ strategy includes a spatial (location, swimming depth) and temporal (when to leave or return) component, but also a group size component, as these are highly variable.

Ultimately, seals should select movement tactics based on these components to minimize the risk imposed by sharks, while sharks should select patrolling tactics that maximize their chance of killing a seal. Within the context of a traditional predator–prey game, the expectation would be that the tactical distributions of both species would represent multiattribute IFDs; this study sought to identify those tactical distributions.

Methods

Study site

We conducted our research around Seal Island, a small island in False Bay, Western Cape, South Africa. The ocean floor around Seal Island drops quickly to depths greater than 20 m off the southern and western sides of the island, while the slope is more gradual on the northern and eastern sides (Fig. 1). Seal Island is populated year-round by 36 000–77 000 Cape fur seals (South African Marine and Coastal Management, unpublished data) and is the only seal breeding colony within False Bay (David 1987). White sharks are transitionally present around the island during the Southern Hemisphere’s winter months (May–September), but scarce during other times of the year (Kock 2002).

For both species, there are distinct variables that together characterize any specific tactical decision: time of day t (indicative of varying light levels), swimming depth (D for seals, d for sharks), location around Seal Island l (differential bottom depths), and for seals, group size g . We collected count data on shark and seal use of each combination of these variables by using acoustic tracking and visual observation.

Acoustic equipment

We tagged 10 adult female Cape fur seals, each one observed nursing a pup, with Vemco Rcode acoustic transmitters (Model V16P; P: pressure sensitivity for swimming depth (D) measurement) on 23 April 2004. Seals were captured on Seal Island with nets, restrained with straps (average 10 min) and had transmitters glued to their dorsal fur using quick-setting epoxy, which the seals would shed during the summer moult.

We tagged 17 white sharks with V16 transmitters (7 were model V16; 10 model V16P for measurement of d). Taggings were spread over the course of the 2004 field season to ensure consistent tagged shark presence around the island. Sharks were enticed to our boat using various forms of attractant (fish oil, sardine, shark liver, whale blubber) and coaxed to stay with large chunks of fish bait. With the sharks close to the boat, we attached a tag subcutaneously using a small plastic barb and a metal spear. Some sharks reacted strongly to the process, but there were no adverse effects. All tagging was conducted under South African Department of Environmental Affairs and Tourism permit V1/8/5/1.

We collected data from the transmitters using six Vemco model VR2 data logging receivers. These were deployed along the ocean floor at various locations (l) around the island (Fig. 1), anchored to the bottom by a truck tire filled with concrete.

Visual records

We also collected information on seal movement using systematic visual observation from an 8 m vessel during June–October 2004, averaging 15 days/month. We divided the waters surrounding the island into six sectors (later regrouped into two zones, see Fig. 1), and time of day into four 2.5 h blocks between 0730 and 1730 hours

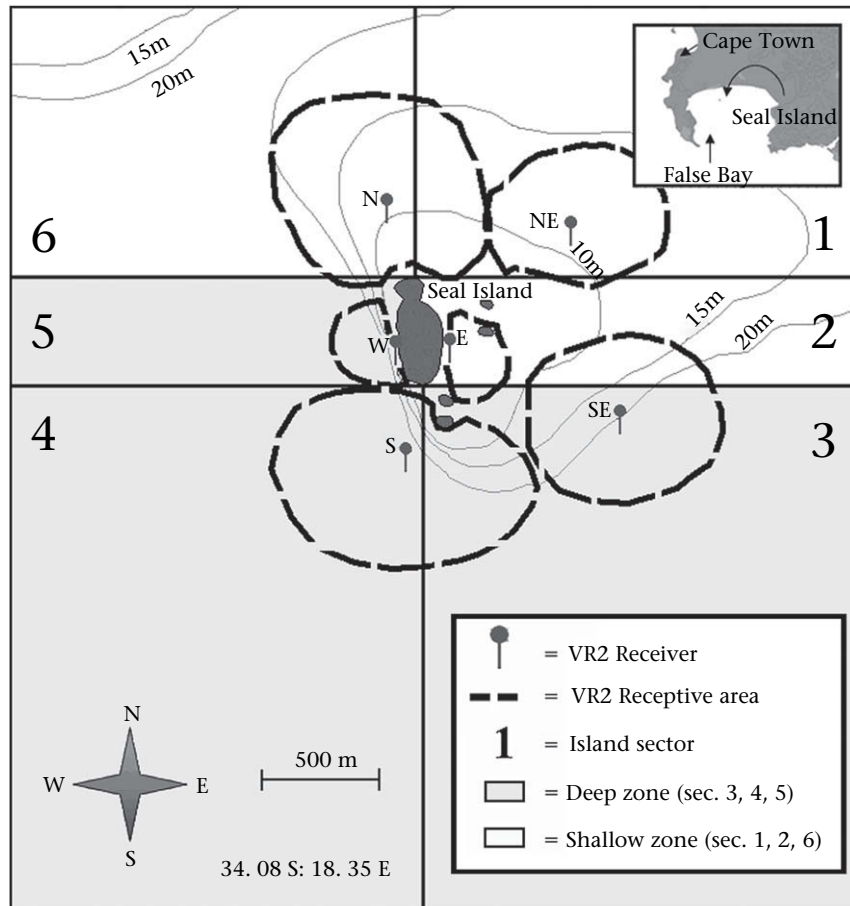


Figure 1. Seal Island, False Bay, South Africa. Indicated on the map are the locations of the six VR2 receivers, as well as the approximate receptive area of each. Waters around the island were divided into six sectors; these were subsequently grouped into two zones, corresponding to the major water depth trends of deeper waters to the south and west, and more shallow waters to the north and east.

(hours were occasionally extended on either side). Our activity was randomly assigned to a specific sector for each time block that we were present using Microsoft Excel's random number function. In total, we were present and collected data during 169 time blocks.

We used two methods to collect visual records. The first involved counting all seal movements observed, noting each group's direction of travel (departing or returning), the group size (g : 1, 2, 3–5, 6–9, 10–15, 16–25, 25+), the average seal size within the group (s , a surrogate variable for age: 1 = neonate, 2 = pup, 3 = juvenile, 4 = adult; receiver records only provided data for adult females), and the sector location (l). We also took note of whether seals were swimming at the surface or diving, for purposes of verifying the receiver records.

We also conducted focal follows ($N = 44$), whereby we followed a group of seals for approximately 750 m, at a distance of approximately 50 m. The follows did not appear to affect seal behaviour, as similar movement patterns were observed while our vessel was anchored. We quantified all behaviours, including swimming speed, percentage of time at the surface (includes porpoising behaviour) and dive distance, if appropriate (when seals dived, the boat was stopped until they were resighted; we would then catch up, measure the distance and resume the follow).

Analysis

Seals. The receptive radii of four VR2 receivers extended to the island itself (Fig. 1), making it impossible to differentiate seal movement data from rafting behaviour. Consequently, the following assumptions were required to isolate discrete instances of seal movement.

(1) Presence outside a small rafting annulus around Seal Island indicates movement.

(2) Seals moving to or from the island do so quickly with as few detours as possible.

(3) Seal mothers leave the island to feed for a few days to a few weeks and then return to nurse (Gentry & Kooyman 1986).

(4) Depth records below 20 m on the south and west, 15 m in other areas, indicate movement (seals could not reach these depths within the rafting zone).

(5) Records from the SE and NE VR2s indicate movement, since the receptive ranges of these receivers did not extend into the rafting zone.

(6) Seals move almost exclusively by either porpoising at the surface or swimming very near to the ocean floor. While moving, they are only found in the middle of the water column on their way between the surface and the bottom.

Assumption (4) creates a reliance on depth records for identifying many instances of movement and it prevented

the inclusion of data from the E receiver, where average depths were too shallow to distinguish between movement and rafting records. This left variable *l* with five categories: N, NE, W, S, SE. Fortunately, the SE receiver probably compensated for the exclusion of E by capturing records of most seals using E waters (see Fig. 1). Assumption (5) seems to create a bias towards increased identification of movement in the SE and NE receivers. However, daytime patterns of movement obtained from all receivers were similar to those expected based on the visual observations, so this does not seem to be an issue. Assumption (6) was necessary for distinguishing movement records from rafting ones, and it also had the effect of forcing all data for variable *D* into one of two categories: deep or surface.

We applied assumption (3) to designate movement records as either 'departing' (movement preceding an extended absence of that individual from the data record) or 'returning' (after an extended absence). We then weighted the data to reflect the variation in receptive ranges for each VR2 (Fig. 1), by measuring the greatest angle subtended by each receiver (radians) against a hypothetical circle centred at the island's midpoint (estimated using Arcview 3.2). We also adjusted the records to reflect time relative to sunrise and sunset, rather than clock time, and grouped time (*t*) into one of four categories: (1) midnight to sunrise, (2) sunrise to noon, (3) noon to sunset, and (4) sunset to midnight.

Three-way ANOVA was used to test the hypothesis that certain tactical combinations of three seal variables (*t*, *D* and *l*; receiver records did not provide information about *g* and *s*) carried less risk, and were thus selected more frequently by seals.

Sharks. Like seal data, shark records were weighted by the receptive area of each receiver (five *l* categories), then adjusted for sunrise/sunset and grouped into one of four *t* categories. We analysed the depth data (metres below the surface) from sharks with V16P sensors in relation to bottom depth in metres, and subsequently aggregated these data to reflect the sharks' presence in each of three depth strata (*d*) of the water column: upper, mid and lower. We defined the 'upper' level as the depths where we assume a surface seal could spot a shark swimming below it, impeding the shark's ability to launch a surprise attack. The 'mid' level upper boundary is then defined as the depth below which we estimate that the attenuation of light allows a shark to remain unseen by a surface seal. The 'mid' level lower boundary is an estimate of the deepest depth still providing profitable opportunities for attacking surface seals, below which the decreasing contrast of surface seals (Muntz 1974) and the increasing time of attack become prohibitive. Finally, the 'lower' level is estimated as the depths at which a seal can remain unseen by a shark at the mean shark-swimming depth. Because the 'lower' level's upper limit does not always coincide with the lower boundary of the 'mid' level, we set the actual demarcation as the average of the two borders. More details of how shark-swimming depth level were estimated are included in the Appendix.

Three-way ANOVA was used to test the hypothesis that certain tactical combinations of the three shark variables (*t*, *d* and *l*) offered better opportunities to kill seals, and were thus selected more frequently by sharks.

Results

Seals

Data on group size *g* obtained from visual records of seal movement indicated that departing seal groups were generally much larger than returning ones (Fig. 2). This difference could theoretically result in a substantial difference in the risk incurred by an individual seal. We therefore analysed the seal data obtained from VR2 receivers separately according to whether the seals were departing from or returning to Seal Island.

Returning seals. Adult female seal movement did not differ with receiver location *l* around Seal Island (i.e. they returned in similar numbers from all sides of the island; three-way ANOVA: *l* effect test: $F_{4,332} = 1.33$, $P = 0.257$; Fig. 3). However, there was a clear difference in movement records with time *t* and depth *D* (Fig. 4). Seals returned to the island substantially more throughout the night under the cover of darkness; they also chose to return primarily at depth. There was a statistically significant interaction between time and depth (three-way ANOVA: *t***D* effect test: $F_{3, 332} = 3.44$, $P = 0.017$), but this was probably a statistical artefact stemming from the small amount of 'surface' movement, rather than from any meaningful biological phenomenon.

Departing seals. Departing seals showed a clear preference for the south side of the island (S and SE receivers; Fig. 3), for swimming at the surface (71% of departing records) and for moving in the dark (78% at night), although departures appeared to be concentrated within approximately 2 h following sunset, rather than spread throughout the night (Fig. 5). There was a highly significant interaction between the three variables (three-way ANOVA: $F_{27,331} = 7.85$, $P < 0.0001$; Table 1), indicating that the preferred seal choice for departing from Seal Island was to porpoise at the surface, in a southerly direction, immediately after sunset.

Seal visual records. We used visual records to determine *g* for the two directions (Fig. 2) and to provide resolution

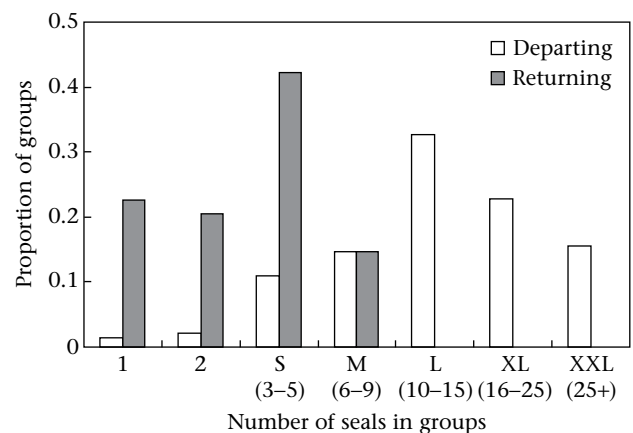


Figure 2. Frequency distribution of seal group sizes for each movement direction. X axis shows group size categories, as well as number of seals per group size category.

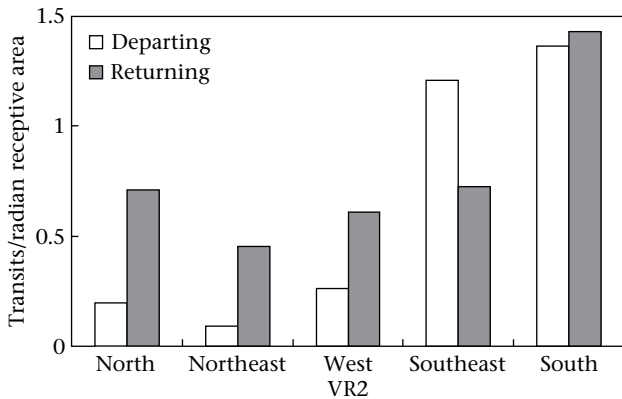


Figure 3. Total movement events of tagged seals per VR2 receiver, weighted by the radians of island circumference covered by each.

of daytime movement on an hourly scale (Fig. 5). Visual records were also used to explore differences in seal behaviour based on age class. Only data for returning seal results are presented here; most departing seals, regardless of age, appeared to use the tactics discussed above.

Between 0700 and 0900 hours, the vast majority of returning seals were pups (Fig. 6). Pups also returned significantly more over the deeper waters from the southerly and westerly directions ($\bar{X} \pm SD = 4.2 \pm 3.3$ counts/h, $N = 258$) than over the more shallow waters to the north and east ($\bar{X} \pm SD = 0.8 \pm 1.1$ counts/h, $N = 126$; independent samples t test: $t_{382} = 12.426$, $P < 0.0001$). Finally, from the focal follows we ascertained that smaller seals did not travel as far underwater as the larger ones, with a difference in mean diving distance of almost 400 m between pups and adults (Fig. 7). Consequently, compared to adults, younger seals were present in much greater numbers at the surface of the water, on the south side of the island, during sunrise.

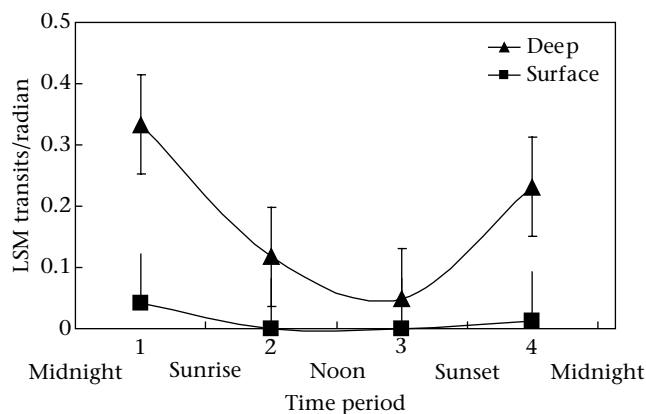


Figure 4. Interaction of time period (t) and seal swimming depth (D) for seals returning to Seal Island. The Y axis shows the least square mean values of seal transits to the island, weighted by the radians of island covered by the respective receivers; the X axis displays the four time periods (1: midnight–sunrise; 2: sunrise–noon; 3: noon–sunset; 4: sunset–midnight). Error bars represent 95% confidence intervals.

Sharks

Shark VR2 records were also explored with consideration for location, time and depth. The sharks showed a preference for the south side of the island, and were present in the greatest numbers in the morning (Fig. 8). Mean shark-swimming depth was approximately the same (between 12 and 14 m) around the entire island, regardless of prevailing water depth (Fig. 9). These depths correspond to the ‘mid’ range of the water column, resulting in a clear preference for swimming at this level ($\bar{X} \pm SE$ least square mean transmissions/m² = upper level: $3.5 \pm 0.14 \times 10^{-5}$; mid level: $11.2 \pm 0.22 \times 10^{-5}$; lower level: $4.4 \pm 0.25 \times 10^{-5}$; one-way ANOVA: $F_{2,4605} = 427.85$, $P < 0.0001$). Depth also explained 65% of the variance observed in a three-way ANOVA model (d effect test: $F_{2,4536} = 251.24$, $P < 0.0001$; model: $F_{71,4536} = 29.56$, $P < 0.0001$), and was therefore removed from the model to explore further the relationship between location and time. The result was a clear interaction between south and morning (two-way ANOVA $t*d$ effect test: $F_{15,4584} = 7.46$, $P < 0.0001$; Fig. 8).

Discussion

It is widely accepted that white sharks hunt seals by swimming at depth to exploit the visual advantage that backlighting provides them against seals at the surface (Strong 1996), and the sharks use this advantage to launch ambush attacks (Klimley et al. 2001; Kock 2002). We will attempt to explain our results within the context of this strategy and how each species responds to the other, discussing tactics in terms of the variables that characterize any particular tactical decision: t , D , d , l and g .

Time of day t

Crepuscular periods may provide the best conditions for hunting seals at Seal Island: low light at night reduces shark visual advantages, while daylight provides greater visibility, forcing sharks to swim lower in the water column to remain unseen (unpublished data), which could increase the time that seals have to detect and avoid attacks. Modest light levels during crepuscular periods provide ample backlighting while maintaining low underwater visibility, allowing sharks to swim undetected relatively high in the water column.

Indeed, sharks were present in the highest numbers at dawn; however, their presence was significantly lower at dusk (Fig. 8). The temporal pattern of seal behaviour could explain this result. While adult seals moved predominantly under the cover of darkness (Fig. 4; Table 1), significant numbers of pups returned to the island at sunrise (Fig. 6); movement of any kind was negligible in the hours preceding sunset (Fig. 5). Thus, there were seals for sharks to hunt at sunrise, but very few at sunset. Shark temporal presence reflected this pattern perfectly, while adult seal temporal pattern reflected a response to shark tactics. Pupa patterns, however, did not appear to account for predation risk; this will be discussed further in the model section.

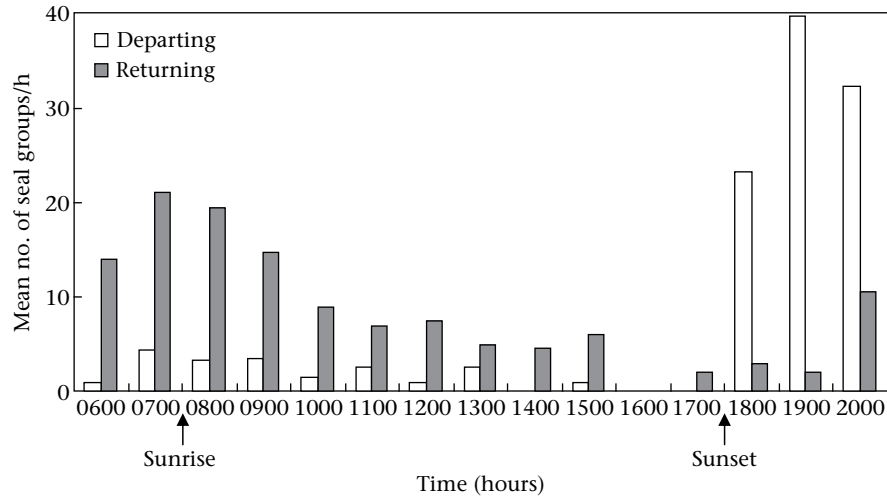


Figure 5. Visual records of seal movement for both movement directions, displayed as the mean number of seal groups observed per hour, for each hour that visual observations were conducted.

Depth d, D and group size g

Avoiding detection by surface seals should favour sharks swimming deeper in the water column, while the diminishing contrast of surface seals as the visibility of Snell’s window decreases with depth (Muntz 1974) should push sharks higher. These two opposing factors could define an optimal hunting depth independent of bottom depth: a pattern evident in our data (Fig. 9).

Given the hypothesized shark hunting strategy, seal surface movement would appear to be a risky tactic. However, surface porpoising is a more energetically efficient means of aquatic movement (Weihs 2002), and also appears to be faster (unpublished data). Furthermore, the benefits accrued from large groups (see Bertram 1978) probably outweigh the costs of being conspicuous at the

surface, suggesting that joining large surface groups may be the most advantageous tactic for the individual seal.

However, aggregating into a large group probably requires coordination of timing. This synchrony is easy to achieve for departing seals already clustered at Seal Island, but may be more difficult for returning ones, because fur seals are typically solitary foragers (Arnould & Hindell 2001). This could force seals to return alone or in small groups. Without the benefits of large groups, surface swimming would again be risky, while swimming along the ocean floor in small inconspicuous groups could potentially defeat the sharks’ hunting strategy. This deep-diving tactic has been observed in other pinniped species (Le Boeuf et al. 1996), and the pattern of large surface-departing groups and small deep-returning groups was clear from our data.

Table 1. Interaction of location, time and depth parameters for departing seals, produced by three-way ANOVA

Location	Depth	Time period			
		Midnight– Sunrise	Sunrise– Noon	Noon– Sunset	Sunset– Midnight
N	Deep	0.064	0	0.065	0
	Surface	0	0	0	0
NE	Deep	0	0	0	0.091
	Surface	0	0	0	0
W	Deep	0	0.162	0	0
	Surface	0	0	0	0
SE	Deep	0	0	0.081	0
	Surface	0.081	0.081	0.161	0.745
S	Deep	0.211	0	0	0
	Surface	0.249	0	0	0.806

Numbers represent least square mean values of seal transits radian. The model was highly significant ($P < 0.0001$ model: $MS = 0.30$, error: $MS = 0.04$, $F_{27,331} = 7.85$), and was driven by the combinations highlighted in bold, which were not statistically discernable from each other. The results suggest that adult seals highly favour departing at the surface, on the south side of Seal Island, some time between sunset and midnight.

Location l

Independent of shark hunting strategy, the physical geography of the surrounding area is probably the most important factor affecting seal choice of departing

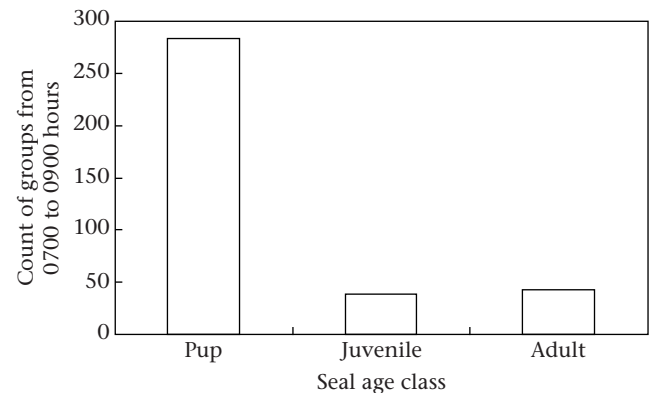


Figure 6. Counts of the number of seal groups observed returning to Seal Island between 0700 and 0900 hours. These are displayed according to the average seal age within the group.

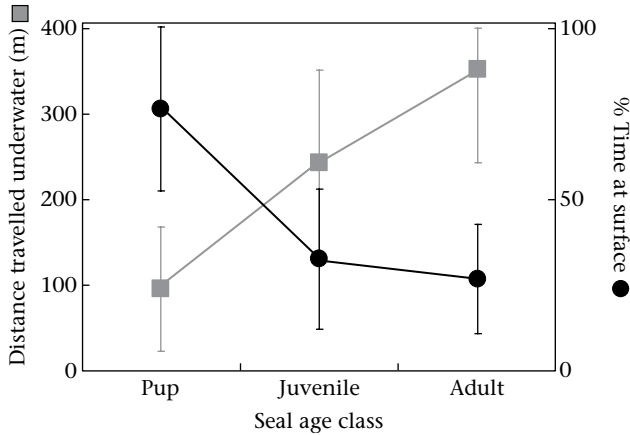


Figure 7. Seal swimming patterns. Left Y axis (light line, squares) represents the mean distances travelled underwater by seals of the different age classes. Right Y axis (black line, circles) shows the percentage of time spent at the surface while moving. Error bars represent 95% confidence intervals.

location. Seal Island is located on the north side of False Bay, which opens to the south (Fig. 1). Therefore, although seals are observed throughout the bay, a majority probably head south to forage. Still, almost all departing records indicated movement to the south; more than expected based on geography alone. This result may be because the benefits of large groups outweigh the costs of a protracted detour. Thus, seals intending to move west, for example, may depart south with conspecifics, only to veer off once outside the danger zone. Returning seals do not benefit from large groups, so their return direction would not be dictated by majority rule. Consequently, seals could return directly to the island from any location, and we did observe more nonsoutherly returns than departures in our data.

Finally, shark choice of location initially appears easy to comprehend: more seals were recorded on the south side of the island, and shark presence followed this pattern.

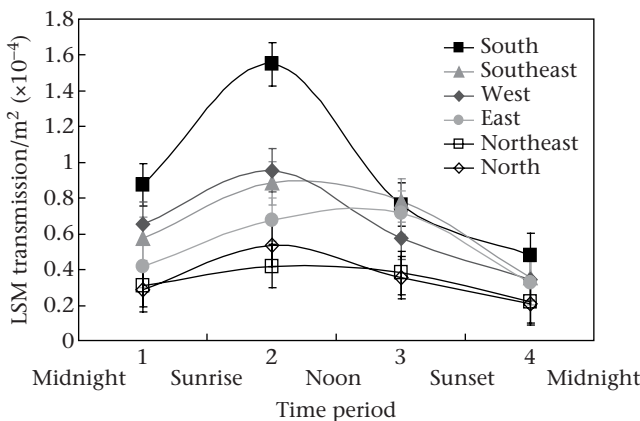


Figure 8. Shark density in relation to location around Seal Island (*l*) and time period (*t*). Y axis shows the least square means of shark transmissions weighted by the receptive area of each receiver; X axis displays four time periods as in Fig. 4. Error bars represent 95% confidence intervals.

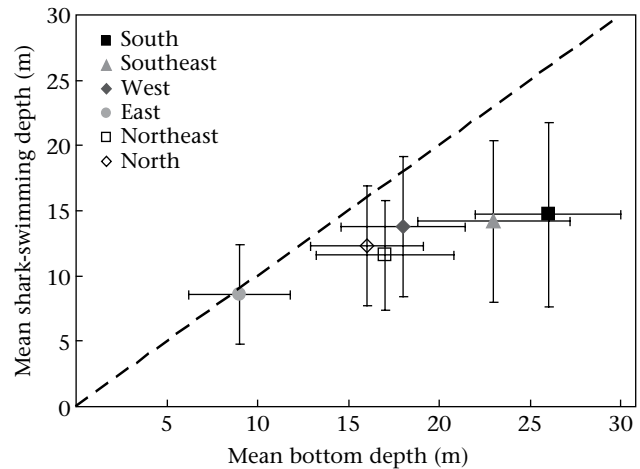


Figure 9. Mean shark-swimming depth for each receiver as a function of the average bottom depth within the receptive area of each receiver. Error bars represent one standard deviation, hatched line indicates 1:1 line of maximum possible shark-swimming depth.

GAME MODEL

Traditional predator–prey game models have considered both predator and prey as uniform groups, with individuals in either group having the same range of tactical decisions available to them, and comparable abilities to select among these tactics (Hugie & Dill 1994; Sih 1998; Brown et al. 1999; J. S. Brown, unpublished data). The general output of these models is a double IFD, where individuals in both groups play evolutionarily stable strategies (ESSs; Maynard Smith 1979) characterized by equal payoffs for every possible tactic.

At least initially, the shark–seal system around Seal Island appeared to be a prime example of such a system: one predator and one prey species, each with a range of tactics available for playing a game within a confined environment. Thus, the expectation from modelling this system was to isolate IFDs with equal tactical payoffs similar to the data distributions recorded for both species. However, the empirical study introduced a caveat: seals of different age appear to behave differently around the island, and thus may not be equal players in the predator–prey game. Consequently, a model in which seals are a uniform group might ignore important factors that drive the tactical decisions of both species.

Having described the range of tactics used by players in the shark–seal game, we now define each in terms of the associated risk to seals and opportunity for sharks. We then use a modelling approach based on multiple linked dynamic programming equations (Alonzo 2002) to explain our observations and predict whether this system has evolved towards ESSs and equal tactical payoffs for two uniform groups of players, or whether the difference between the seal age classes playing the game affects the ultimate equilibrium distributions.

General Structure of the Model

For both shark and seal, the payoff for any tactical decision was defined by the probability of an attack

occurring while adopting that tactic: for seals, the payoff is the probability of avoiding an attack (and thus staying alive); for sharks, the payoff is the probability of being able to launch an attack (and perhaps obtain a meal). Thus, the model ignores the actual kill, under the reasonable assumption that the behavioural tactics adopted by each species are likely to reflect the chances of an attack occurring, regardless of the outcome.

The model developed consists of three submodels that predict predator (sharks) and prey (departing and returning seals, which differ in available group sizes, as defined in Fig. 2) behaviour and tactical distributions. These submodels are linked: the distribution of shark tactics determines the probability of attack payoffs in both the departing and returning models, while the sum of tactical distributions from both seal models determines the probability of attack payoffs in the shark model (departing and returning distributions were summed because sharks probably do not distinguish between seals based on movement direction; Fig. 10a). Consequently, all three submodels

must be solved simultaneously. We used the best response method described in Houston & McNamara (1999) and Clark & Mangel (2000), the 'error' method from Clark & Mangel (2000), and a damping method described in Alonzo (2002) to solve the equations and predict evolutionarily stable strategies for both species.

For a seal, the same variables measured during the empirical study are now modelled to characterize any specific movement tactic: time of day t (varying light levels), swimming depth D , location around Seal Island l (differential bottom depths), group size g , and seal size s (surrogate for age class). Unlike the first four, the last of these is not a tactical choice, but rather a state variable over which the seal has no control. Regardless, it may have a substantial effect on the risk incurred by an individual seal (because of differences in experience, physiological ability, etc.), and must therefore be considered when modelling the likelihood of an attack. In the interests of simplicity, only four time periods were considered (which ignores the difference between crepuscular periods

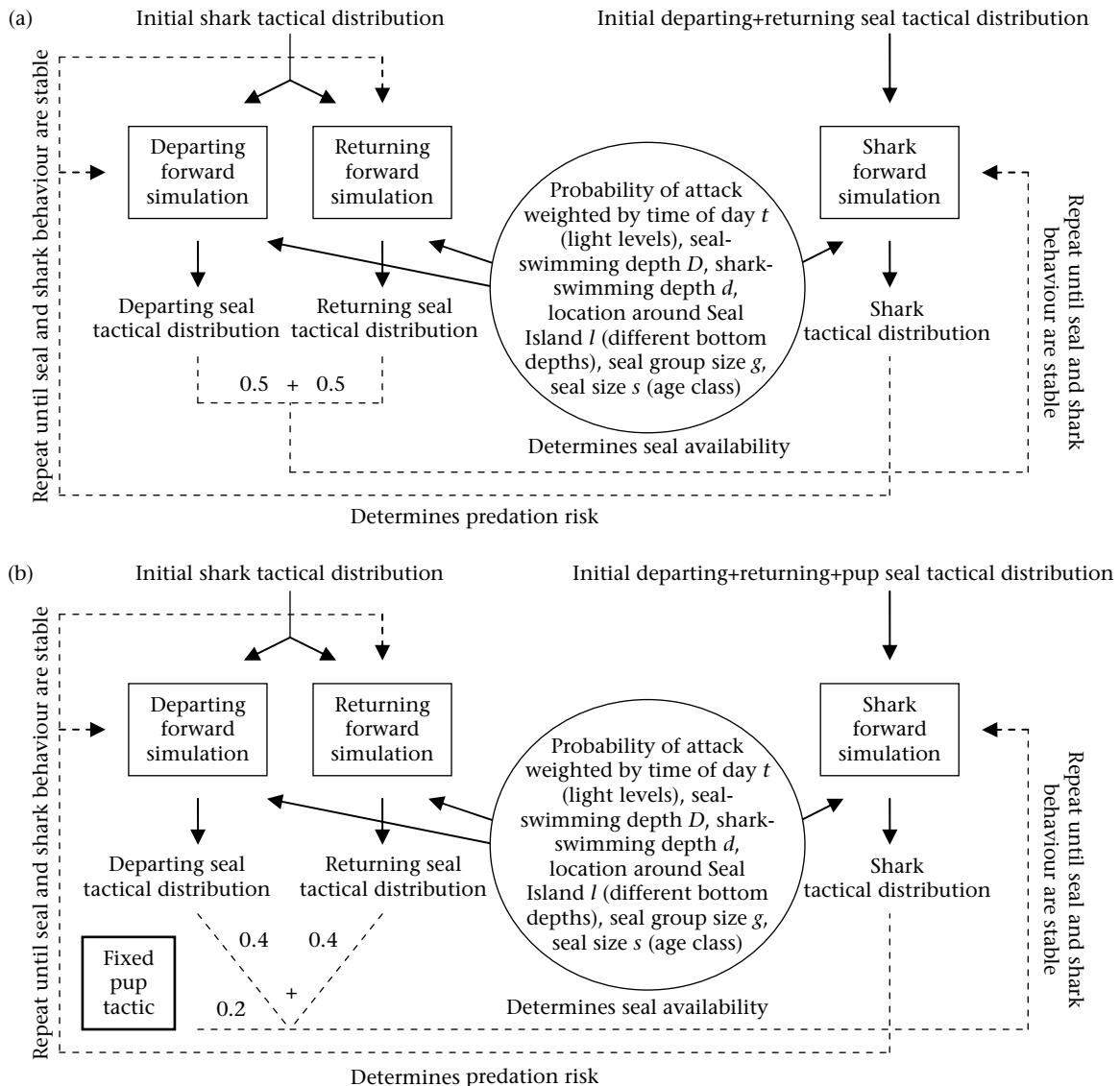


Figure 10. The computer algorithm used to solve both versions of the dynamic predator–prey game. See text for details.

and full daylight), and the physical geography of the bay was not incorporated (eliminating a potential driving force for departing group direction).

To solve the model, we assume equal starting distributions for all possible seal and shark tactics (the choice of starting distribution has no effect on the results). Then, the probability Q_{tDlgs} of a seal of size s adopting tactic $tDlgs$ and successfully navigating the waters around Seal Island without being attacked is

$$Q_{tDlgs} = \max \left\{ 1 - \left(\frac{\sum_d P_{tDlgs} \times M_{tdl}^v}{\sum_s N_{tDlgs}} \right), 0 \right\} \quad (1)$$

where N_{tDlgs} is the proportion of seals of size s also adopting tactic $tDlgs$, M_{tdl} represents the proportion of sharks adopting tactic tdl where d is one of the three shark-swimming depths, $v = 0.5$ is a predator competition coefficient representing weak competition (personal observation from Seal Island; [Alonzo 2002](#)), and P_{tDlgs} is a scenario-specific relative weight estimated to reflect the combined effect of t , D , d , l , g and s on the probability of an attack occurring. The value of P_{tDlgs} is estimated relative to the combination of these variables, which almost certainly lead to the greatest probability of attack: a seal pup (s) swimming alone (g) at the surface of the water (D) during daylight hours (t) on the south side of the island (l ; seal pups observed using this tactic were almost always attacked), and a shark swimming in the ‘mid’ level of the water column (d) at the same time and location. The scenario defined by this combination is assigned a value of 1 (i.e. the probability of an attack occurring in this scenario is modelled to be dependent solely on the proportion of seals and sharks); every other possible combination is then assigned a fractional value relative to this (i.e. every other scenario is associated with a reduced probability of an attack occurring; see [Appendix](#) for a detailed description of P_{tDlgs} calculations).

Given the full range of attack probabilities Q_{tDlgs} , seal tactic selection is predicted by the tactic for which the seal has the greatest probability of not being attacked:

$$Q^* = \max_{tDlgs} \{ Q_{tDlgs} \} \quad (2)$$

Let C_{tDlgs} represent the canonical cost of a seal of size s selecting tactic $tDlgs$

$$C_{tDlgs} = Q^* - Q_{tDlgs} \quad (3)$$

The probability that a seal will select a particular tactic is then given by

$$H_{tDlgs} = \frac{E}{E + C_{tDlgs}} \bigg/ \sum_t \sum_D \sum_l \sum_g \sum_s \frac{E}{E + C_{tDlgs}} \quad (4)$$

where $E = 0.01$ is a shape parameter that determines the relative chance of an error. This probability then gives the proportion of seals using each tactic for use in subsequent iterations of the model; that is,

$$H_{tDlgs} = N_{tDlgs} \quad (5)$$

The tactical distributions for both departing and returning seals are calculated in this manner, and the totals for

each add up to 0.5, such that the sum of departing and returning proportions for any particular tactic provides the total seal proportion N_{tDlgs} for use in the shark model ([Fig. 10a](#)).

The probability that a shark using tactic tdl will be able to attack a seal is given by

$$U_{tdl} = \max \left\{ \frac{\sum_s \sum_g \sum_D P_{tDlgs} \times N_{tDlgs}}{M_{tdl}^v}, 1 \right\} \quad (6)$$

For simplicity, we assume that sharks show a linear functional response to prey.

The probability of sharks selecting each tactic is calculated in the same way as for the seals, and the game is solved using the same best response and error method. The behavioural predictions from all three submodels are used in forward simulations to find the distribution that would result if the entire population of both species adopted the predicted strategies, and these steps are repeated until stable solutions are found.

We solved to ESS using two separate s distributions, both times restricting returning seals to a maximum group size of medium (direction thus translates into a group size effect; see Results of empirical study). The first time, both the departing and returning populations were each broken into proportions of 0.2 female adult seals, 0.2 pups, 0.095 juveniles and 0.005 bulls (estimated based on personal observation at Seal Island). These age classes did not interact or play against each other, and the final seal tactical distribution applies to all ages.

For the second run, the two seal submodels (departing and returning) were designated as adult female seals (for simplicity), and each was set to comprise 0.4 of the total seal tactical distribution. We assigned the remaining 0.2 to a third group of seal pups ([Fig. 10b](#)) frozen on the riskiest movement tactic (daylight, alone, surface, south). Consequently, 20% of the total seal tactical distribution available to sharks always consisted of seals with the greatest probability of being attacked, and the remaining 80% (adult female seals) selected tactics based on shark response to this fixed group.

Model Results

General ESS results from both versions of the model are presented in [Table 2](#) (full results in [Supplementary Material, Table S 2](#)). In the first version, where all seals could respond to sharks, the results predicted a rather uniform tactical distribution for both species. Shark proportions were practically equal across tactics, except for being slightly higher during the midnight–sunrise time period at all depth levels. Seal proportions were not as uniform, but there was only an approximate 10-fold difference between the lowest and highest proportions (0.001–0.014 departing; 0.002–0.021 returning). For departing seals, the model predicted the highest proportions in the largest groups at the surface at night, and the lowest in small groups at the surface during the day. For returning seals, the highest proportions were in small groups in deep water at night, and the lowest proportions were in small groups at the surface during the day.

Table 2. Results of both versions of the game-theoretic model for sharks, and departing and returning seals

Version of model	Result	
Pups play	Sharks	Uniform distribution across all tactics
	Seals	10-fold difference between tactics selected by highest (Max) and lowest (Min) proportions of seals
	Departing seals	Max: largest groups, surface, night Min: small groups, surface, day
	Returning seals	Max: deep, night Min: surface, day
Pups fixed	Sharks	0.3 proportion morning, mid, south Remainder spread among all tactics
	Seals	100-fold difference between tactics selected by highest (Max) and lowest (Min) proportions of seals
	Departing seals	Max: xx-large groups, surface, night Min: small groups, surface, day
	Returning seals	Max: small group, deep, night, south Min: surface, morning

In the first version of the model, all seal age classes, including pups, play the game against the sharks, and the results for this version represent the tactical distributions for all seal age classes. In the second version, a seal proportion of 0.2 is fixed as 'pups adopting tactic surface, sunrise–noon south, and group size of 1', the tactic assumed to carry the greatest risk. The remaining proportion of 0.8 seals are all assumed to be adult females, so the results only represent the tactical distribution for this age class.

In the second version, where 20% of the total seal population were pups fixed on the riskiest possible tactic, over 30% of sharks were predicted to adopt the tactic best suited for exploiting this group (morning, mid, south), while the remainder were spread almost equally among tactics (approximately 1.1% for each tactic, slightly higher in the other morning-south depth levels). This changed the proportional differences between seal tactics (100-fold differences: 0.0005–0.045 departing; 0.0012–0.12 returning), and the model now predicted that a majority of seals would adopt safer night-time tactics: nearly 50% of departing seals should leave in extra-large groups at night, while 58% of returning seals should swim deep at night (12% using deep, sunset–midnight, small group, south). Overall, only 11% of seals (departing and returning combined) in this version were predicted to move in the morning, and of these the majority selected the least risky options of departing at the surface in very large groups and returning in deep water in small groups.

Model Discussion

The first version of the game allowed all seals around Seal Island to play the predator–prey game equally, regardless of age class. The basic expectation, then, would be of a double IFD for predator and prey with equal payoffs for all tactics.

The results of the first model suggest that both species would distribute themselves based on the cost of seal errors. As these increase (by setting P_{tDalg} near 1 for many tactical combinations), or the probability of erring decreases (by decreasing the error term E), seal ESS distribution shifts further from dangerous day tactics towards the safer night tactics. This implies that seal distributions in the model do not represent a perfect IFD with equal tactical payoffs, because the error term ensures that a proportion of seals consistently select suboptimal tactics. However, unless the parameters are set such that the proportion of seals selecting riskier tactics reaches zero, sharks

still select almost all tactics equally, because shark payoffs remain essentially equal (i.e. the payoff from a tactic with few seals but a high probability of attack will be equal to that from a tactic with many seals but a low probability of attack). The ratio of successful predatory events at Seal Island to the number of seals moving only from 0600 to 1000 hours is very low (approximately 1:100, unpublished data; Martin et al. 2005 recorded a mean of only 141 successful predations per season over seven seasons); this suggests that the cost of making errors is not high enough to decrease their occurrence in the model to the point of upsetting the shark ESS. The result then, as expected, is an IFD for sharks with equal payoffs, and a near IFD for seals maintained as an ESS by the chance of making errors.

These results predict that our empirical data should reveal an equal distribution of sharks at all times, depths and locations, and a distribution of seals slightly biased towards night movement. Clearly this was not the case. Our homogeneous predictions also differ from those of previous theoretical predator–prey models (Hugie & Dill 1994; Sih 1998; Brown et al. 1999). These models, however, do not incorporate an error term, and they all consider games where prey respond to resources as well as predation; in our model, prey consider predation risk only when selecting tactics.

Pup seals, however, do not appear to account for risk. In our study, they occasionally adopted adult tactics, but also moved at dawn (Fig. 6), spent more time at the surface (Fig. 7), and returned to the island from a southerly direction more frequently than adults did. The second version of the model attempted to capture this pup behaviour by fixing 20% of the total seal population as pups adopting this risky tactic. The result was that adult seal errors were no longer the driving factor, and the model output approximated the tactics measured around Seal Island much more closely, with sharks concentrating in the morning, mid-water, to the south, and adult seals moving predominantly at night. The suggestion, therefore, is that seals differ in their response to

shark tactics, and sharks focus primarily on those that adopt riskier tactics.

GENERAL DISCUSSION

The initial goal of this study was to describe the tactics used by both sharks and seals around Seal Island, and to evaluate these within the evolutionary framework of a traditional predator–prey game model. Our preliminary expectation was that the shark–seal system would be a prime candidate for such a model: one predator and one prey species playing a game within a highly confined environment. We thus predicted it would be possible to calculate approximately equal payoffs for every tactic available to each species, based on the data collected describing the current tactical decisions of their own species and those of their opponents.

However, it became evident that the Seal Island system may not fit traditional models as well as predicted. Of particular note were the number of attacks on pups and small juvenile seals that were swimming alone or in small groups in the hours around dawn, at the surface of the water, on the south side of the island. This particular combination of variables described almost 80% of recorded predatory events, with nearly 10% of the remainder involving only a change in location of the attack (unpublished data). Partially serving to explain this observation was our finding that pups made up similar proportions of the seals swimming in the water at dawn (Fig. 6); what was, and remains, unclear is why pups choose these movement tactics, when traditional game models would suggest that their tactical choices should evolve towards selecting safer tactics like those used by adult seals.

Pup behaviour could reflect a degree of naïveté, and their timing may represent a miscalculation of travelling time when returning to the island. Such apparently naïve juvenile behaviour has been observed across a wide variety of taxa (e.g. gobies, Utne-Palm 2001; geese, Klaassen et al. 2006; moose, White et al. 2001). However, it is also possible that seal pups are somehow constrained from responding to predation risk, or that they trade off risk against some other important factor. Such trade-offs have similarly been shown in juvenile animals across many taxa (trade-off foraging: tortoises, Halstead et al. 2007; sheep, Hutchings et al. 2001; trade-off development: treefrogs, Gomez-Mestre & Warkentin 2007). Alternatively, the young ones may perceive a lower cost of predation by virtue of having lower survivor's fitness and higher marginal value of energy. In addition, Seal Island may be an open system where breeding seals have been weaned at other colonies under different selective pressures (i.e. where the 'riskiest' tactics from Seal Island are not actually risky). Genetic heterozygosity has been linked to risk-taking behaviour in other species (Vilhunen et al. 2008). Unfortunately, identifying the reason for risky pup behaviour was beyond the scope of this study, leaving it as a question for further research.

Regardless, the result obtained by adding the fixed pup element to the game model leads to an important

conclusion. Most predator–prey game models consider prey as a uniform group (but see Jackson et al. 2006), although some extend this to include a distribution of prey energy states (Alonzo 2002). However, as this study clearly shows, a prey population, particularly that of a larger vertebrate, may be composed of subunits that differ markedly in behavioural patterns. In our study these subunits were based on age, but other possible factors could include size, sex, experience, or social rank. Such subunits actually feature prominently in many other types of game models (e.g. hawk–dove games, Smith & Price 1973; sperm competition games, Parker 1990), but have been largely ignored when modelling predator–prey interactions. This study shows the importance of considering these behaviourally distinct groups when modelling the choices and actions of a predator and prey, because without such consideration the end result could misrepresent ecological processes and obscure important inter-specific and intraspecific relationships.

Indeed, constraining the pups to a risky tactic had the ultimate effect of transforming the first version of the game-theoretic model to one that predominantly modelled an intergenerational behaviourally mediated indirect interaction (BMII; a form of trait-mediated indirect interaction; Dill et al. 2003), where seal pup behaviour influences the behavioural tactics adopted by the sharks, which in turn dictate the tactics used by adult seals. Indirect interactions have been explored extensively in the literature (reviewed in Werner & Peacor 2003), although typically in systems with at least three species. However, distinct functional units within a population can create similar indirect interactions in two-species systems. Other recent studies have suggested that two-species indirect interactions may be common across a variety of systems, although these studies have focused primarily on size differences in predators (Rudolf 2006) and intragenerational size differences in prey (Greenberg et al. 1997; Persson & De Roos 2003). To our knowledge, this is the first study to show a BMII between prey generations mediated by their common predator. This result is surprising, given that new offspring are often more vulnerable to predation than their elders, and that minor differences in vulnerability between prey groups can dramatically affect predation rates and overall fitness for individuals within these groups (e.g. Jackson et al. 2006). However, in this context, assessing fitness differences between groups is complicated by the nature of the interaction, in that the fitness of parents is inextricably linked to that of their offspring. Future models and empirical research could provide valuable insight into how widespread such intergenerational indirect interactions are, how important they are in driving the evolution of behavioural traits, and what the long-term effects are on population and community dynamics.

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Supplementary Material

Supplementary data associated with this article can be found in the online version, at [doi:10.1016/j.anbehav.2008.06.025](https://doi.org/10.1016/j.anbehav.2008.06.025).

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Appendix

Shark-swimming Depth

We analysed the depth data (metres below the surface) obtained from white sharks with V16P sensors according to bottom depth in metres, and subsequently aggregated these data to reflect the sharks' presence in each of three levels of the water column: upper, mid and lower. These three levels do not correspond to fixed depths around the island, but rather are defined in relation to mean shark-swimming depth, the attenuation of light with increasing depth, and consideration of how the interplay between these factors affects the ability of white sharks and Cape fur seals to detect each other, based on the assumption that light levels and vision are the key elements that shape the patterns of predatory interaction between these species (Strong 1996; personal observation).

We thus defined the 'upper' level as the depths at which we assume a seal could spot a shark swimming below it, impeding the shark's ability to launch a surprise attack. The assumed 'mid' level upper boundary is defined as the depth below which it is estimated that the attenuation of light allows a shark to remain unseen by a seal at the surface. The 'mid' level lower boundary is then an estimate of the deepest depth still providing optimal opportunities for attacking seals at the surface. Below this depth, the decreasing resolution of Snell's window as a result of light scattering by suspended particles (Muntz 1974) should lead to a reduction in contrast between a seal and the surface, probably making surface seals more difficult to detect. The 'attack time', or time between initiation of the attack and the actual strike, also increases with depth. The result should be increased opportunities for the seal to detect the shark and avoid it, or even an increased chance that the seal will alter its course at random, thus inadvertently defeating the shark's predation attempt. Both of these factors combined probably render successful attacks increasingly difficult from greater depths, and we defined the lower 'mid' level boundary as the depth at which these costs become prohibitive. Finally, the 'lower' level is estimated as the depths where a seal, swimming along the ocean floor, can remain unseen by a shark present at the mean shark-swimming depth. Because the 'lower' level's upper limit is not always identical to the lower boundary of the 'mid' level, we set the actual demarcation between the two levels as the average of the two borders.

P_{tDdlgs}

The probability of an attack occurring is defined as being contingent on the proportion of seals selecting

a particular tactic, on the proportion of sharks selecting the corresponding tactic and on the nature of the tactic itself (see text, General Structure of Model). Five variables are considered to define every possible seal tactic: time of day (t), swimming depth (D), location around Seal Island (l), seal group size (g) and average seal size in a group (s). Unlike the first four, the last of these is not a tactical choice, but rather a state variable over which the seal has no control. Regardless, it no doubt has a substantial effect on the risk incurred by an individual seal (as a result of experience, physiological ability, etc.), and must therefore be considered when modelling the likelihood of an attack. Three variables are considered to define every possible shark tactic: the time of day (t), swimming depth (d), and location (l). Each possible combination of seal and shark tactics therefore characterizes a unique tactical scenario $tDdlgs$, to which is assigned a specific probability modifying weight P_{tDdlgs} (Supplementary Material, Table S1). Unfortunately, insufficient data exist to explicitly quantify each possible P . Instead, the relative effects of the specific environmental, group size, and seal size conditions on the probability of attack occurring are estimated as weighting values scaled against a baseline value of 1, which is allocated to the scenario of a seal pup (s) swimming alone (g) at the surface (D) above the South receiver (l) during daylight hours (t), versus a shark swimming at the 'mid' level of the water column (d), during the aforementioned conditions. This scenario was chosen because any seal pups that we observed using this tactic were almost invariably attacked, making it the scenario that appears to have the highest associated probability of attack. Consequently, by assigning a value of 1, we define the probability of an attack occurring in this specific scenario as being solely contingent on the proportions of predator and prey (see text, General Structure of Model), and therefore as not being context dependent in any way. All remaining weights are assigned as fractional values relative to this scenario, meaning that, in all other scenarios, the probability of an attack occurring is negatively contingent on the nature of the context.

The actual P_{tDdlgs} weights used in the model are calculated based on the products of values estimated for discrete categories of each variable (t , D , d , l , g , s). The specific numbers comprising each of these individual values remain educated guesses, and are therefore open to debate. However, the patterns that form the basis for these approximations are each rooted in scientific theory and common sense, and thus probably represent the general trends occurring at Seal Island.

Visual Conditions: t , D , d

The visual conditions for a particular scenario were defined by the interaction of t , D and d . As a result, we did not attempt to tease apart the effects of each of these variables, but instead assigned a relative weighting value to each possible combination of their discrete categories.

The overall probability of attack is estimated to be lower at night, as extremely low light levels would all but eliminate any visual tactical advantages. The sharks and seals should

therefore have to rely predominantly on their other senses, and, since these are well developed in both species, their ability to detect each other should be approximately on par for most night-time scenarios. Consequently, the night-time relative scenario weights are estimated to be much lower than 1. For example, deep seals are probably at the most risk from sharks in the lower segment of the water column (Fig. A1a), where they should be on approximately equal footing. However, seals swimming along the bottom eventually have to come up for air, where they are at increased levels of risk from sharks at all depths. Consequently, the relative night weight for deep seals is estimated to be the highest against lower sharks at 0.11, while for mid sharks it is set at 0.1, and for upper sharks at 0.01. Deep seals would most likely face no risk at all from upper sharks were it not for these brief intervals of surface breathing, for it would seem highly unlikely that a shark could identify a seal 20 m below it in the dark.

Departures from the baseline value of 1 are similarly large in the relative weights estimated for seals swimming at the surface during the night (Fig. A1b). A weight of 0.1 is assigned to the combination of surface and upper, as this is assumed to be equivalent to the scenario of deep seals and lower sharks, without the extra risk associated with having the sharks below the seals when the seals surface. However, instead of the weighting factors decreasing as differences in swimming depth increase (as they do for deep seals), they are assigned a marginal increase. This is based on the potential effect of moonlight: during our study, there were numerous occasions where moonlight would have provided ample light for visual hunting. This should put surface seals at substantial risk from sharks at the mid and lower levels, although less so from the latter because, even in the brightest moonlight, it is probably difficult to detect seals at the surface from 20 m

deep. Still, despite this potential for increased risk, the relative rarity of these extremely bright nights limits the increase in relative weight that we estimate for these scenarios.

The general trends estimated for night conditions are carried over into the day, as the interactions are assumed to be governed by the same general principles. However, given the likely importance of vision to the sharks' hunting strategy, the increase in light levels with daylight are estimated to increase the relative weights beyond those for night, meaning an increased probability of an attack occurring in the daytime (Fig. A1c,d). This is particularly the case for surface seals, which find themselves at the greatest of all visual disadvantages against sharks below them. This scenario is probably the one that leads to the majority of observed predatory events and includes the baseline scenario assigned a value of 1. Surface seals also face considerable risk from lower sharks, although probably less so than from sharks in the middle of the water column, because contrast of surface seals decreases and attack time increases at greater shark depths.

Location Around Seal Island I

The relative weighting values assigned to each combination of t , D and d form the initial basis for P_{tDdgs} . However, l , g and s also define specific attack scenarios. We therefore derived a function for each of these, based on relative weighting values estimated for each of their discrete categories, and these are multiplied by the values that define the visual environment to obtain the final scenario-relative weight P_{tDdgs} . Values for each of these secondary variables are estimated in the same manner as previously described (i.e. scaling the relative effect for each category of a specific variable against the category

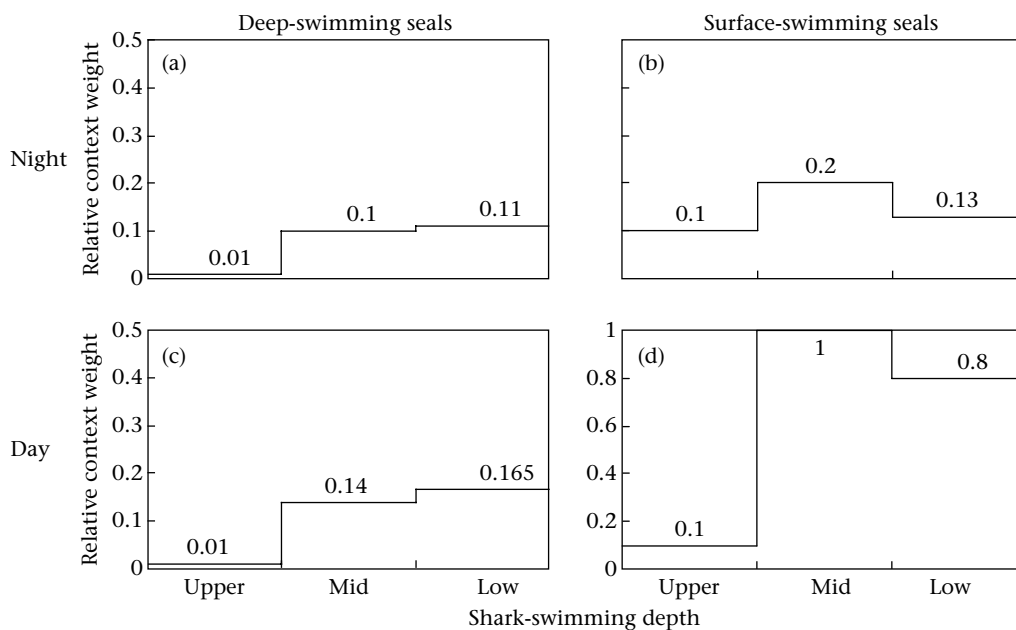


Figure A1. Relative scenario weights for visual conditions, as defined by light levels (day or night), and by the swimming depths of both species.

of that variable from the baseline scenario (defined above), which is assigned a value of 1).

The first of the secondary variables considered is the location around Seal Island, as defined by the receptive areas of each VR2 receiver. Location is actually a surrogate variable for water depth, and is therefore only relevant when the depth of the location is pertinent to the probability of an attack occurring. All scenarios where the shark is at the surface, as well as when seals are at the surface and sharks are mid, are deemed to be equivalent to the baseline scenario, and are therefore assigned weighting values of 1 (Fig. A2).

Location, and hence water depth, is estimated to have an inverse effect on the probability of an attack occurring. The basis for this assertion is the absorption and scattering of light in water; being further away from something underwater decreases its visual contrast and thus its detectability (Muntz 1974). This phenomenon is compounded by environmental conditions (wind, swells, currents; all of which are prevalent at Seal Island), which lead to increases in suspended particulate matter, and an increase in the scattering of light. The result is that waters around Seal Island typically have poor visibility; in the range of 3–10 m (unpublished data collected using a secchi disk).

Visibility is assumed to have little effect on the north and east sides of the island, where average bottom depths rarely exceed the mid shark level. However, on the southern and western sides, the bottom drops off very quickly to greater depths. Thus, sharks swimming near the bottom, in the lower level, probably have a reduced view of the surface; similarly, sharks swimming mid-water are probably not able to detect seals swimming along the bottom, as they might be over 10 m away. The end result is that the increased depths on the southern and western sides of Seal Island are assumed to decrease the probability of attack within certain scenarios.

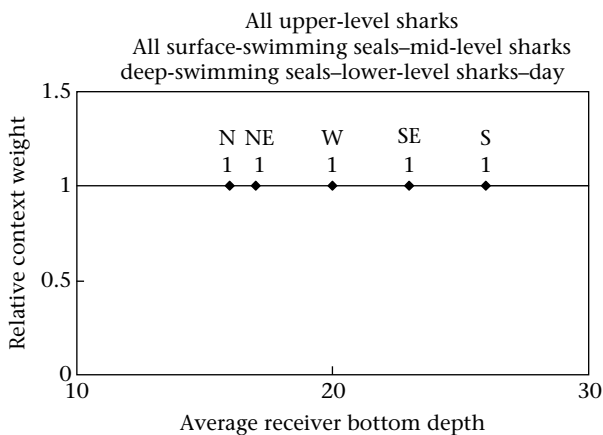


Figure A2. Relative scenario weights based on varying bottom depth. N, NE, W, SE and S refer to receiver location. Water depth was not estimated to have an effect on any scenarios where sharks were in the upper level of the water column, as well as any scenarios defined by seals at the surface and sharks at mid level, and the scenarios comprising deep seals and lower sharks during the day.

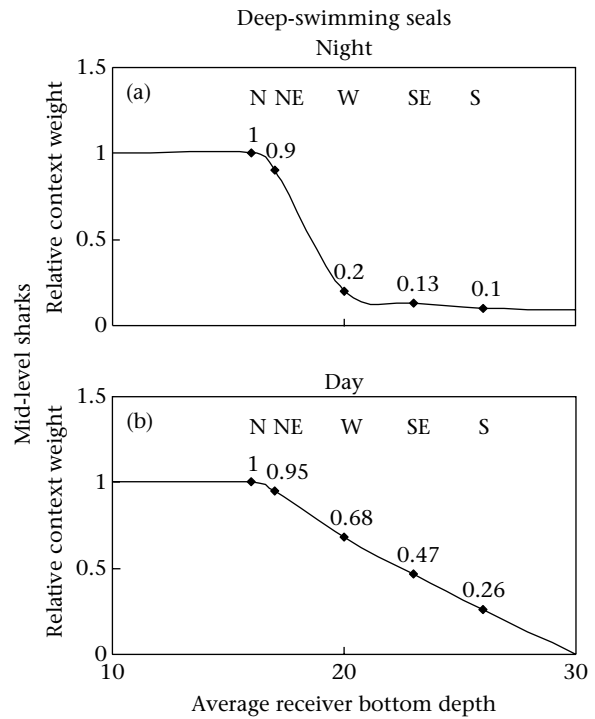


Figure A3. Relative scenario weights based on average receiver bottom depth for deep seals and mid sharks during both light level conditions. N, NE, W, SE and S refer to receiver location.

The greatest decrease in associated attack probability is estimated to occur at night for deep seals versus mid sharks (Fig. A3a), where low light conditions probably make it extremely difficult for a shark to detect a seal only a few metres below it. Thus, a precipitous drop in weighting values is assigned between the mid-range average depths of the northern VR2s and the lower-range average depths of the southern and western ones. This same reasoning is also applied to the combination of deep seals and mid sharks during the day (Fig. A3b). However, this decline is estimated to be more linear, because

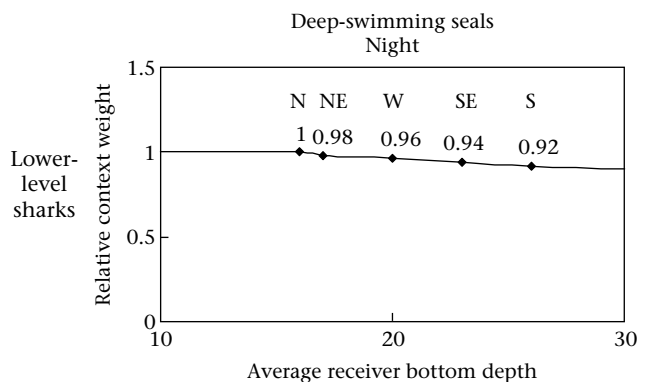


Figure A4. Relative scenario weights based on average receiver bottom depth for deep seals and lower sharks at night. N, NE, W, SE and S refer to receiver location. During the day, location was assumed to have no effect on the deep seal – lower shark relative weight (Fig. A2).

the greater visibility provided in daylight probably makes it easier for mid sharks to spot deep seals, even in southern waters.

Relative weighting values are also estimated to decrease slightly with average bottom depth for the combination of deep seals and lower sharks at night (Fig. A4), while during the day it is estimated that there is no effect (Fig. A2). This difference is once again based on light levels. Greater depths towards the south mean a greater separation distance between the ocean floor and the upper boundary of the lower level. Thus, seals might manage to escape totally undetected at night, when sharks are obliged to rely more heavily on short-range senses, and might therefore be less likely to have full cognizance of seal movement in the entire level at once. However, this opportunity will not exist during the day, as light levels probably allow sharks to monitor the entire lower level at once.

Finally, the combination of surface seals and lower sharks is also estimated to produce a declining probability of attack with depth, once again because underwater contrast decrease with distance and attack time increase (Fig. A5a, b). However, these effects are again presumed to be greater at night, given the further constraints imposed by low light levels.

Group Size *g*

It is well documented in the literature that an individual within a large group will gain a measure of antipredatory benefit in the event of an attack (Bertram 1978). However, what is also well documented is that these benefits must

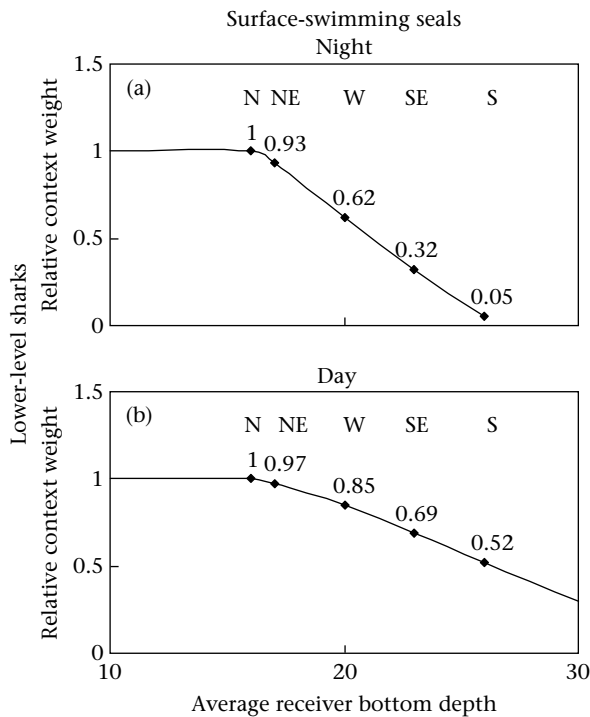


Figure A5. Relative scenario weights based on average receiver bottom depth for surface seals and lower sharks during both light level conditions. N, NE, W, SE and S refer to receiver location.

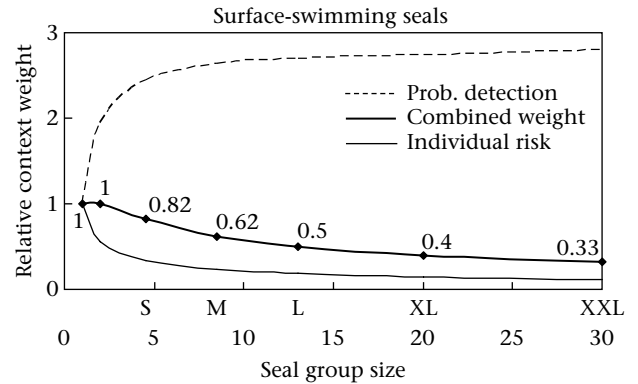


Figure A6. Relative scenario weights assigned as a function of surface seal group size. These weights were modelled to have an ‘effect on detection’ component and a ‘risk to an individual seal’ component, which were multiplied together to give the final group size weight.

be tradedoff against detectability; large groups are often easy for predators to detect and hunt, yet large groups remain advantageous to individuals within the group because of an overall decrease in the chance of predation (Taylor 1979). These principles probably apply just as well to seals moving to or from Seal Island. Consequently, the weighting values assigned for group size are derived from the interaction between a weighting function estimating the risk to an individual seal within a group, and a second weighting function estimating the relative effect of group size on detection. These functions were derived such that their products total the weighting value used to calculate P_{Dalg} .

Separate weighting functions were created for deep and surface seals, given the dramatically different visual conditions associated with each tactic. Surface seals are undoubtedly easy to detect visually, regardless of group size. Consequently, the values estimated for the curve are based predominantly on sound, such that it increases quickly with more than one seal (more seals means more noise) but levels off as seal numbers reach a point where

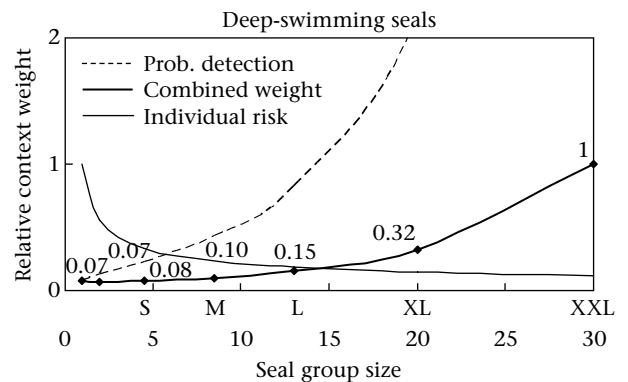


Figure A7. Relative scenario weights assigned as a function of deep seal group size. Weights were modelled using the same method as for Fig. A6. However, the effect on detection curve was modelled to increase sharply with group size, rather than level off (as for surface seals), to express the importance of stealth in the deep swimming tactic.

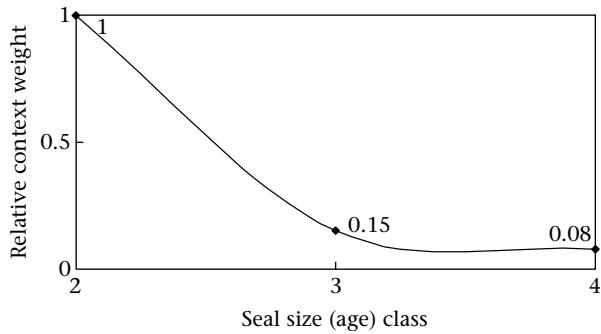


Figure A8. Relative scenario weights assigned as a function of seal size, used as a surrogate for seal age: size 2 = pups; size 3 = juveniles/female adults; size 4 = mature bulls, which were too large for many of the sharks around Seal Island to attack.

any extra surface noise makes little difference. Conversely, risk to an individual seal is estimated to decrease with group size, although marginal benefits diminish as group size increases. The product of the two curves estimates that the relative weighting value used to calculate P_{tDdlgs} decreases with group size (i.e., a decrease in the probability of attack for surface seals with increasing group size), although the additional benefits accrued become minimal as groups get extremely large (Fig. A6).

Deep seals face an entirely different set of circumstances. They move in an environment where visual conditions are in their favour, allowing them to detect sharks above them while remaining undetected below. Thus, in deep scenarios, the expectation is of a premium on stealth, at the expense of group benefits. Consequently, the effect of group size on detection is modelled to increase exponentially, reflecting the noncryptic nature of extremely large groups, while the decrease in individual risk is modelled in the same manner as for surface seals. The relative product weights reflect our estimate that smaller group sizes are more beneficial for deep movement (Fig. A7).

Seal Size s

The final factor defining P_{tDdlgs} is seal size, used as a surrogate for age class. It is a nearly ubiquitous fact in nature that juvenile animals are more susceptible to predation

than adults, and the relative weighting values for s are modelled to reflect this trend (Fig. A8). Seal sizes: 1 = neonates; 2 = young-of-the-year pups; 3 = juveniles/adult females; and 4 = mature bulls (Fig. A8). Neonates were not observed, since pupping occurred 4 months before our field season began. The baseline value of 1 is assigned to a solitary pup swimming at the surface, and thus seal size 2 is assigned a weighting value of 1. These pups are relatively physiologically limited, and are essentially naïve explorers of a new environment. As seals age and grow, they no doubt become better equipped to evade an attacking shark. Thus, the weighting value decreases with increasing size (i.e. the probability of attack decreases as seals get older). Size 4 seals are assigned a very low weight, as it is estimated that their imposing size could intimidate many of the smaller sharks around Seal Island, even further decreasing the overall chance of an attack occurring.

Final Product: $tDdlgs$

The final scenario-relative weights P_{tDdlgs} are calculated as the product of the individual weighting values assigned to each variable that defines a specific scenario. Thus, for example, in a scenario where a size 3 seal (weight: 0.15) is swimming at the surface in a small group (weight: 0.82) on the south side of the island at night versus a shark at the lower depth (visual condition weight for low in surface seals – night: 0.13; location weight for south in surface–lower–night: 0.05), the estimated relative weight was 0.0008. This number is a relative weight that defines the effect of scenario on the probability of an attack occurring. It signifies that the effect of this particular scenario is to decrease the probability of an attack occurring by three orders of magnitude as compared to the baseline scenario of a pup seal swimming alone at the surface in the daylight on the south side of the island versus a shark in the mid level of the water column. Calculated weights for all P_{tDdlgs} values are presented in [Supplementary Material, Table S1](#). The full ESS results from both versions of the game model are presented in [Supplementary Material, Table S2](#), each using equal starting tactical distributions for both species, and $E = 0.01$ and $\nu = 0.5$.